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FILTER FEEDING IN FLAMINGOS (*PHOENICOPTERUS RUBER*)¹ LIBRARY

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Abstract. We propose a model of filter feeding in Caribbean (*Phoenicopterus r. ruber*) and Greater Flamingos (*P. r. roseus*) that is based on a description of the oropharyngeal integument, using SEM and radiography, and analysis of kinematics and performances. Our model extends that of Jenkin (1957). We propose a lingual back-and-forth pump, that causes a lateral in- and outflow of water. Outflow of water is manipulated by directing water more distally to pass somewhat larger lamellar meshes, or more proximally to pass slightly smaller meshes. Performance analysis of filtering monotypic suspensions of seeds ranging from 0.1 to 10.0 mm cross-section shows peak performances at 2–4 mm. Sizes smaller than 0.5 mm and larger than 6.0 mm are not filtered. Performance analysis of filtering suspensions of two seed types shows that discrimination capacity, though not perfect, is accurate if food of preferred size is offered. In addition to touch, taste also controls discrimination. We present a provisional morphospace of avian filter feeding mechanisms derived by nomological deduction from an initial pecking mechanism and develop in this domain preliminary historical-narrative hypotheses of the evolution of avian filter mechanisms. The morphospace connects chicken-like pecking, considered as the initial type of feeding, through initial probing, to five categories of filtering. These categories are: accidental filtering (as in *Phalaropus*), ram filtering (as in *Pachyptila*), grasp-pump filtering (as in *Anser*), (inverted) back-and-forth pump filtering, causing a lateral in- and outflow (as in *Phoenicopterus*), and through-pump filtering, causing distal inflow and proximal outflow (as in *Anas*). The evolutionary hypotheses consider probing as developed from ancestral pecking, and filter feeding as branching early from that route.

Key words: *Filter feeding mechanism; flamingo; Phoenicopterus ruber; morphology; morphospace; evolution.*

INTRODUCTION

The beak in flamingos (*Phoenicopterus*) is remarkably well adapted to gather large quantities of small food organisms by filtering in shallow lagoons and lakes. However, relatively large particles are grasped with the beaktips and trans-

ported through the mouth by a "catch and throw" mechanism. Smaller-sized particles like insect larvae and seeds are filtered from the water. Very small items such as micro-organisms are gathered through scraping top soil and ingesting mud, or by very specialized filtering.

Present knowledge about the mechanism of filtering is based on three sources: (1) anatomical dissection of the integument of mouth and tongue, (2) analysis of food present in the environment and that found in stomach-contents, and (3)

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studies that detail ecobehavioral observations and analyses in the field and in zoos. However, direct measurements of filter kinematics by film-analysis and performance analysis of filter capacity are unavailable.

Models for filter mechanisms in flamingos are proposed by Allen (1956) and Jenkin (1957) and subsequent authors refer to these studies (see review in Kear and Duplaix-Hall 1975). Allen (1956:89) described filtering as follows "(flamingoes) . . . dragged their mandibles through the mud and water, rocking their heads from side to side . . . pumping movements of the gular region, and the twin jets of muddy water that were shot outward from the corner of the mouth [were observed] . . . Certainly a suction was being set up in the mouth opening . . . evidently a combination of a pumping and a sucking through the opening of the gullet. Then, as the upper mandible clamped shut, streams of mud and water were found forced outward, certain portions being retained within . . . processes along the upper edge of the tongue . . . with an additional straining effect from the lamellae on the mandibles." Allen also writes that these birds eat mud and that small molluscs are sieved from the mud in the same way.

Jenkin (1957) proposed a different mechanism for filtering. She developed a reconstruction of the filter mechanism by identifying the anatomical elements that are possibly responsible for exclusion (to keep from entering the mouth) and for filtering (to keep within the mouth). Therefore she compared sizes of the grit particles sieved. She estimated the functional mesh-size of the filter and concluded that neither the inner lamellae of the upper mandible nor those of the lower mandible contribute to the filter process. Moreover, Jenkin stated that the idea that only the outer marginals serve as filter must be reconsidered: "The filter differs from the previously assumed by having spaces between the upper hooks and leaflets subdivided by submarginals and the lower outer lamellae" (1957:466). The meshes produced in this way allow the filtering of particles larger than 0.5 mm. Jenkin postulated that the exclusion of particles larger than 4 mm occurs by manipulating the gape.

Rooth (1965) confirmed Jenkin's ideas, and he added a second type of filtering by which particles <0.5 mm can be filtered. In this mechanism the beak is presumed to be closed while the tongue pumps water through the filter, the water being expelled at the base of the beak.

Allen (1956) and Jenkin (1957) differ as follows. Allen assumed that a series of processes at the back of the tongue are the major filtering elements, while the outer marginal lamellae on the upper mandible have a secondary functional role. Jenkin, however, assumed that the lingual processes serve for food transport, while the large outer marginals in combination with the smaller submarginals of the upper mandible are the only filtering elements. Both authors describe the jet streams at the base of the beak and the back-and-forth stream of the water along the lamellae.

Sanderson and Wassersug (1990, 1994) concluded that, apart from a preliminary paper of de Jong and Zweers (1981), a functional anatomical model for filtering based on direct measurements from kinematics and filter capacity is still lacking. The current study is designed to understand the filter mechanism from cinematic analysis, to measure performances of filtering of food particles under different circumstances, and to determine the specific integumental adaptations for filter feeding. Such an analysis requires detailed description of the oral cavity and oropharyngeal anatomy. Therefore we will extend Jenkin's (1957) careful description of the integument of the mouth. In a separate study we will address how the pump and filter are driven by muscular actions, what specific adaptations the muscle-bone apparatuses of jaws and tongue have, and how they relate to the evolution of avian filter feeding systems.

Filter feeding has also been analyzed in several taxa of Anatidae and Procellariidae. The filter mechanism in Mallards (*Anas platyrhynchos*) has been described (Zweers 1974, Berkhoudt 1977, Zweers et al. 1977, Kooloos et al. 1989). Van der Leeuw and Zweers (1994) analyzed filter feeding in geese. Morgan and Ritz (1982), Harper (1987), and Klages and Cooper (1992) analyzed filtering in prions (Procellariidae). Feduccia (1976, 1978, 1980) and Olson and Feduccia (1980a, 1980b) proposed a filter mechanism for the extinct *Presbyornis*. Rubega and Obst (1993) suggested that surface tension feeding in phalaropes is a potential step in the evolution of avian filter feeding. We intend to integrate present knowledge of these systems by developing a preliminary morphospace of avian filter feeding mechanisms based on maximizing the avian pecking mechanism for filter feeding requirements, following the methodology of Zweers (1991a, 1991b) and Zweers et al. (unpubl. ms.). Provisional evolutionary hypotheses for the development of avian filter feed-

ing mechanisms are then developed using a modification of the methodologies of Baum and Larson (1991) and Losos and Miles (1994).

MATERIALS AND METHODS

NOMENCLATURE, DISSECTION, AND SEM

We adapt the systematic nomenclature of Kear and Duplaix-Hall (1975) and the anatomical nomenclature of Baumel et al. (1993), Baumel and Witmer (1993) and Vanden Berge and Zweers (1993). We dissected two skulls and four heads (two fresh) of adult specimens of the Caribbean Flamingo (*Phoenicopterus ruber ruber* L, 1758), and one skull and two heads of the Greater Flamingo (*Phoenicopterus ruber roseus* Pallas, 1811). The study of lamellae and other integumentary structures, e.g., taste bud outlets, by scanning electron microscopy and pontamine skyblue, follows techniques described by Berkhoudt (1976, 1977).

EXPERIMENTAL ARRANGEMENT

Conditioning. Specimens borrowed from the Avifauna Zoo (Alphen aan den Rijn, Netherlands) of the Caribbean and Greater Flamingo were available for close-up, high-speed filming in the lab. We transported the birds following techniques described by Sprunt (1975), and Sprunt and Crego-Bourne (1975). Birds were kept in a concrete basin of 370 × 120 × 16 cm. One half of the basin was covered with 10 cm sand and the other half was filled with water at 10–15 cm depth (Kear 1974). The backwall was tiled, whereas left and right walls were hardboard, 1.5 m high. The front was a wire-netting, 40 cm high. Four birds were restrained in a harness in the experimental cages for a few days after their arrival. They were conditioned stepwise to the experimental set-up in the next six weeks and experimentation was done over the next five months. The birds eventually were filter feeding at 90 cm in front of the camera. Tests could only be performed if birds had other birds nearby.

Cinematography. A Teledyne Camera, 100–125 fps., 1/650 sec exposure, was used. Birds were protected from the heat of the spotlights by a perspex sheet of 30 × 20 cm which formed one side of the feeding box. The box had an adaptable width of 7–15 cm. We were able to train only one bird for experimental purposes and therefore all specific data collected is based on observations of this single specimen.

The birds were filmed while feeding from a homogenous suspension of seeds. Filter feeding was analyzed by a frame-by-frame analysis. For the kinematic analysis the terminology of Zweers (1982) was used. We were not allowed to physically mark the birds, but the following points of identification were used (letters refer to Fig. 1): a) tip of the lower mandible; b) tip of the upper mandible; c) a spot halfway along the lower mandible; d) distal tip of the nostril; e) center of the eye; f) intersection of an arc from e) and the silhouette of the head; g) fronto-nasal border of the feather cover; h) center of the seed kernels; i) the most ventral projection of the retracted tongue in the throat; j) intersection of an arc from c) and the bony silhouette of the lower mandible; k) intersection of perpendicular from i) at the line c/j.

These points of identification allowed measurement of the following parameters: 1) gape, as the distance between the tips of the mandibles; 2) dorso-ventral motion of the tongue; 3) rostro-caudal motion of the tongue; 4–11) represent the X- and Y-coordinates of the identification points at the eye (4, 5), the fronto-nasal edge (6, 7), the tip of the upper and lower mandibles (8–11); 12) the angle (α) of upper mandible and skull; 13) the angle (β) of lower mandible and skull; XY-coordinates of kernels (h).

The dorsoventral motion of the tongue was measured by placing a cardboard model of the bony lower mandible over the silhouette of the lower mandible at each frame measured. Then the ventral silhouette-line of the bony mandible was drawn at an XY-table, while a line was drawn connecting spot c) and the intersection of an arc from c) with the bony, mandibular silhouette line (j). The length of the perpendicular from the top of the bulging skin of the throat on the constructed line represents the dorsoventral motion of the tongue. The distance between spot c) and the intersection of the perpendicular and the constructed line represents the rostrocaudal motion of the tongue. To measure 12) and 13) a line was drawn representing the head, connecting the center of the eye and the intersection of an arc from the eye center and the head silhouette (line S in Fig. 1). The line representing the lower mandible connects the beak tip and the spot on the lower mandible. The line representing the upper mandible connects the upper mandible tip and the rostral tip of the nostril.

Capacity to filter and to discriminate specific seed sizes. A diet was composed following Ridley

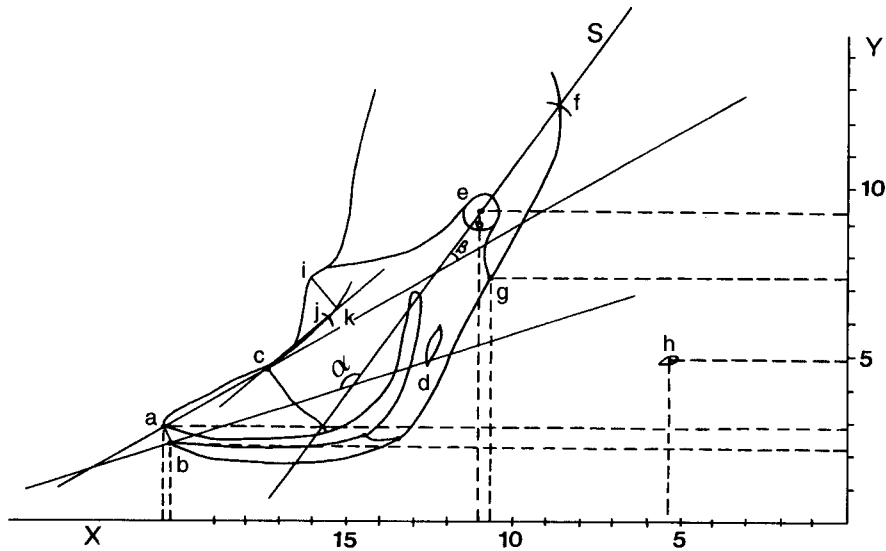


FIGURE 1. Identification points and measured parameters for the analysis of filter kinematics. Line a/b = length of gape; Line a/c = axis of the lower mandible; Line b/d = axis of the upper mandible, Line e/f = axis of the head; Angle α = intersection of Line b/d and Line e/f, and defines the excursion of the upper mandible on the skull; Angle β is the intersection of Line a/c and the Line e/f, and defines the angular excursion of the lower mandible on the skull; Line i/k = dorsoventral motion of the tongue; Line c/k = rostrocaudal motion of the tongue. See the text for the key to the letters and numbers.

