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Diversity of feeding adaptations in certain columbid birds: A functional morphological approach

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Abstract. With gradual increasing complexity in higher vertebrate structure and function, the birds as a class have acquired very high degree of feeding adaptations for diverse food-niches. A comparative functional morphological study of the feeding apparatus of 6 species of columbid birds showing diversification in their food-habits reveals that some correlations exist between the form-function complexes of the feeding apparatus and the extent of diversity of food-habits shown by these birds.

Among the species of columbid birds selected for the Study, *Columba* and *Streptopelia* are ground feeders and predominantly grain-eaters, although quite often they invade diversified food-niches. *Treron* and *Ducula*, on the other hand, are almost exclusively fruit-eaters, plucking and swallowing fruits from the lofty tree branches, While *Columba* and *Streptopelia* show better kinesis of their jaws for ground-pecking, *Treron.* and *Ducula* possess wider gape as well as stronger grasp of their bill for plucking off, grasping and swallowing large-sized fruits. Consequently, the size and pinnateness of the jaw muscles in these fruit-pigeons have developed far greater than those observed in *Columba* and *Streptopelia.* Further, in *Treron* and *Ducula,* the thick and broad 'venter externus' slip of the M. pterygoideus ensures complete closure of the bill and possibly prevent any excess lateral expansion of the mandibular rami.

Similar correlations have also been observed between the tongue features of columbid birds and the diversity of their feeding adaptation.

Keywords. Columbidae; morphology; feeding apparatus; osteology; myology, ecomorphology; adaptation.

1. Introduction

Birds as a class of vertebrates possess some unique features which have equipped them with the adaptations for diverse conditions of life. The structural adaptations of the feeding apparatus of birds project an interesting subject for functional morphological studies. To quote Bock (1974): "a knowledge of functional morphology is essential for all types of morphological studies, including systematic investigations".

Throughout the present century many notable contributions were made on the diversity of food and feeding adaptations, as well as, on the morphology and mechanics of a part or whole of the feeding apparatus of birds, including the columbids, by a number of authors such as Blanford (1895, 1898), Lucas (1897), Mason and Maxwell–Lefroy (1912), Hofer (1950), Beecher (1951), Rooth (1953), Starck and Barnikol (1954), Dubale and Rawal (1962), Merz (1963), Bock (1964, 1966, 1974), Bock and Wahlert (1965), Goodwin (1967), Burton (1974), Bhattacharyya (1980, 1989, 1990), Zweers (1982a, b) Homberger (1986), and Van Gennip (1986).

The present paper deals with the diversity of food and feeding adaptations of 6 species of columbid birds in relation to the form-function complexes of their feeding apparatus on a comparative basis. Attempts have been made to correlate the diversity of feeding adaptations with the structural modifications of the feeding apparatus.

2. Materials and methods

Apart from using information available in the literature, the food-habits of birds selected for the study have been observed in nature as far as possible. All the birds, except the two species of *Ducula*, have been collected from the suburbs of Calcutta and from the district of Birbhum, West Bengal. Some of the domestic pigeons and doves were kept alive in the laboratory with several food-items like rice, puffed rice, beaten rice, seeds, pulses, etc. Their consumption of food according to preference was noted down.

Dissections to observe the structural modifications of their feeding apparatus were performed in the laboratory either in freshly killed specimens or in those preserved in a suitable fixative (Bhattacharyya 1982).

The following species of birds have been selected for study:

Order Columbiformes

Family Columbidae

Columba livia Gmelin; blue rock pigeon
Streptopelia chinensis (Scopoli); Indian spotted dove
Streptopelia decaocto (Frivaldsky); Indian ring dove
Treron phoenicoptera (Latham); common green pigeon
Ducula aenea nicobarica (Pelzeln); Nicobar green imperial pigeon
Ducula badia insignis Hodgson; Hodgson’s imperial pigeon

3. Results

The observations have been mainly recorded under two major subdivisions, namely, (i) diversity of the food and food-habits of birds selected for the study and (ii) form-function complexes of the feeding apparatus and their biological roles.

3.1 *Diversity of food and food-habits of birds selected for the study*

3.1a *C. livia:* The food of the rock dove chiefly consists of grains of rice, maize, millet and other cereals, pecked from the ground. This species also feeds on banyan figs and other berry-like fruits and sometimes insect eggs and larvae.

3.1b *S. chinensis:* The Indian spotted dove feeds mainly on grains of paddy, maize, millet and other cereals, but also on grass and weed seeds. All the grains and seeds are pecked from the ground.

3.1c *S. decaocto:* Besides grains of paddy, wheat, millet, jowar (*Sorghum* sp.) and other cereals and pulses, Mason and Maxwell–Lefroy (1912) state that the Indian ring dove very often feeds on seeds of mustard, linseed and various weeds. Rana (1991) reports that the ring dove changes its food-habit quite frequently, depending on the availability of food; in the monsoon, the birds also feed on insects.

3.1d *T. phoenicoptera:* This fruit-pigeon is almost exclusively and voraciously fruit-eating, feeding on fruits of nearly all the species of *Ficus* (*e.g.*, banyan, peepul, etc.). It feeds on drupes, berries and wild figs of various kinds. In the western part of West Bengal, the ripening fruits of guava attract large number of these birds during winter.

3.1e *D. a. nicobarica:* This pigeon is exclusively frugivorous, feeding on figs of *Ficus* sp., nutmegs of *Myristica* sp. and other wild fruits. The nutmeg which comprises its favourite item of food is plucked off from the lofty tree branch and then swallowed entire with the help of its wide gape of the mouth and enormously distensible gullet. The hard pericarp of the fruit is later expelled orally.