(1954), Ridley et al. (1955) and Wackernagel (1975). Data from feeding of the Greater Flamingo were analyzed. Foods and seeds offered in tests were mostly ovoid: cut grass, broken millet, poppy seed, millet, grass seed, barley corn, milo, mung beans, corn, peas, marrow fats, pieces of bread. The largest cross sectional seed-diameter is taken as a reference for comparison since that is the major constraint for filtering as

well as exclusion of seeds. Mass, volume and form parameters are shown in Figure 2 and Table 1. These data refer to 40 kernels of each type. The specific gravity of these seeds is slightly higher than 1. This feature and the strong turbulence in the suspension caused by the filter feeding beaks assure an almost homogenous offer of seed suspensions in the performance tests. Suspensions for kinematic analysis comprise >2,000

TABLE 1. Form and size of seeds offered in test sessions. Width and depth represent the smallest and largest cross sectional diameters. Averages are taken from 40 particles; standard deviations are in parentheses; SG is specific gravity; particles eaten by filter feeding are shown in the right column.

Food	Width	Depth	Length	SG	Filter
1. Cut grass	<0.25				-
2. Cut grass	0.25-0.50				-
3. Broken millet	0.52 (0.10)	0.80 (0.21)	1.42 (0.20)		-
4. Poppy seed	0.59 (0.09)	0.96 (0.09)	1.23 (0.08)		-
5. Millet	1.45 (0.25)	1.74 (0.11)	1.95 (0.30)	1.36	+
6. Grass seed	1.52 (0.11)	2.03 (0.11)	2.87 (0.18)	1.26	+
7. Barley corn	2.77 (0.23)	3.58 (0.26)	8.03 (0.51)	1.10	+
8. Milo	2.62 (0.25)	3.94 (0.35)	4.37 (0.28)	1.02	+
9. Mung bean	3.61 (0.32)	3.62 (0.30)	4.81 (0.59)	1.20	+
10. Broken corn	3.75 (0.48)	4.99 (0.76)	8.30 (1.14)	1.26	+
11. Pea	8.19 (0.51)	8.84 (0.63)	10.8 (0.62)		-
12. Marrow fat	8.19 (0.54)	10.3 (0.99)	11.8 (0.84)		-
13. Bread	>10	>10	>102		-

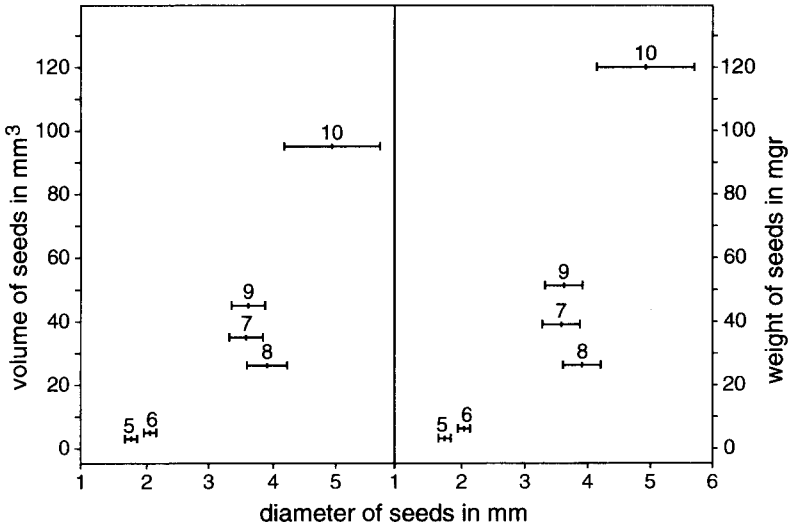


FIGURE 2. Volume and mass of the seeds used to analyze kinematics and capacities of filter feeding. Key to the numbers: 5, millet; 6, grass seed; 7, barley corn; 8, milo; 9, mung bean; 10, broken corn.

particles of cut grass, 1,000 parts broken millet, 1,000 parts of poppy seed, 500 parts of barley, grass seed, millet, milo and mung bean, respectively, 100 parts of large peas, and 50 marrow fats.

Suspensions for performance tests were offered after 24 hr of food deprivation. The results of the first 60 sec of uninterrupted straining were used for analysis. Homotypic suspensions of 800 particles of millet, grass seed, barley, milo, mung bean and broken corn were used to test filter capacities. In addition, single discrimination tests were performed by offering mixtures of two seeds (Table 2). The seeds offered represent form and size of the natural food of Greater and Caribbean flamingos.

RESULTS

ANATOMY OF THE ORAL CAVITY AND OROPHARYNX

Jenkin (1957) reviews the literature on the integument of the oropharynx including Owen (1832), Gray (1869), Milne Edwards (1869-1871), Weldon (1883), and Shufeldt (1901) and adds her own accurate description. Neither the review of Kear and Duplaix-Hall (1975) nor more recent papers add to the work of Jenkin (1957). We describe these anatomical areas adding new details from X-ray and SEM analyses.

Beak (Fig. 3). The deep beak of the Caribbean and Greater Flamingo curves as much as 50°

sharply ventrad just rostral to the nostrils. The oblong apertura nasalis may be closed by the large valvula nasalis. The midsagittally keeled upper mandible fits closely along the broad mandibular rims of the deep trough-like lower mandible. The external shape of the slender distal part of the upper mandible is straight and flattened dorso-ventrally, with a longitudinal ridge

TABLE 2. The total seed number in mixtures offered for discrimination tests and the number filtered per 60 sec. Test 3 has been done twice; these data are added in parentheses.

Mixture	Offered numbers	Filtered numbers	Depth
1. Broken millet	>1,000	120	0.8
Grass seed	>1,000	1,200	2.0
2. Poppy seed	>1,000	—	1.0
Grass seed	>1,000	—	2.0
3. Grass seed	800 (550)	254 (219)	2.0
Barley corn	800 (550)	278 (20)	3.6
4. Grass seed	800	660	2.0
Milo	800	14	4.0
5. Grass seed	800	1,074	2.0
Mung bean	800	2	3.6
6. Milo	800	260	4.0
Barley corn	800	235	3.6
7. Milo	800	6	4.0
Mung bean	800	—	3.6
8. Poppy seed	4,800	570	1.0
Milo	800	420	4.0

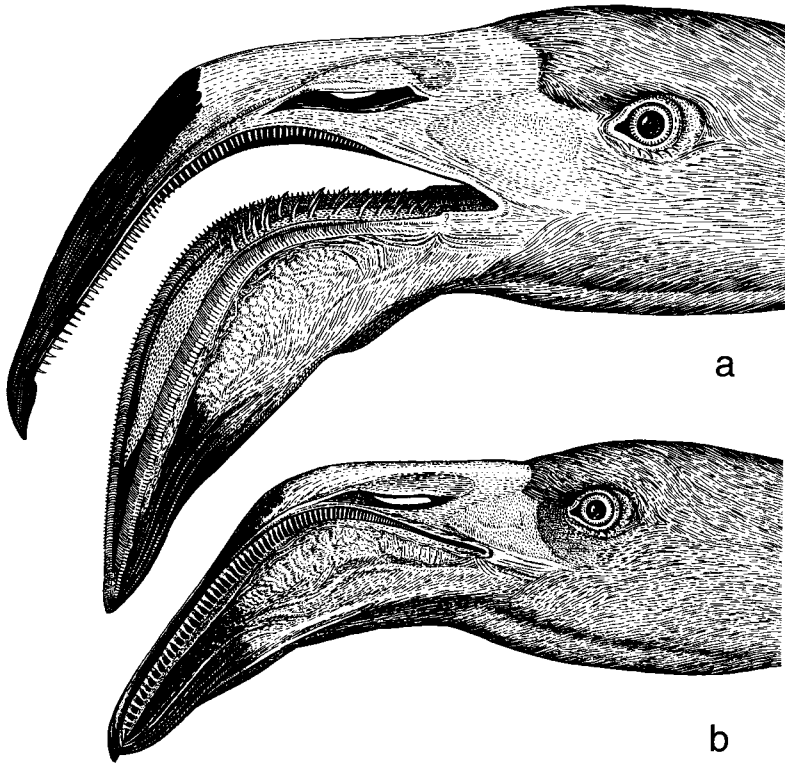


FIGURE 3. Head of the Caribbean Flamingo (*Phoenicopterus ruber ruber*). a. A wide open beak. The smooth tongue surface clearly follows the curvature of the beaks. On the proximal half of the tongue lies a series of large caudally pointing spines, and the main body of the tongue clearly lies in the trough-like lower mandible. The flexible skin of the throat ventrocaudally of the lower beak shows a slight bulging. This is the area that will bulge outward when the tongue is retracted. b. Head with closed beak. Presence of a series of lamellar meshes along the beaks is clearly visible. Distal meshes differ in shape from the proximal ones at the curvature of the beaks.

laterally just dorsal to the tomial edge. Within the lower mandible lies a large and fleshy tongue that closely fits along the inner rami. Ventrally, the external integument of the distal lower mandible is very hard with a few longitudinal shallow grooves. The lateral walls of the mandible extend caudad with a hard keratin cover, but midventrally the skin becomes soft and flexible at the level of the distal end of the beak curvature.

Tongue and mouth floor (Figs. 3, 4, 5; numbers in parentheses refer to fig. 4). The lateral, external appearance of the tongue follows the curved shape of the beaks. The large fleshy tongue completely fills the mouth when the beak is closed and the tongue protracted. The flexible distal part of the tongue (3) is dorso-ventrally flattened and pointed, followed caudally by lateral extensions forming the lingual bulges (4). Radiograms (Fig. 5) show that the fleshy proximal portion of the

tongue is very much larger and that it is supported by bilateral, large, semi-circular paraglossals giving the ventral tongue-body a non-flexible circular shape. Retraction of the tongue requires therefore much space in the mouth floor, but this space is not present. However, the flexible throat skin allows a strong bulging outward of the throat when the large body of the tongue is retracted.

Dorsolaterally on the tongue lies a bilateral series of about 20 flexible spines, the papillae linguae rostralis (5), almost entirely in the non-curved proximal part of the beak. The spines point dorsally, slightly caudo-laterally and decrease in size from 5 to 3 mm rostral to caudal. When the beak is in closed position and the tongue protracted, these spines lie along the maxillar keel (16). During tongue retraction they are in a position to sweep along the inner lamellar series

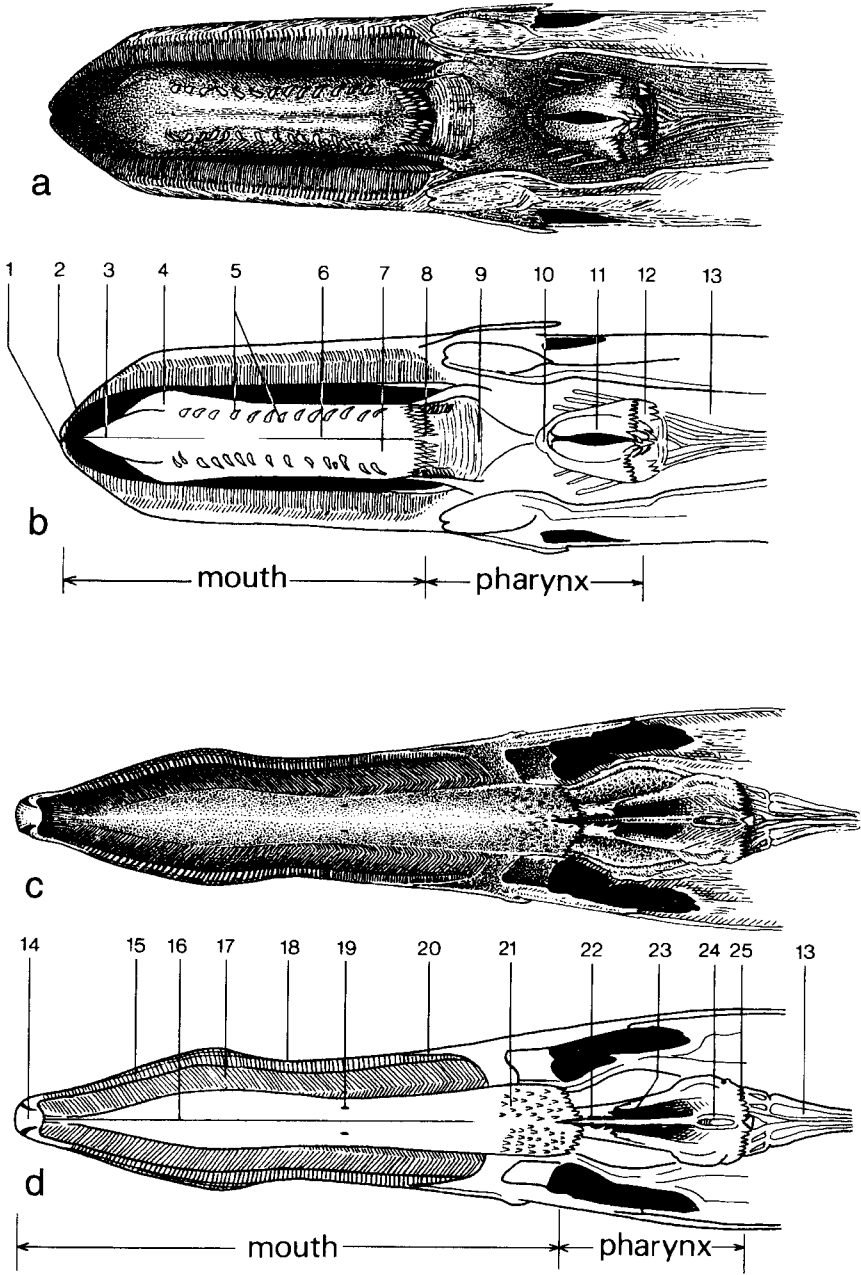


FIGURE 4. Integument of oral cavity and oropharynx. a, b. Dorsal view of the floor of mouth and pharynx. The rami of the lower mandible are spread laterad. c, d. Ventral view of the roof of mouth and pharynx. Key to the numbers: 1) Mandibular nail, 2) Symphysis, 3) Lingual tip, 4) Lingual bulges, 5) Papillae linguae rostralis, 6) Median lingual groove, 7) Torus linguae, 8) Papillae linguae caudalis, 9) Basis linguae, 10) Rostral tip of cricoid bone, 11) Larynx, 12) Papillae pharyngis caudo-ventralis, 13) Esophagus, 14) Maxillary nail, 15) and 17) Outer and inner maxillary lamellae, 16) Median maxillary ridge, 18) Maxillary tomial edge, 19) Orificis glandulae maxillaris, 20) Rictus, 21) Papillae pharyngis rostralis, 22) and 23) Narrow and wide parts of internal choana, 24) Infundibulum, 25) Papillae pharyngis caudo-dorsalis.

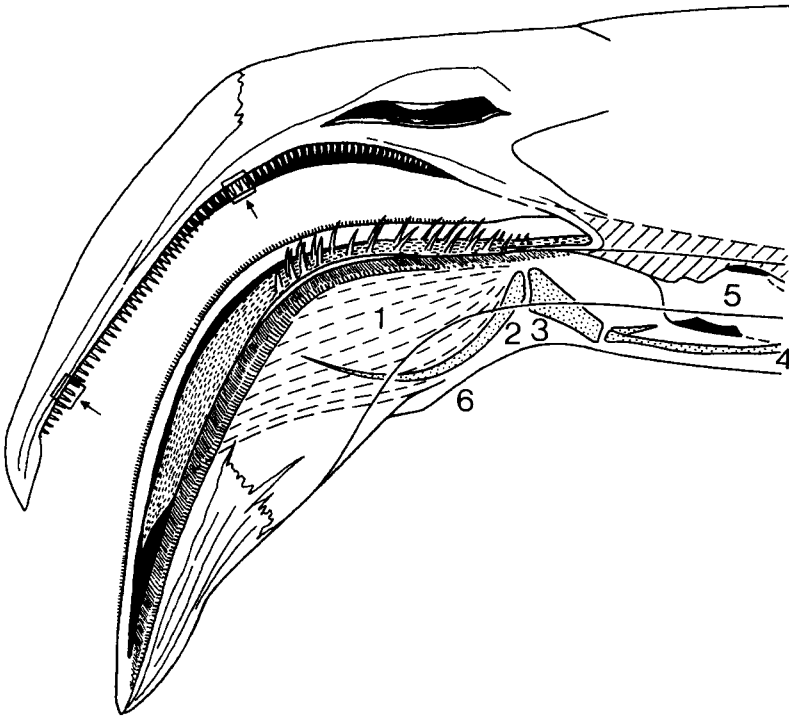


FIGURE 5. Scheme of the open mouth. The position and view of the SEM pictures in Figure 6 are indicated by the two rectangles along the upper mandibles. Dashed lines indicate the outlines of the fleshy portion of the tongue (1); stippled areas are the curved semi-circular paraglossal (2), the stout basihyal (3) and ceratobranchial (4) (taken from radiograms). The torus lingualis overlies the paraglossale-basihyale joint. The larynx (5) lies dorsal to the ceratobranchiale, the dorsal black spot is the ossified portion of the arytenoid and the ventral spot, the ossified portion of the cricoid. The flexible throat skin (6) will bulge out if the tongue is retracted. The oblique shaded area represents the pharynx.

of upper (17) and lower (2) mandibles. A shallow median lingual groove (6) runs between these series of spines. At the end of the series lies a slight elevation of the lingual mass forming a lingual cushion, the torus linguae (7), that runs along the mouth roof if the beak is closed.

Pharynx floor (Fig. 4). At the caudal end of the lingual cushion lie two parallel, transverse series of some 20 flexible spines pointing caudad, the papillae linguae caudales (8). These series mark the entrance into the oropharynx and the transition from the external tongue into the lingual base (9). Radiograms (Fig. 5) show that this external transition is marked internally by the articulation of the median, pronounced basihyal and the curved bilateral paraglossals. The lingual base carries rostrally a lateral series of 10 soft, caudad pointing spines, the papillae pharyngis. The lingual base also shows numerous transversal folds, indicating that the area can be extended

over a relatively large distance. The elevated larynx (11) forms the caudal part of the pharyngeal floor. The glottal mound is characterized by a rostrally elevated tip of the cricoid (10)—forming the caudal border of the lingual base—and bilateral longitudinally orientated arytenoids. The caudal border of the larynx is a transverse series of 20 spines, the papillae pharyngis caudovertralis (12), marking the transition from the pharynx into the esophagus (13).

Mouth and pharynx roof (numbers in parentheses refer to Fig. 4). The shallow maxillary keel is smooth. Lateral to the keel is a bilateral shallow groove converging rostrally and ending in the very hard keratin nail at the beak tip (14). Two conspicuous bilateral series of lamellae run along the whole beak rim, the outer (15) and inner (17) maxillary lamellae. The smooth roof changes caudally at the corner of the mouth (rictus) (20) into slightly bulging structures carrying

some 40 caudally pointing spines (21), marking the entrance into the oropharynx. This palatal area ends with a transverse series of 10 spines; then follow the narrow (22) and wide (23) parts of the secondary choana and the midsagittal, small infundibulum (24). Just caudal to the latter runs a second transverse row of 10 caudally pointing spines, which marks the entrance into the esophagus (13).

Maxillary lamellae (Figs. 3, 5, 6). Jenkin (1957) describes lamellar sizes and structures of several flamingo species. Our SEM analysis shows the following details. The maxillar rami carry inner and outer series of keratin lamellae. The outer maxillar lamellae are of two types: large, marginal lamellae and smaller submarginal lamellae. The following data are from three specimens, the larger specimen representing the higher values.

The large marginal lamellae are again of two types. There are 40–50 tooth-like, inward pointing marginals along 60–70 mm of the distal straight portion of the maxilla (Fig. 6). Interlamellar distances vary from 1.1–1.9 mm. Their height varies from 3.2–4.0 mm, and on the average it increases from distal to proximal. They are flexible in rostro-caudal direction, but much less flexible in lateral direction.

In the curvature of the maxilla the shape of these lamellae rapidly becomes blade-like, pointed, thin, and convex (Fig. 6a). There are 60–80 of these transversely positioned marginals. They gradually decrease in size and disappear. The first 10 blade-like lamellae along the curvature are 3.4–3.7 mm high, with an interspace of 0.5–1.0 mm.

Just medial to the outer tooth-like marginals lies a series of 100–130 smaller, inner, tooth-like submarginals. They often show up as a pair of small teeth behind and between a pair of the larger teeth (Fig. 6b), but this is not a rule (e.g., one or three submarginals may be present per interspace). If two or three submarginals are found, often the rostral one is larger than the caudal one. The height of the largest submarginals per interspace varies from 0.8–1.1 mm in the region of the tooth-like marginals. In the region of the caudal blade-like marginals they are half this size and merge more caudally with the inner maxillary lamellae. The inner maxillary lamellae are much less pronounced and appear as transversal rows of very small blades. These blades are aligned in rows that run from rostro-lateral to caudo-medial (Fig. 6).

Mandibular lamellae. There is a series of blade-like, serrated mandibular marginals that opposes the series of outer maxillary marginals. As a rule, opposite each 10 maxillary marginals stand 25–28 mandibular marginals. This number decreases to 20 caudally. They are 1.1–1.4 mm high and each lamella runs from latero-rostral to medio-caudal. Their height decreases to 0.6–0.8 mm at the curvature of the beak. The inner mandibular lamellae are much less pronounced, run transversely, and are less than one-third of the height of the lateral marginals.

Functional meshes. The functional mesh-sizes in *Phoenicopterus ruber* are formed by the large marginal and the smaller submarginal maxillary lamellae in juxtaposition with the marginal mandibular lamellae (Fig. 12). If the beak is closed and the upper mandible tip is pushed against the lower, a slit of about 2 mm high is left between the beak rims, equivalent to the height of maxillary marginals. The mesh-sizes along the beak change in size and shape from rostral to caudal. The functional mesh-size with the beak in closed position along the distal portion with the tooth-like marginals varies considerably: $1.6(\text{height}) \times 1.7(\text{width})\text{mm}$ (± 0.4). The mesh size at the curved portion of the beak with the blade-like marginals also varies: $2.0(\text{height}) \times 0.7(\text{width})\text{mm}$ (± 0.2).

Tuning the gape adjusts mesh-size. The gape along the straight, distal portion of the beak is almost constant over the full length of that portion when the beak tips gape to about 3 mm. About the first 1.5 mm of such gaping produces an increase of the functional mesh since that is the height of the mandibular marginals, representing the overlap with the maxillary marginals. The fact that the marginals rub along each other by the caudo-rostral shift of the mandible in this stage of gaping does not influence the mesh size since the lamellae are flexible in rostro-caudal direction. The other 1.5 mm of such gaping produces an extra, constant slit of 1.5 mm between the tips of the upper and lower marginals along the distal portion of the beak. Wider gaping is assumed to be non-functional for filter feeding since much wider distances develop proximally than distally. This does not allow size discrimination.

Taste and touch organs. Jenkin (1957) found no evidence of taste organs in the beak or tongue. However, Bath (1906) described a group of taste buds in the mucosa of the ventral esophagus,

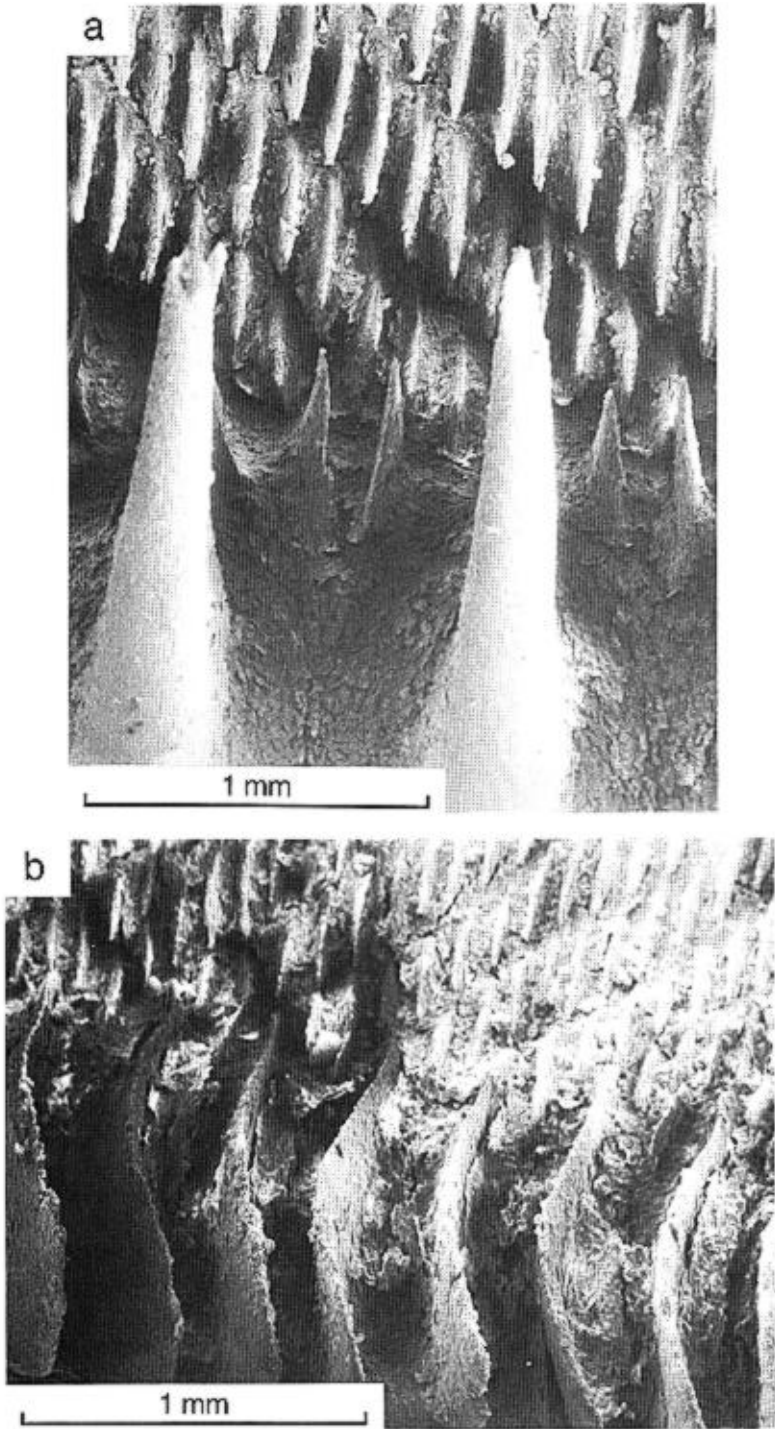


FIGURE 6. SEM-prints of the maxillary lamellae. a. Two distal, tooth-like, large marginals are shown. Just medial to the marginals lie two pairs of smaller submarginals. Behind these lamellae, more medially are parallel series of the inner lamellae. They lie in both diagonal and transversal series. b. Seven plate-like lamellae are shown at the curvature of the beaks. The submarginal lamellae are present as the most lateral lamella of the inner lamellae. They are positioned in transverse as well as in diagonal rows.

caudal to the tongue, in two bilateral folds supported by the hyoid horns, adjacent to the larynx. These regions of taste buds have not been observed in ducks (Berkhoudt 1977, 1985), which suggests the possibility that their location in flamingos is an adaptation to the inverted positioning of the filter mechanism when flamingos filter feed. Further, just proximal to the maxillar curvature the orifices of the monostomatic glandulae maxillares (gl. palatina anterior; 19 in Fig. 4) open bilaterally. SEM and rapid surface staining with pontamine skyblue show that each is surrounded by about 10 orifices of taste buds (Fig. 7a). These glandular outlets and taste buds are near the bill tips in ducks, as in most birds (Berkhoudt 1977, 1985), which suggest again an adaptation of their location to specific filter feeding in flamingos. Much higher numbers of taste bud pores were found in the circumference of the openings of the numerous gll. sphenopterygoideae, 3 to 6 around each duct-outlet (Fig. 7b).

Dissections of the maxillar, ophthalmic and mandibular trigeminal rami all along the beak show that directly under the maxillar and mandibular marginals, there lies a dense field of corpuscles of Herbst (also cf., Schildmacher 1931). They are innervated by numerous nerve branches from these very large trigeminal rami.

KINEMATICS OF FILTER-FEEDING

Behavioral phases of filter feeding. A behavioral scene of filter feeding contains four phases. The pattern starts with food searching by a head depression and the immersion of the straight, distal beak portion in a nearly horizontal position. The head may then be swept sideways while the birds walk slowly. A filter phase follows in which cyclic motion patterns of beak, tongue and head produce a stream in and out the mouth while particles are collected by sieving. The head is rocking each cycle and either one or the other side of the beak may be pushed in the top soil serving as the leading side for lateral head motion.

Gradually the filter phase changes into a transport phase in which the food collected at the level of the beak curvature is transported from the mouth into the pharynx, the food having been left on the lingual base. This occurs by a somewhat different cyclic motion pattern of mandibles and tongue while the head is elevating. A swallowing phase of a few cycles follows in which the food bolus, collected at the lingual base, is transported from the pharynx into the esophagus. This is accomplished by cycles of depressed

protractions and elevated retractions of the larynx. Finally, the papillae pharyngis caudovernalis sweep the bolus into the esophagus. Often the bolus can be seen travelling downward as a swelling even though the bolus may follow an oblique course.

The search, filter, transport, and swallow phases each have characteristic, cyclic motion patterns. The filter and transport phases are highly repetitive and merge gradually into each other. Similar patterns are found for seeds ranging from 2 to 4 mm in cross-sectional diameter. In the next section we show that the filter capacity peaks sharply for these seed sizes and the motion pattern is most clearly visible when millet, grass seed, barley corn or milo is filtered. Representative portions of phases have been selected for frame-by-frame analysis.

Filter cycle in suspensions of monotypic seeds (Figs. 8, 9). The motion characteristics of the filter cycle derived from filtering barley corn and grass seed are as follows. The frequency is about 12.8 Hz and the cycle duration about 78 msec. If the head is kept in the inverted position, which is normal for filtering, the horizontal motions of the identification points at the lower and upper mandibles are rather small, and those at the frontal and the eye are almost zero. However, the vertical motions of these points at upper and lower mandibles are considerable, while those at the frontal bone and the eye are again almost zero. Thus, the head is rocking each cycle around a center near the eye and frontal bone in such a way that the beak tips move up and down each cycle. The amplitude of the upper mandible is somewhat larger than that of the lower mandible, which may be due to a larger independent motion of the upper beak relative to the head motion.

The generalized picture for filtering the optimal food size of 2–4 mm is derived from representative figures as shown in Figure 8. The generalized filter cycle for grass seeds is as follows (Fig. 9). The gape increases during the first stages; is steady during the second half of stage 2 and decreases during stage 3; the beak is kept closed during stage 4. Lingual retraction is very fast during stage 1, comes to a halt in stage 2, then slow protraction occurs in stage 3, followed by fast protraction in stage 4. Lingual elevation/depression occurs in stages 1 and 2, and depression/elevation in stages 3 and 4. Hence, the lingual body retracts elevated and protracts depressed. The rocking head pushes the straight portion of the beaks (horizontally) down and forward in

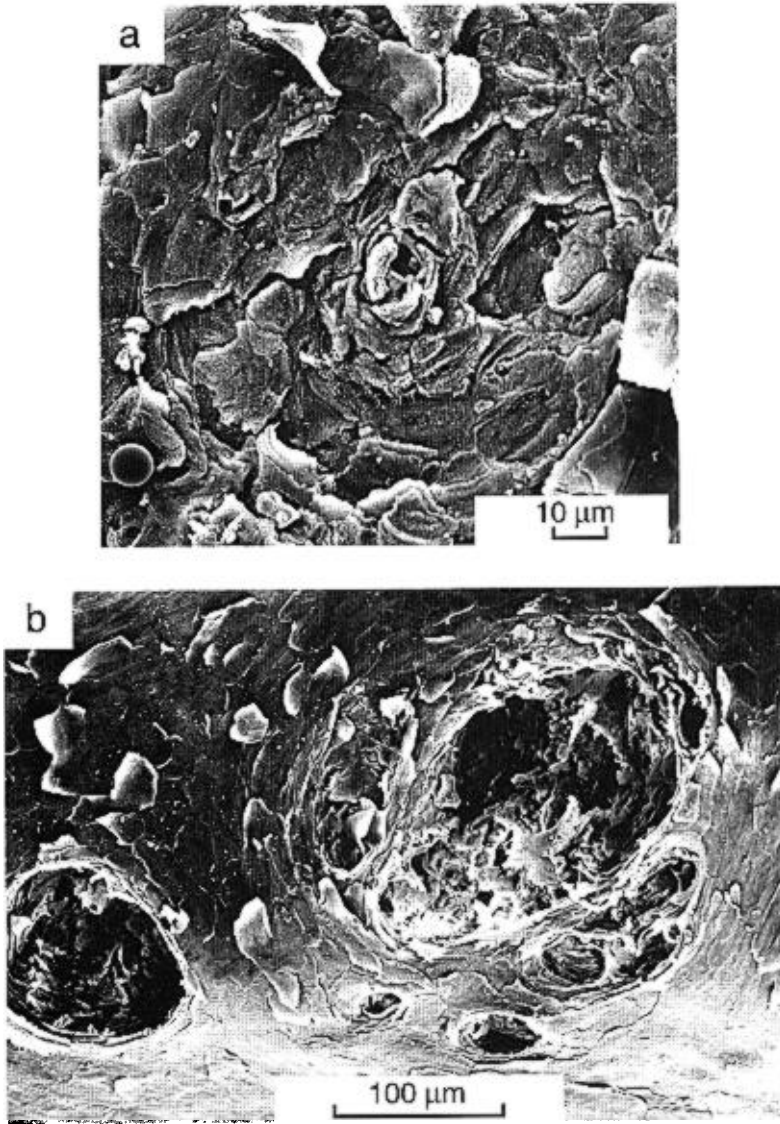


FIGURE 7. SEM-prints of bud orifice. a. Orifice of taste bud around the outlet of the monostomatic gl. maxillaris. b. Orifices of taste buds around the numerous outlets of the gl. sphenopterygoideae.

stages 1 and 2, and pulls it up and backward in stages 3 and 4. In lateral motion the head is often tilted so that the leading beak rim is pushed further down than the contralateral rim.

Motion of seeds shows that the water suspension flows in only along the distal, straight portion of the beak when the gape increases. Water flows out when the tongue protracts and the beak has been closed in the last part of the cycle. The outflow of the water is all along the beak rim.

We have observed water expelled as a beam from the beak tip and also by two jet streams caudally at the curvature of the beak. Generally water is expelled along the straight, distal portion of the beak when the beak is or has been closed.

Filter cycle in mixtures of different seed sizes. If smaller millet is filtered, the difference from the generalized pattern is that gape amplitude is smaller, 1 mm, while the major water-outflow is directed at the beak curvature. If larger-sized

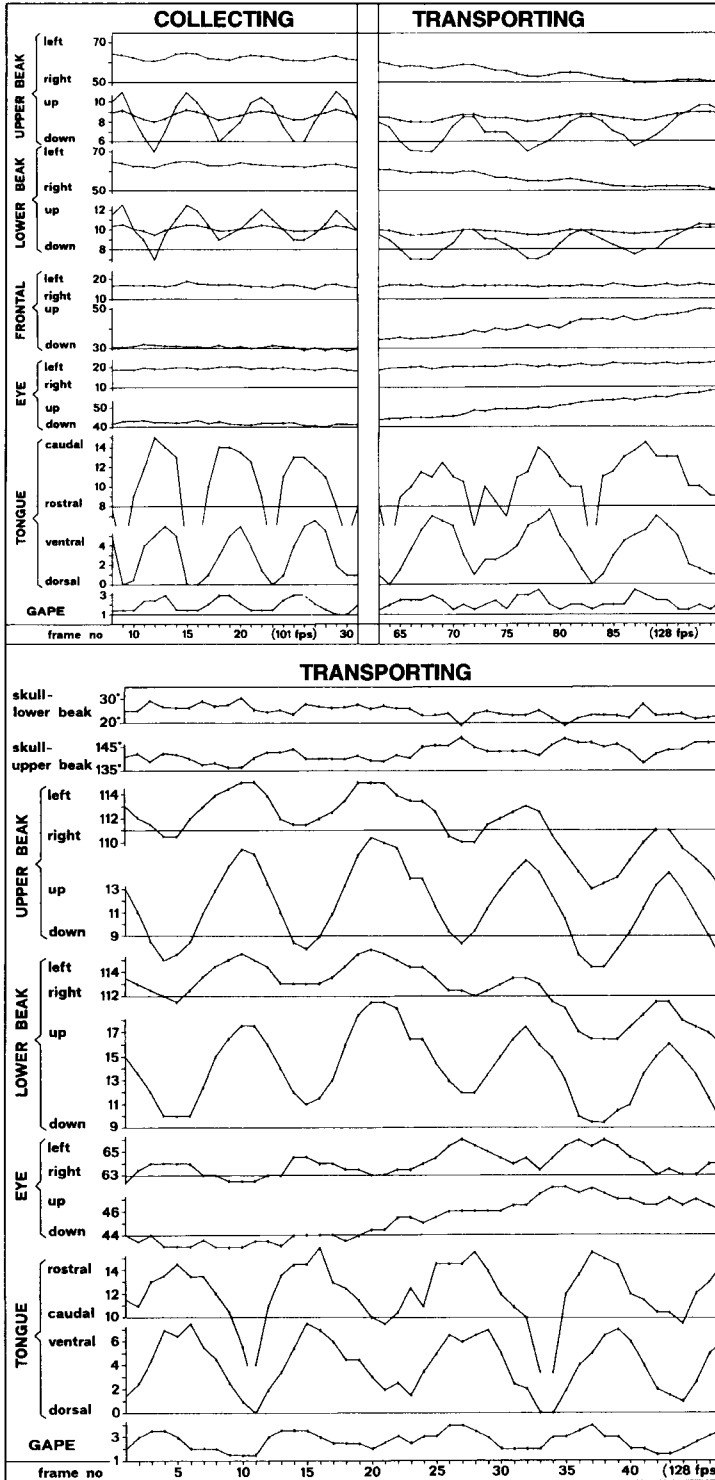


FIGURE 8. Kinematics of filtering. Motion patterns of head, eye, mandibles and tongue while filtering barley corn (upper figure) and mung beans (lower figure). Two types are recognized: collecting and transporting food. See text for explanation.

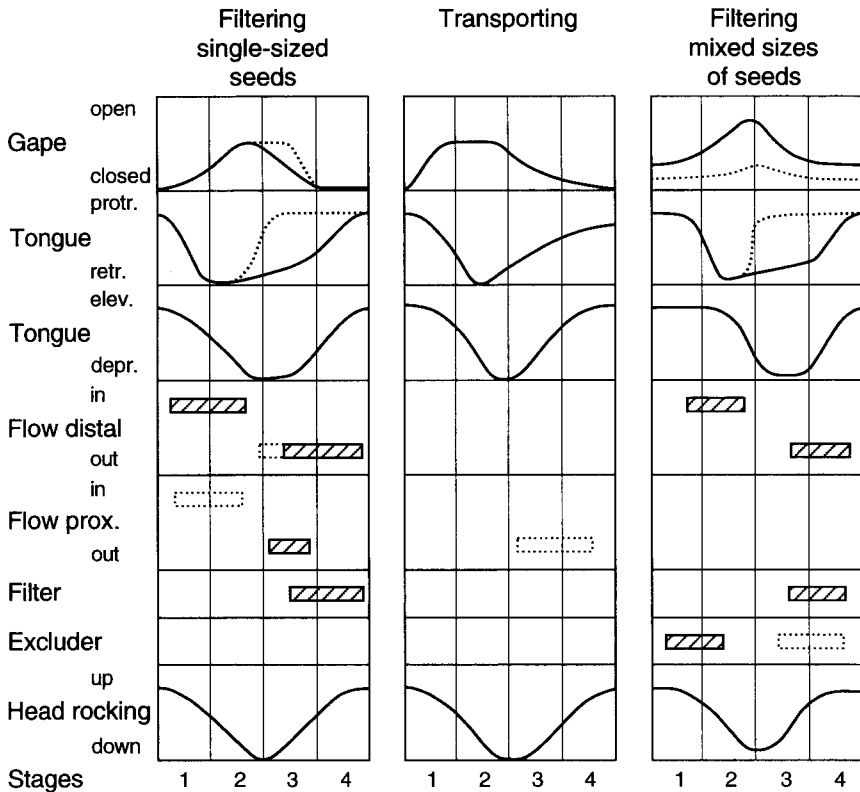


FIGURE 9. Generalized picture of waterflow, lingual and gape changes during filtering and transporting. Left column: Filtering seeds of 1.7–4.0 mm in cross sectional diameter in monotypic suspensions. Middle column: Filtering seed mixtures where the larger seed is filtered and the smaller one is washed through the lamellar meshes. Right column: Filtering seed mixtures where the larger seed is excluded and the smaller one is filtered. See text for explanation.

mung beans are filtered the gape is wider, about 3 mm, while the water flows out along the vertical beak portion and the beak curvature. If a mixture of grass seed and mung bean, or barley corn or milo is filtered, gape changes per cycle are from 1 mm (maximally “closed” position) to 3 mm (maximally “open” position).

Transportation cycle. The characteristics of the transportation cycle are illustrated for barley corn in Figure 8. In Figure 9 the cyclic pattern is shown to be almost similar to the filter cycle. Of course, other anatomical elements are set to function now. The differences are as follows. The cycle lasts a bit longer, about 86 msec, hence the frequency is about 11.6 Hz. The rocking motion is slightly less; the head is elevating, and the gape motion appears less regular. The water is expelled mostly along the proximal part of the beaks at the beak curvature and caudal to it. Lingual

pro- and retraction run parallel to lingual elevation and depression.

FILTER PERFORMANCES

Acquisition capacity and tolerance. Cut grass and broken millet are pumped in and out through the filter while the beak is kept closed during the full motion cycle. The birds lose interest very fast in filtering cut grass. Poppy seed is also readily refused as food to filter. All other types of seeds are accepted after a short period of conditioning. The birds show a normal filter motion pattern, if they filter peas or marrow fats, however their motivation decreases fast. After a few trials they apparently accept that they cannot filter these large seeds; however, they do not change to pecking. Pieces of bread are taken by pecking only. Performance measurements are taken in the tol-

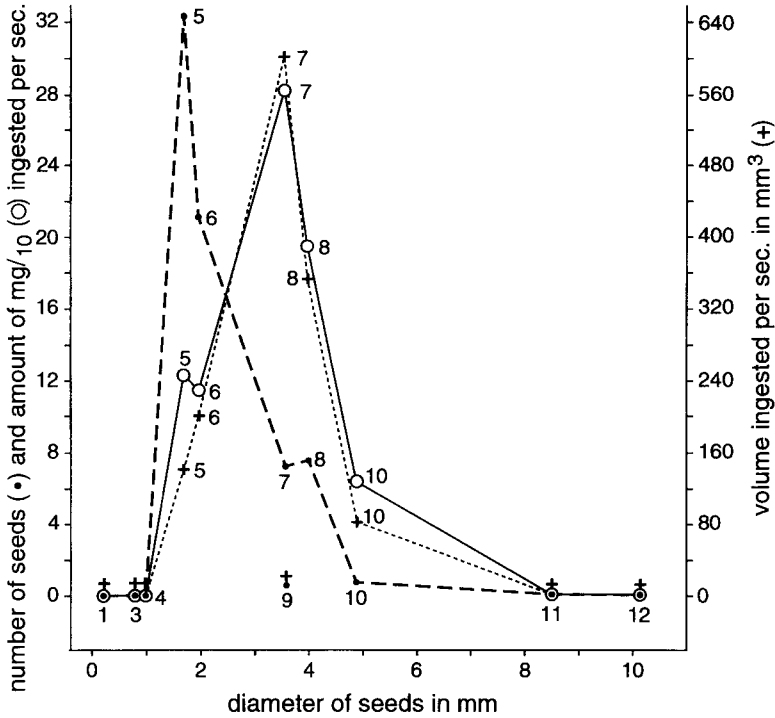


FIGURE 10. Graph illustrating the number, mass and volume of seeds filtered per second from a homogeneous monotypic suspension. Key: 1, very small cut grass; 2, cut grass; 3, broken millet; 4, poppy seed; 5, millet; 6, grass seed; 7, barley corn; 8, milo; 9, mung bean; 10, broken corn; 11, pea; 12, marrow fat.

erance range that runs from millet to broken corn. After a few trials the birds refused to filter milo.

The filter capacities for different seed sizes in monotypic suspensions are summarized (Fig. 10). In terms of numbers of food items filtered, the system peaks sharply for millet and grass seed which have cross-sectional size-levels of 1.7 to 2.1 mm, respectively. Also, in terms of ingested volume or mass the system peaks sharply, but now the peak has shifted to barley corn and milo at size-levels of 3.6 and 4.0, respectively. No intake is found for very small items as cut grass, broken millet and poppy seeds, or for very large items such as peas and marrow fats.

Almost all seeds must be sucked in with a beak slightly gaping since the functional mesh width with closed beak is about 1.6×1.7 mm. Only the cross sectional diameters of the smallest seed, millet (about 1.4–1.8 mm), allow filtering while the beak is kept closed. In the case of the larger seeds, the water is washed away while the beak is still slightly gaping. Apparently, not only the large marginals retain food, but also the internal

lamellae may play a role by fixating the seeds during water expulsion.

DISCRIMINATION CAPACITY

In the field, flamingos meet much more complex situations than single-sized food items. Caribbean flamingos in the Bahamas and Yucatan feed exclusively on small molluscs (*Cerithium*) (Klingel 1942). Allen (1956) concludes from reviewing the literature on food presence in the natural environment that the diet comprises (1) small molluscs (*Cerithiidae*), (2) organic ooze consisting of 80% bacteria, algae, diatoms, nematods, molluscs and arthropods, as well as seeds of euryhalin plants like widgeon grass, *Ruppia* and *Salicornia*, (3) brine shrimp (*Artemia*), and (4) larvae and chrysalids of salt fly (*Ephydra* sp.). Jenkin (1957) mentions from analysis of stomach-contents that *Cerithium* (5×25 mm) and *Artemia* (3×20 mm) are gathered by filtering, while green and blue algae (*Spirulina*; 0.03×0.1 mm) and diatoms (0.02×0.07 mm) are gathered by scraping and ingesting organic ooze. Rooth

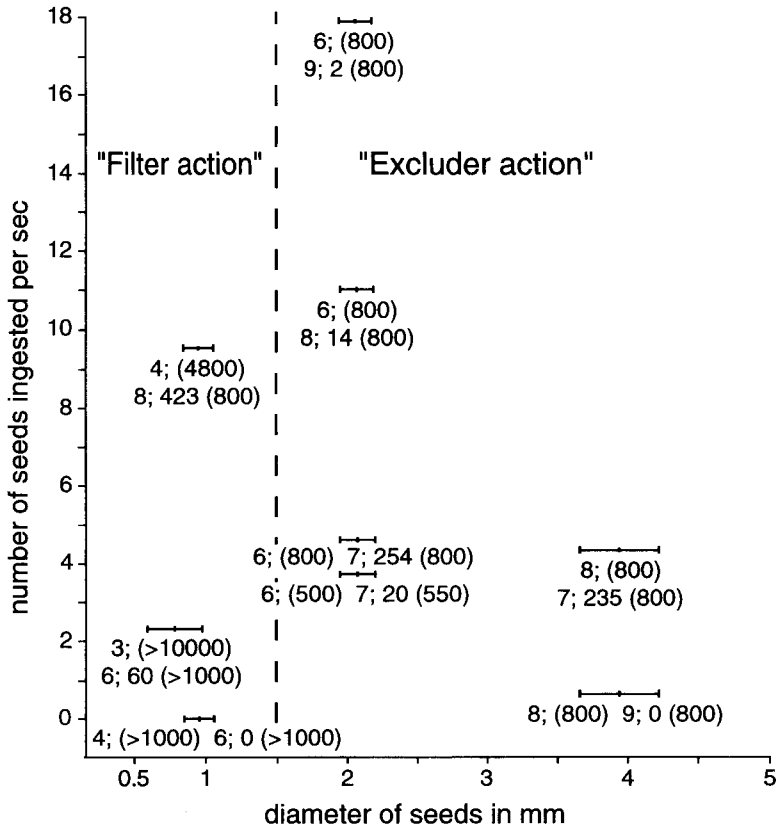


FIGURE 11. Results of the experiments where homogenously mixed suspension of two seed types were offered for filtering. The graph shows the number of seeds of the type that was most frequently ingested. Numbers in parentheses indicate the amount of seeds of both types offered. The amount of seeds that is filtered from the lesser filtered seed type is also shown. To the left of the vertical line are mixtures shown in which seeds are filtered while smaller seeds are washed through. To the right of this line are mixtures where the larger seed is excluded while the smaller one is filtered. See Figure 10 for the key to the lettering and see text for explanation.

(1965) adds that larvae and chrysalids of the salt fly (*Ephydra gracilis*; slender and 12 mm long) form the staple food, while the following taxa are also filtered: *Cerithium minimum*, *Cerithidea costata*, *Artemia salina* (5–10 mm), organic ooze and small cyprinoids. The Caribbean and Greater Flamingos are able to greatly alter their diet. Rooth (1975) observed a change in staple food from the salt fly (*Ephydra*) to small molluscs (*Cerithium* sp. and *Cerithidea* sp.) as a result of a drastic change in habitat. Extensive diet changes are also recorded in zoo populations. Poulson (1975) mentions that mixed food pellets, dried shrimp, and lucern and peppers (*Capsicum*) suffice well. Jenkin (1957) mentions that many seeds of 2–4 mm are filtered from *Cyperus*, *Medicago*, *Juncus*, *Lesia* and many Papilionaceae.

We tested whether the birds had size-discrim-

ination capacities. These tests were completed with only a single bird, and could not be repeated because of demands based on duration of the initial loan of the birds and the required physical conditions for the testing. However, these tests, although limited, do lead to the following results (Fig. 11, Table 2).

Grass seed is in the peak of filter capacity. Therefore, the discrimination capacity for grass seed was tested against four other seed sizes:

(1) A mixture of grass seed and broken millet was offered. There were 1,200 grass seeds (2.0 mm) ingested per minute, but only 120 broken millets (0.8 mm). This means that broken millet is sucked in with the grass seed and is then washed away through the meshes present when the beak is closed, while the grass seed is filtered. The outflow of broken millet can only occur along

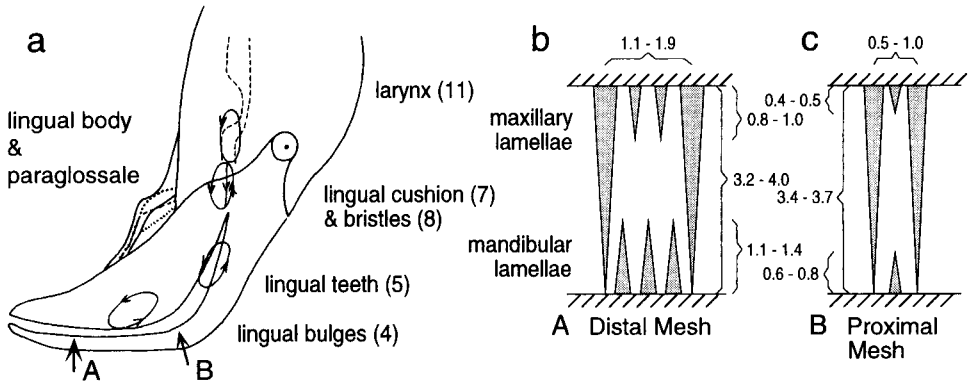


FIGURE 12. a. Main motions of lingual and laryngeal elements. Numbers refer to Figure 4. a, b. Generalized picture of the minimal lamellar mesh size along distal (b) and proximal beak rims (c). Maxillary marginal and submarginal lamellae as well as mandibular marginal lamellae are shown.

the distal portion of the beak, since the proximal meshes are too small. The system is not perfect since both seed sizes and mesh sizes vary.

(2) A mixture of grass seed and poppy seed was offered. There were no grass seeds (2.0 mm) ingested when it was mixed with poppy seeds (1.0 mm). Poppy seeds are not fully spherical, but are somewhat crescent-like, therefore they may jam the filter since they can stick between the maxillary marginals and submarginals if the beak is fully closed. The lamellar filter apparently cannot discriminate this mixture by filtering.

(3) There were two tests made with grass seed (2.0 mm) mixed with barley corn (3.6 mm). In the first test 254 grass seeds and 278 barley corns were filtered. In the second, however, there were 219 grass seeds and only 20 barley corns. Thus the filter mechanism acts in the first test as a *filter* for sizes ranging from 2.0 to 3.6 mm, but in the second the same apparatus operates as an *excluder* for the larger barley corns.

(4) A mixture of grass seed and milo was offered. There were 660 grass seeds (2.0 mm) filtered, but only 12 milos (4.0 mm). Thus, the lamellar sieve works almost exclusively as an excluder for large milo and as a filter for grass seed.

(5) From a mixture with mung beans (3.62 mm) there were 1,074 grass seeds ingested and only two mung beans. Thus, the lamellar sieve again operated as an excluder for the larger mung beans and as a filter for grass seed. To see whether the bird discriminates differences among larger sized seeds by setting the lamellar sieve, the following tests were done.

(6) From a mixture of barley corn (3.6 mm)

and milo (4.0 mm) the bird ingested 235 barley corns and 260 milos. Hence, both seeds were accepted. This does not mean that the birds cannot discriminate these sizes by tuning the gape. They like both types as food and moreover the barley corn is almost twice as elongated (8.0 mm) as milos (4.4 mm). Therefore, the following test was conducted.

(7) The birds apparently preferred not to accept the mung beans. Since mung beans have almost the same size range as milos (3.6 mm vs. 4.0 mm), both were offered in a mixture. There were six milos and no mung beans filtered. Hence, although with low overall efficiency, the lamellar filter was used as a filter for milos and as an excluder for mung beans. This was seen in the film when a specific mung bean was followed entering the mouth accidentally. When the mung bean touched the lower mandibular lamellae it was apparently 'recognized' as non-acceptable and worked away by an outflow. This 'recognition' may be done in two ways. First the mung bean is slightly larger (3.6 × 3.6 × 4.8 mm) than the milo (2.6 × 4.0 × 4.4 mm), and second it has a hard smooth cover. Thus, apparently the generality in this filtering is that barley corn is filtered and mung beans are excluded.

To determine whether the jamming of the filter by poppy seeds is due to the mesh size of the filter in the outflow if grass seeds and poppy seeds are mixed, poppy seeds were also offered in a mixture with milos. Milos (4.0 mm) are much larger than grass seeds (2.0 mm) in cross section and therefore they may allow a larger mesh size in the outflow to let poppy seeds (1.0 mm) pass.

(8) The test shows that 570 poppy seeds and

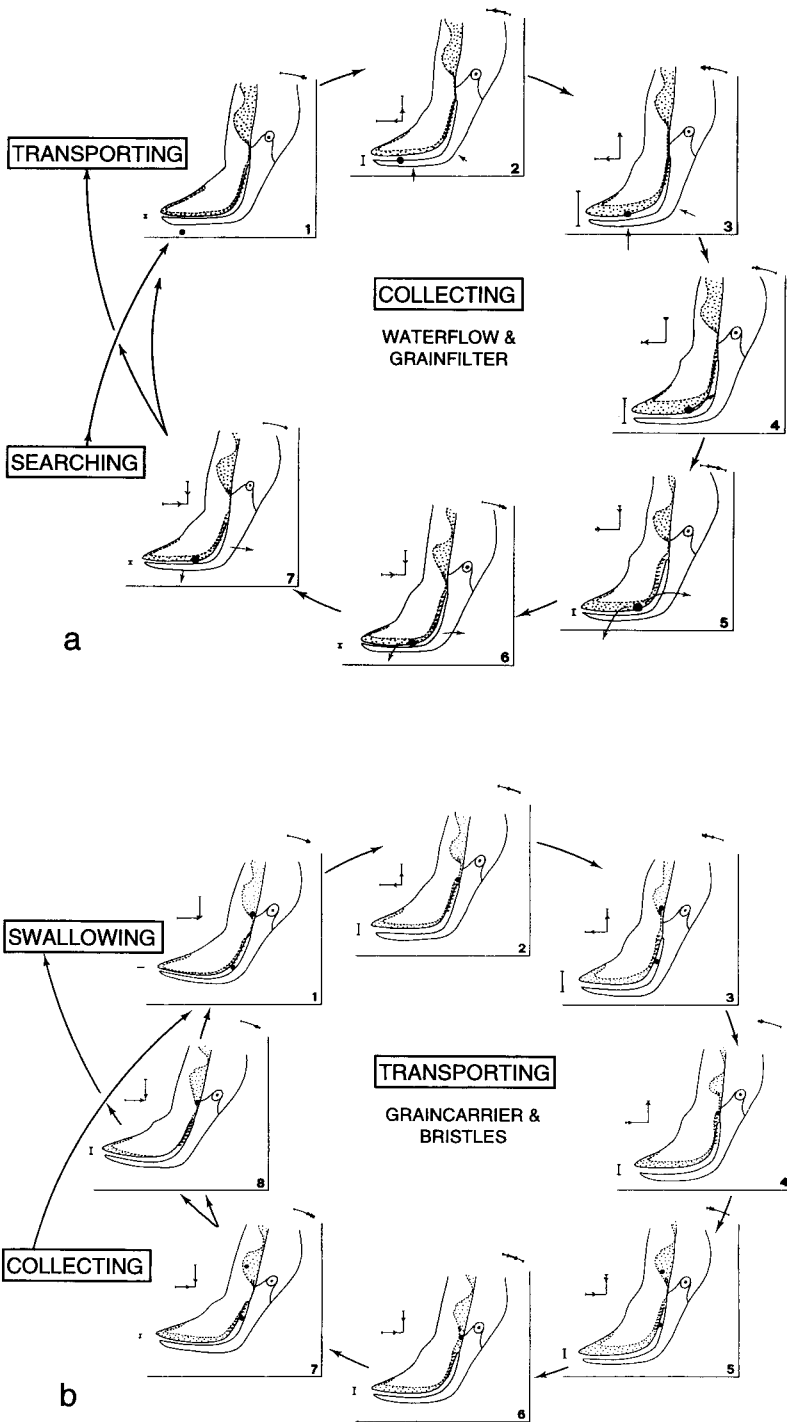


FIGURE 13. Filtering and transporting of seeds. Beak rims and throat are drawn in full lines. The lingual tip, lingual bulges, papillae linguae rostralis, torus lingualis, papillae linguae caudalis, basis linguae and larynx are drawn by dashed lines. Dotted areas represent cavities of mouth, pharynx and esophagus, respectively. The gape is represented by the bar to the left of the beak tip. The arrow above the head represents the rocking of the head. The perpendicular arrows to the left of the throat indicate lingual motion. The vertical bar represents pro-

420 milos are filtered. We conclude that the filter is not jammed, and poppy seeds are also filtered. This may be the effect of the fact that the concentration of poppy seeds was very high (4,800 items) compared to 800 milos. Thus, about 12% of all poppy seeds and over 52% of all milos were ingested. Given that the system is not perfect because mesh size and seed size vary, the discrimination efficiency is high.

DISCUSSION

LINGUAL BACK-AND-FORTH PUMP CAUSING A LATERAL IN- AND OUTFLOW

Filter patterns. Kinematic analyses of films show that filter feeding has four phases (1) head approach including grasping; (2) collecting food; (3) transport of food into the pharynx, and (4) swallowing—each having a specific cyclic motion pattern. The filter cycle is characterized by mutually tuned mandibular, maxillary and lingual motion patterns. There are two adjustable features recognized in the generalized mandibular-lingual motion cycle. First, size and duration of the gape are manipulated to adjust the mesh size of the inflow and outflow to filter preferred food size in the range of cross sectional diameters of 1.0–4.0 mm, and to exclude other food sizes. Second, the amplitudes of lingual motions are manipulated to adjust pumping capacity. In addition, the timing of lingual protraction-retraction relative to lingual elevation-depression is manipulated to direct a portion of the water outflow along proximal rather than distal lamellae to match mesh size to filtering of smaller food size.

Video recordings of a six-week-old flamingo show that kinematics of filter feeding are present, including the water pumping (unpubl. data). However, at this age flamingos have no lamellae, and filter capacity must be extremely low. We therefore conclude that filter behavior is already present before it is functional.

Tolerance and acquisition tests show that filter capacity peaks at cross sectional seed sizes of 1.7 to 2.0 mm in terms of numbers of seeds filtered; it is also high in terms of ingested total mass up

to diameters of about 4.0 mm. The discrimination studies lead to the conclusion that the lamellar system can act as a filter in the outflow and as an excluder in the inflow. Lamellar meshes vary along the beak, therefore size discrimination cannot be perfect. Nevertheless the accuracy of the filtering system is about 0.5–1.0 mm, both for excluding and filtering in the range of 1.0 to 4.0 mm for the largest cross sectional diameter of elongated, oval-like seeds.

Back-and-forth pump causing a lateral in- and outflow. The following model for the filter mechanism is proposed (Figs. 9, 12–14). A generalized pump-filter cycle is described from Figure 13 (upper part). In stage 1 the beak has been closed and the elevated tongue has been protracted. In stage 2 the beak opens, the tongue depresses and retracts while the torus lingualis is kept against the palate, and as a result the volume of the mouth cavity increases and water is sucked in laterally along the distal beak portion. The rocking head rotates and the beak rims are pushed in the suspension. In stage 3 all these motions proceed and inflow increases. In stage 4 the gape is closing, lingual retraction reverses into protraction, while lingual depression continues. This increases the space at the beak curvature and a flow caudad is generated by the momentum of the water suctioned in. Outflow occurs since the torus linguae is kept elevated. Mandibular marginal lamellae and maxillary marginal and submarginal lamellae sieve the grains. In stage 5 the beak closes very fast, the lingual bulges protract and begin elevating, causing a strong outflow of water along the curvature and distal portion of the beak. Also distal lamellae sieve the grains. In stage 6 the beak has been closed and the lingual bulges protract and elevate producing a strong outflow along the distal portion of the beak so that grains are filtered. In stage 7 lingual motions forcefully squeeze out all water. These motions end in stage 8 and thereafter the cycle starts again. It is clear that in the course of pumping the waterflow is reversed and that part of it is pumped through as a result of its own momentum. The birds apparently are able to manipulate this balance. While surface filtering, the through-flow

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and retraction, and the horizontal bar elevation and depression. a. A generalized collecting/filtering cycle shown in 7 stages. The black dot represents a seed. The seed is drawn in and filtered. Small arrows along the beak indicate relative size and direction of the water flow. b. A generalized transporting cycle shown in 8 stages. The black dot represents a seed. The seed is transported into the pharynx, by action primarily of the papillae linguae rostralis.

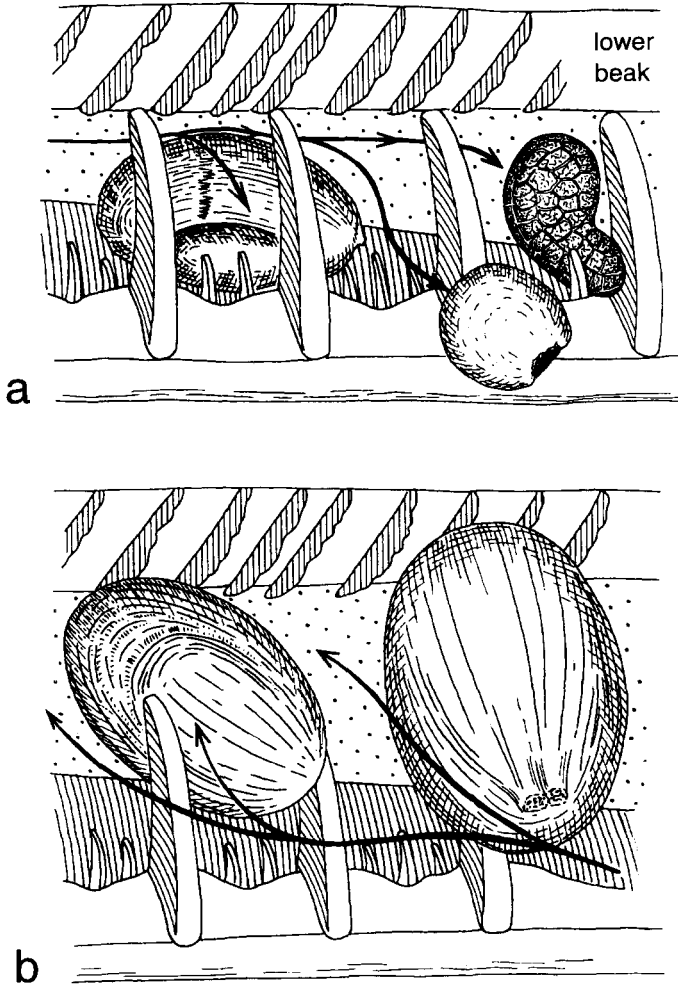


FIGURE 14. Filtering, washing out, and excluding of seeds. a. The outflow of the food suspension in a closed beak while filtering. The beak is drawn in upside down position which is normal for filter feeding. The relatively large grass seed is filtered by direct impact. The smaller, crescent-like poppy seed jams the mesh since it is caught between a large maxillary marginal and a small maxillary submarginal. The small millet is washed out with the water. The size of the mesh is determined by the lamellae. b. The inflow of the food suspension in a slightly gaping beak. The relatively smaller grass seed is sucked in with the water stream, while larger milo is excluded. The size of the mesh is now clearly determined by tuning of the gape.

portion may prevail; while feeding submerged in dense mixed suspensions, the back-and-forth flow prevails (Fig. 14).

A remarkable feature of filter feeding is that beyond seed sizes of the range of 1.5–4.0 mm, filter and discrimination capacities strongly decrease. This may be connected to a specific anatomical feature of the jaw apparatus, unknown in any other avian taxa. Exerting mechanical pressure on the frontal bone above the orbit and simultaneously at the same level on the mandible opens the beaks to a maximal gape of about 3

mm, producing a maximal size of about 4 mm for ingested food in the inflow. We assume that tuning and restricting the gape is now controlled by the sliding mandibulo-jugal articulation that lies far rostral to the quadrato-mandibular joint. This feature may be a specific adaptation of the jaw apparatus to filtering staple-food sizes most economically.

The anatomical studies show that the functional mesh size varies as follows. With closed beak distal meshes along the straight portion of the beak are about 1.6 mm wide and 1.7 mm

high. They effectively allow passage of oval-like, cross sections that have diameters not larger than 2×1.5 mm. Along the curvature of the beak meshes become smaller, 2.0 mm high \times 0.7 mm wide. The crescent shape of the marginals reduces the mesh to be passed effectively from 0.6–1.0 mm. They allow the washing through of oval-like cross sections that have diameters of about 0.6–1.5 mm. However, more caudally they disappear at the corner of the mouth. These mesh-sizes clearly fit to accurately filtering the staple food-sizes. In addition they allow the accurate discrimination of preferred sizes in the range of 0.1 to 4.0 mm, assuming that the maximal gape for filtering is 3 mm.

The significance of the straight distal beak portion is important for accurate discrimination of particular sizes. Sanderson and Wassersug (1990) and Bildstein (1993:131) noted that "as a result of nearly parallel curvature, the distance between the upper and lower mandibles of a partially opened decurved beak varies less over the length of the bill than it would in straightened bills of the same length. A long straightened bill would open relatively more near the tip of the bill and less near the base than does the decurved version. For example, flamingos, which filter-feed . . . are able to do so effectively because strongly decurved bills enable them to space their upper and lower mandibles equally along most of the gape." This feature produces rather uniform mesh sizes along the distal portion of the beak.

Aspects of sensory control of filtering. A sophisticated direct-touch system is required to control fine tuning of the gape. The sensors needed for such a system are present as a network of corpuscles of Herbst directly underneath each marginal of upper and lower mandibles. A highly developed bill tip touch organ as found in waterfowl and probing waders may be present, but not yet described. An equivalent control system has developed laterally along the tomial edges in flamingos.

Many birds (e.g., waterfowl, fowl and pigeons; Berkhoudt, 1985; Bath, 1906) have taste buds around the two orifices of the rostral maxillary glands. These glandular orifices lie just caudal to the maxillary nail where the hard keratin changes into the soft palatal mucosa. In flamingos, however, the position of the maxillary taste buds has shifted to caudal. This conforms to the point where best food discrimination by taste is expected. The location of that point must meet the demand that all gathered food pass that point

and that rejection is performed as early and as easy as possible in the food processing route.

Transport through the mouth. The transporting cycle is characterized by the same motion pattern as found in the filter cycle. The difference is that different anatomical structures are set to function. In Figure 13 (lower part) the odd numbered stages represent the transport by papillae linguae rostralis. The even numbered stages illustrate the transport along the lingual torus. In stage 1 one seed of a bolus gathered by filtering is drawn, the tongue is protracted and elevated. In stage 3 the depressed tongue retracts so that rostral lingual teeth take the seed caudad. In stage 5 lingual retraction reversed into protraction and lingual depression into elevation, so that the caudad pointing papillae slide underneath the seed leaving the seed caudal along the palate. In stage 7 this procedure is continued. In a next cycle the seed is assumed to arrive at the level of the torus linguae as shown in stage 2. In stage 4 the tongue is maximally retracted and slightly depressed so that the torus becomes depressed also. The elevated larynx protracts along the palate closing the choanae which prevents flow of food and water into the nasal cavity. Evidence for this assumption comes from the fact that air bubbles leave the nostrils at this stage. In stage 6 the torus protracts. The seed is held back by the papillae pharyngis rostralis while the torus protracts. In stage 8 the lingual protraction and elevation comes to an end, leaving the seed just caudal to papillae linguae caudalis at the basis lingualis in the pharynx (see stage 1).

Filter and transportation cycles occur simultaneously, but the lingual elements that function shift caudad during a full behavioral scene of filter feeding. First, the lingual bulges are involved in pumping, hence collecting seeds, and then the rostral lingual papillae start functioning to sweep the seeds beyond the beak curvature caudad. Thereafter, the torus lingualis and caudal lingual papillae transport the seeds into the pharynx. Our tests therefore confirm Jenkin's phoenicopterid filter feeding model (1957), but we extend that model considerably.

COMPARISON OF FILTER FEEDING MECHANISMS IN BIRDS

Filter feeding has been analyzed for several avian taxa. Morgan and Ritz (1982) propose for Short-tailed Shearwaters (*Puffinus tenuirostris*) that the bill architecture produces a lower pressure in the mouth while it is pushed through the water,

thereby gathering water and krill. This is called 'ram filter feeding' (Sanderson and Wassersug 1994). Caudally pointing lingual papillae overlap with rows of caudally pointing, recurved, palatal papillae. As the water is squirted out over a permanent rictal ridge, krill are trapped by the papillae which are erected by the water outflow. For Fairy Prions (*Pachyptila turtur*), they suggest a gular pouch sucking in and squirting out water, while krill are being filtered, although the papillae are much smaller. Harper (1987) and Klages and Cooper (1992) confirm that observation and suggest that suction is created by the voluminous tongue; water and copepods are collected in a large mandibular pouch that squeezes water out while copepods are filtered.

Rubega (1990) and Rubega and Obst (1993) describe a prey transport, known as surface-tension feeding in *Phalaropus lobatus*. Here, prey is transported in a water drop that runs very rapidly up along the beak due to surface tension, while the beak is opening. Then the mouth closes abruptly, the throat skin is elevated, water appears at the rictus running distally along the beak to collect in a drop at the tip, and vigorous head shaking throws the drop off. Rubega (pers. comm.) suggests that this type of transport may be widespread among shorebirds. Gerritsen (1988) photographed a similar kind of drop transport in sandpipers (e.g., *Calidris alpina*) but did not observe prey in a drop. Both Zweers (1990) and Rubega and Obst (1993) propose that this type of water transport is a potential step in the evolution from pecking to filter feeding. Feduccia (1980) and Olson and Feduccia (1980a, 1980b) consider *Presbyornis* as a filter feeding ancestor of modern ducks starting from an ancestral shorebird stock, based on features such as beak shape, the large sized proc. retro-articularis and additional post-cranial elements as evidence. They consider the line to flamingos diverged before *Presbyornis* appeared.

Zweers (1974) and Zweers et al. (1977) propose for Mallards (Anatidae) a suction pressure pump in which the tongue draws water in at the beak tips and expels it latero-caudally along the beak rims. This pump is a "through pump" in which the water enters at one end and leaves at the other end. During their elevated retraction, the lingual bulges and cushion serve as pistons with a closed valve in the cylinder-like beak so that the water is expelled caudally along the beak rims. During their depressed protraction, the lingual

bulges serve as a piston with an open valve allowing the water to flow caudad over the lingual bulges by its momentum. Kooloos et al. (1989) have studied filter feeding in Mallards, Tufted Ducks, and Shovelers (*Anas platyrhynchos*, *Aythya fuligula*, and *Anas clypeata*, respectively). They concluded that filtering occurs by inertial impact at the lamellae in Shovelers. However, in Tufted Ducks and Mallards, in addition to direct impact, they hypothesize that food items smaller than the interlamellar mesh are centrifuged out the main stream by vortices that develop along the lamellae. The filtered particles are transported into the pharynx left and right along (not over) the lingual cushion by a bilateral series of strong scrapers.

Van der Leeuw and Zweers (1994) analyzed filter feeding in geese (e.g., *Anser anser*). Filter feeding has a collection and a transport phase. During the collection phase, water and food are grasped and sucked in at the beak tips during bill opening, mainly by a retracting tongue with a depressed tip and lingual bulges, while the lingual cushion is kept elevated, serving as a piston. Water is largely expelled laterally by bill closure and a protracting tongue with an elevating tip. The food is retained since the tongue presses it against the mouth roof, where caudally pointing spines add to retainment while the tongue protracts. The transport phase is characterized by large vertical movements of the lingual cushion, causing an over-tongue transport of the food and a food retainment by the spines in the mouth roof during protraction. Grass is transported in a similar way.

Comparison of the anatid model with that for flamingos shows that flamingo pumping is basically a "back-and-forth pump" causing a lateral in- and outflow, while the anatids have 'a grasp pump or a through-pump' causing frontal inflow and lateral outflow. Comparison of the duck model and the geese model shows that they differ in pumping and in transporting food. Ducks use the lingual bulges primarily as a piston and a valve, while geese use them primarily to retain food and to aid in suction. Ducks have a smooth mouth roof, while they scrape the filtered food laterally along the lingual cushion, which is kept elevated during filtering; geese, however, transport the food over the lingual cushion, while caudally directed flexible spines retain it during lingual protraction. During development in geese, first pecking and then grazing develops by com-

bing a grasp and a headshake, followed by a lingual inertial (slide and glue) transport through the mouth; thereafter filter feeding develops.

MORPHOSPACE AND PHYLETIC EVOLUTION OF FILTER FEEDING MECHANISMS

Methodological remarks. Here, we first develop the concept of a morphospace, and then introduce the correlation that exists between the morphospace and historical narrative explanations (see Bock 1988, 1991; and Zweers 1991a, 1991b for further explanation of terminology and methodology). We initially analyze one (yet unexplained) morphology by deducing it from a known morphology, transforming the latter through an explanatory theory. The explanatory theory, in turn, is a maximization of a known initial system, for the functional requirements of a different system in which the morphology is to be explained. For example, we consider the avian pecking mechanism to be the initial system and then maximize its morphology for the functional requirements of a probing mechanism by analysis of the latter for tolerance and performance. This deductive methodology produces a branching transformation pattern which describes the domain of structures of probing mechanisms as deduced from a pecking mechanism. By using "maximization for certain functional requirements," a polarity is introduced which is purely of a nomological deductive nature. To establish a correlation between such a morphospace and an historical narrative evolutionary explanation, we must consider historical initial and boundary conditions. We consider a pecking mechanism to be the "historical initial condition" for the avian feeding mechanism (Zweers 1991a, 1991b; Zweers et al. 1994). We define certain anatomical and behavioral changes to be "boundary conditions"; that is, some changes are permitted and others are not. For example, we would specify that the particular configuration of bones in a jaw apparatus is *not allowed* to change, but the size, shape, and orientation of the bones *would be allowed* to change. Such initial and boundary conditions are often vaguely described as "phylogenetic constraints."

Morphospace and evolution. Based on the methodology as outlined above we summarize a provisional morphospace for avian filter feeding, deduced from a pecking mechanism and hypothesize evolutionary routes in that same mor-

phospace. (In Figure 15, numbers in parentheses refer to numbers in the text, and the taxon names at the top line refer to the appearance of known filter mechanisms.) We recognize that a functional and performance analysis of the filter feeding is only known in flamingos and ducks and not for other filter feeding mechanisms. Moreover we restrict the development of the morphospace and of evolutionary hypotheses of avian filter feeding to the following guidelines derived from proposals by Baum and Larson (1991), and Losos and Miles (1994): 1) Identification of integumental characters in routes that were crucial in the change from pecking to filter feeding; 2) Identification of functional capabilities leading to performance advantages for filter feeding; 3) Identification of new selective regimes driving new developments. We first summarize maximization and evolutionary route of the pecking mechanism for probing requirements and then show how filter feeding development may branch off from this line. Finally, we show how different types of filter feeding can be deduced and how they may have evolved by increasing intake capacities and filter specialization. We include here only the integument, and omit the muscle-bone apparatus and its mechanics.

We assume that the ancestral avian feeding mechanism was a grasping mechanism (1), like that assumed for *Archeopteryx*. This mechanism is characterized by a long beak, teeth along the mandibles, and (probably) a prokinetic skull, though less advanced than in modern birds (Bühler 1985). We also assume that the grasping mechanism was a precursor to the pecking mechanism, the latter is considered as the ancestral feeding mechanism of modern birds (2). That mechanism comprises conical, tooth-less, keratin-covered beaks, and a prokinetic skull. Food is transported by "catch and throw," comprising head jerks, as well as by a lingual inertial transport in which only the tongue moves. That initial mechanism is defined as the de-specialized pecking mechanism in the chicken (*Gallus*), i.e., the top soil breaking specializations are omitted (7). See Zweers (1990) and Zweers et al. (1994) for a discussion of its ancestry and appearance.

A remarkably modifiable feeding design had been developed with this mechanism. Zweers (1990) and Zweers et al. (unpubl. ms.) predicted by deduction, and tested, transformation from initial pecking to initial probing (3), to air/water hole probing (4), and subsequently to mud pen-

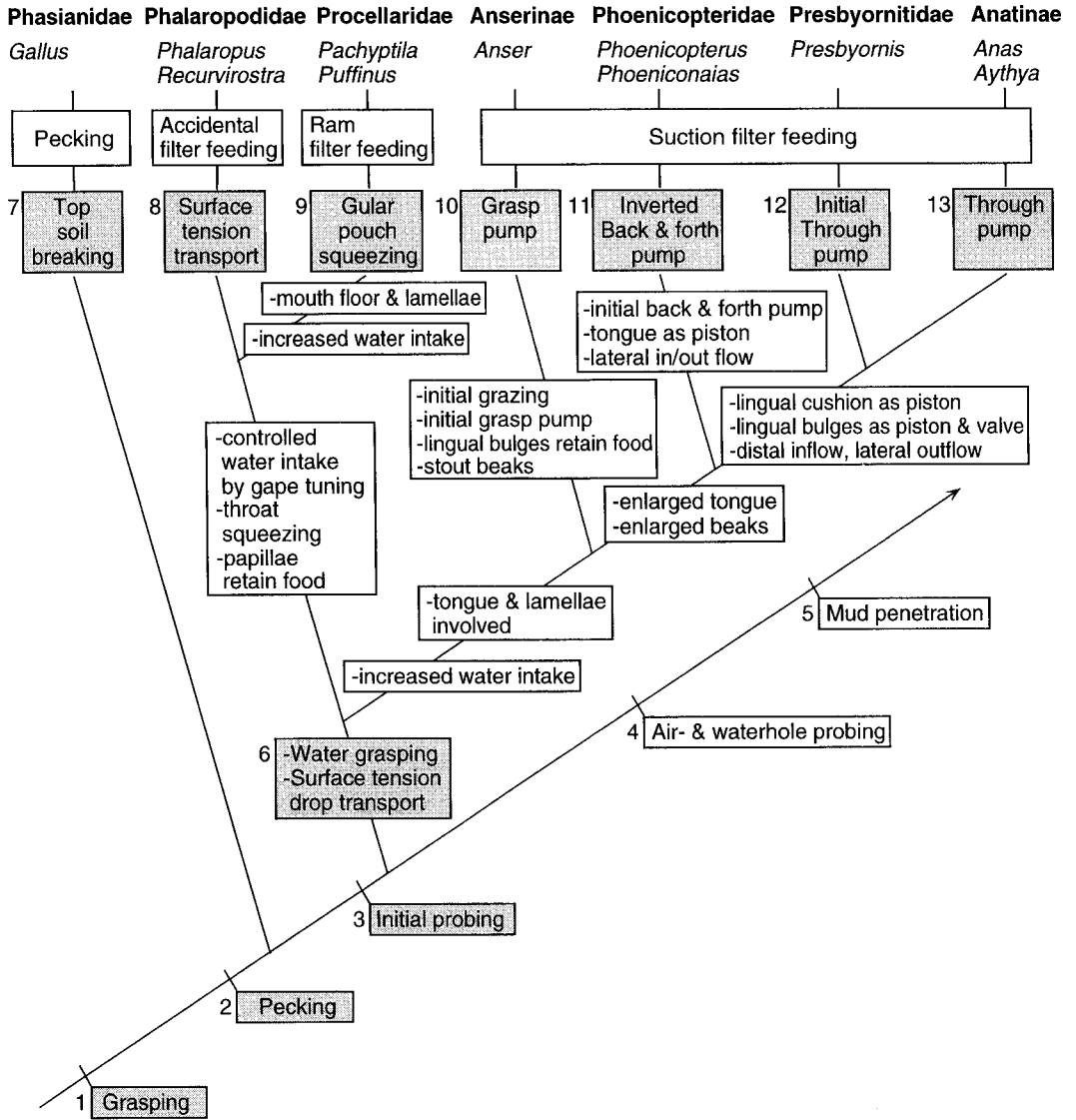


FIGURE 15. Preliminar morphospace for filter feeding mechanisms. Five steps of deduction are shown. 1) A pecking mechanism (2) is the initial feeding mechanism that is deduced from a grasping mechanism (1) and defined as the despecialized pecking mechanism in chicken (e.g., top-soil breaking specializations are omitted) (7). 2) The morphospace of filter feeding mechanisms is considered to branch from the morphospace deduced by maximizing the pecking mechanism for probing requirements (3–5). That branch occurs at the level of an initial, probing wader that forages along shores. Branching is assumed to be allowed by the integration of two epiphenomena (6). These are: water is grasped while the bird pecks at submerged food, and surface-tension drop-transport occurs along the mouth while the beak is opened slightly to transport the pecked food. Once these two features are integrated, this configuration can accidentally filter feed (8). 3) Maximization of the water intake volume forces the deduction to a transition from the surface-tension transport mechanism to two parallel lines, one of gulping in which mouth floor motions occur (9), and one of suction mechanisms in which lingual motions are involved (10–13). 4) Depending upon the type of lingual actions in combination with mandible motions three types of suction-pump mechanisms are deduced (10, 11, 13). 5) In addition to the deduction of suction mechanisms the filter capacity is maximized by deducing lamellae along the tongue and/or the tomial edges of the mandibles (10–13).

etration (5). They showed that a slightly lengthened and slenderized beak must first progressively elongate, and then become secondarily wedge-shaped. The beak may curve or recurve, and finally develop rynchokinesis and a remote touch sensory system in the beak tip.

Filter feeding, however, cannot directly be deduced from pecking by maximizing it for filter feeding requirements. First, an intermediate stage must be defined. The reasoning for that stage is as follows. If the initial probing mechanism of slightly slenderized and lengthened mandibles (3) is deduced for birds that feed by run-and-peck hunting along shores and in shallow waters (as seen in *Charadrius* sp.), then two epiphenomena (concomitant features) (6) necessarily accompany the transformation. These are: (a) If these birds peck their prey in water they must necessarily grasp water, and (b) If these birds thereafter open their beak slightly, the water necessarily runs up along their beak as a result of surface tension. Such a configuration, the surface tension transport (8), is found in *Phalaropus* (Rubega and Obst 1993), possibly in *Recurvirostra* (M. Rubega, pers. comm.) and in *Calidris* (Gerritsen 1988). A similar situation occurs when these birds grub, grasp or graze vegetation in shallow waters.

For an evolutionary interpretation of this deduced line we assume that birds have the behavioral capacity to anticipate such epiphenomena and experience them; that is, they can "learn" that grasped food can be transported in the drop that is moved along the beak. Given that learning potential, an intake mechanism can be developed that is faster and more economical than the ancestral type of transport in the pecking mechanism. Selection can then work on this mechanism. This configuration may accidentally show simple filter feeding if papillae are effective to retain food particles while the water is squeezed out by throat elevation (as observed in *Phalaropus* by Rubega and Obst 1993).

Branching to a line of advanced filter feeding, which could have occurred several times, is deduced as follows. The surface tension transport mechanism soon reaches the limits of its capacity. To enlarge the intake volume, mechanisms of gulping or suction must take over from those of surface tension. The take-over may be provided by several gulping and pumping mechanisms (see below: a-d). They are deduced subsequently according to the parsimony principle, which leads to deduction of increasing specialization.

(a) First, gulping requires a gular pouch, and enlarged beaks that are dragged through the water to collect food (i.e., "ram filter feeding," Sanderson and Wassersug 1990). The gular pouch is squeezed empty by an elevating mouth floor. An enlarged elevating tongue holds particles against the mouth roof. Additionally, in the outflow, elements that retain food particles may develop. This configuration, the gular pouch squeezing (9), is deduced to branch off from the surface-tension/water-grasping line, since throat squeezing was already present in that line. Alternatively, gular pouch squeezing could have been deduced as the first line branching away from the "increased water intake" line, since it is the simplest configuration for increasing water intake. It is present in *Puffinus* and *Pachyptila* (Morgan and Ritz 1982).

For an evolutionary interpretation we assume that, once the benefit of water as a transport mechanism for food is selected upon, selection tends to drive increase of the intake-volume of the food-suspension, as well as development and improvement of structures that retain food particles from that suspension.

(b) Second, enlarged beaks and lingual volume for a simple lingual pumping mechanism are deduced for increased water intake, and structures in the mouth that retain food particles for an increased filter capacity are deduced. Grasping water, sustained by a small effect from surface tension, and a larger effect from lingual suction, can develop from the two mentioned epiphenomena (6) by adding simple lingual retraction. The closing beak and the protracting tongue squeeze the mouth empty and simultaneously secure the particles between tongue and mouth roof. There is still and over-tongue transport (food is transported over the lingual cushion) into the pharynx as has been defined for the initial pecking mechanism. This configuration, the grasp pump (10), may occur as the first branch along the pump-line. It is found in *Anser*. For an evolutionary interpretation, Van der Leeuw and Zweers (1994) propose that this maximization is an adaptation to pump specialization which may occur simultaneous with adaptation to grazing that leads to a compromise that is dominated by grazing demands for a stout broad based beak. That grazing develops first during ontogeny and filter feeding somewhat later adds to the parsimony argument to position this type of filter feeding as the first branch along the pump-line.

(c) Third, deduction of even more enlarged

beaks and a lingual pumping that is now disconnected from the sieving are deduced as further increase of water flow capacity. For the functional requirement of filtering the superficial soil layer in shallow water by skimming, primary specializations are an inverted head posture connected to a curved beak with a straight distal portion. Specialized filtering is served by lamellae along the beak rims and the lingual pumping is basically a protraction and retraction of the tongue that forces the water flow laterally in and out the mouth. This configuration, the back-and-forth pump (11), branches off as the second branch along the pump-line. It is observed in *Phoenicopterus* and *Phoeniconaias*. For an evolutionary interpretation, we assume that strong selection on top-soil filter feeding of uniformly sized particles has driven the development along the deduced lines.

(d) Fourth, widened and lengthened, straight beaks, and an enlarged tongue that acts as piston and valve in a suction-pressure pump mechanism are deduced for a different, parallel line of increasing the water flow capacity. The lingual bulges may add to food retention, but primarily lamellae in the outflow sieve particles by inertial impact and a vortex mechanism. Filtered food is transported laterally along the tongue (lateroventral to the lingual cushion) into the pharynx. This configuration, the through-pump (13), is the last branch along the pump-line. It is present in *Anas* (Zweers et al. 1977, Kooloos et al. 1989). For an evolutionary interpretation, we assume that a wide trophic diversification has occurred once this very effective multi-purpose mechanism had been developed, since it was easily scalable, and compromizable to a variety of other requirements.

We recognize that only bony elements are known from *Presbyornis*. We therefore follow the suggestion of Feduccia (1980) and Olson and Feduccia (1980) to consider the *Presbyornis* feeding type an offshoot (12) close to, but earlier, than ducks.

Several studies have led to phylogenetic hypotheses which include the above filter feeding taxa (Feduccia 1976, 1987, 1980; Olson and Feduccia 1980a, 1980b; Olson 1985). They describe phylogenetic relationships that were based partly on the fossil record and partly on feeding mechanisms. Sibley and Ahlquist (1990) developed cladistic analyses at the DNA level to formulate phylogenetical relationships, and Cra-

craft (1981, 1988) proposed phylogenetic relationships from cladistic analysis at the organismic level. However, it would be premature to compare phylogenetic hypotheses to our provisional morphospace and historical-narrative hypotheses for development of filter feeding mechanisms.

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