3.1f *D. b. insignis*: The food of Hodson's imperial pigeon is very similar to that of *D. a. nicobarica.* However, unlike *D. a. nicobarica,* this bird rarely descends down from the lofty tree-tops. The fruits are collected from the tree-tops where the bird flies from one branch to the other for plucking of fruits.

3.2 *Form function complexes of the feeding apparatus and their biological role*

The diversity of the feeding adaptations in birds is reflected in the form-function complexes of their feeding apparatus. The biological roles played by such complexes are influenced by any change in the food-niches of the environment. The feeding apparatus in birds consists of three major sub-divisions, namely, the jaw apparatus, the tongue apparatus and the laryngo-glottal apparatus, each being composed of several osteological, arthrological and myological form-function complexes. The laryngo-glottal apparatus which is also a part of the respiratory system has not been discussed here for the sake of brevity.

3.3 *Osteology and arthrology of the jaw and tongue apparatus*

The osteology and arthrology of the skeletal and connective tissue components of the jaws, tongue and hyoid account for the variability in the size, structure, location and fibre-arrangements of the muscles which produce differential forces in the movements of the jaws.

3.3a *Osteology:* The measurements of certain skeletal components of the skull in different birds provide a clue to understand the nature, of morphological adaptations of the muscles attached to them. The relative increase in the length of the bill in proportion to that of the cranium is considered as an advantageous adaptation to the insectivorous birds, but not to the columbids in general. In both *Columba* and *Streptopelia,* the bill-length being considerably shorter than that of the cranium, becomes more advantageous for ground-pecking of grains and seeds, whereas in the nearly-arboreal and fruit-eating *Treron* and *Ducula,* the bill-length is only slightly shorter than that of the cranium but the wide bill-base, massive structure of the bill and hooked tip of the upper beak (figure 1) are helpful adaptations of these birds in plucking and grasping large-sized fruits. Likewise, the greater width of the cranium and of the retroarticular surface of the mandible, the greater length

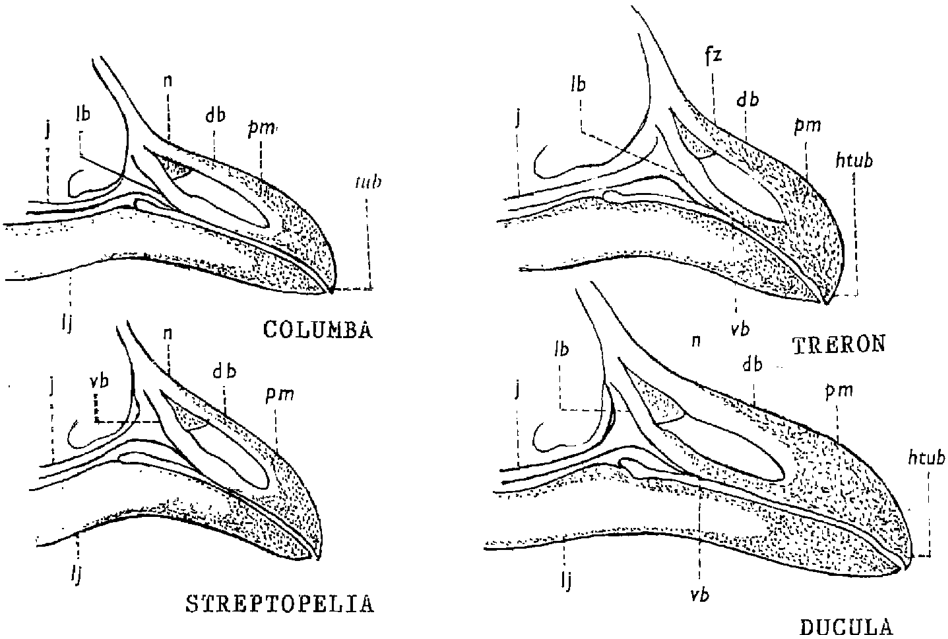

Figure 1. Bill shape and length in a few columbid birds (lateral view).

and width of the orbital process of the quadrate in *Treron* and *Ducula* (figure 2) are a few among many adaptive features in the osteology of the skull.

In the osteology of the tongue apparatus, the skeletal components of the tongue and hyoid in *Treron* and *Ducula* are comparatively much longer and thicker than those observed in *Columba* and *Streptopelia.* The greater length and width of the ceratobranchial and epibranchial bones provide extensive surfaces for the origins and insertions of the Mm. ceratoglossus and branchiomandibularis respectively.

3.3b *Arthrology:* Some structural variations are observed in the morphology of the joints, joint-capsules, ligaments and flexion-mines. In general, these structures are better developed in *Treron* and *Ducula* than in *Columba* and *Streptopelia.* The articular and linkage ligaments, the cotyla medialis mandibulae (ctm) and the condylus medialis quadrati (cmq) are very well-formed in *Ducula* (figure 2). In both the fruit-eating pigeons, especially in *Ducula,* the Lig. depressor mandibulae is stretched widely across the squamosal and exoccipital regions, thereby affording wider site for the origin of the deepest layer of the M. depressor mandibulae. However, *Columba* and *Streptopelia,* possessing two flexion-zones in their upper jaw, show better jaw kinesis than that observed in *Treron* and *Ducula.*

3.4 *Myology of the jaw and tongue apparatus*

The functional morphological study of the jaw and tongue muscles reveals certain interesting correlations between the modifications of muscles and the diversity of feeding adaptations.

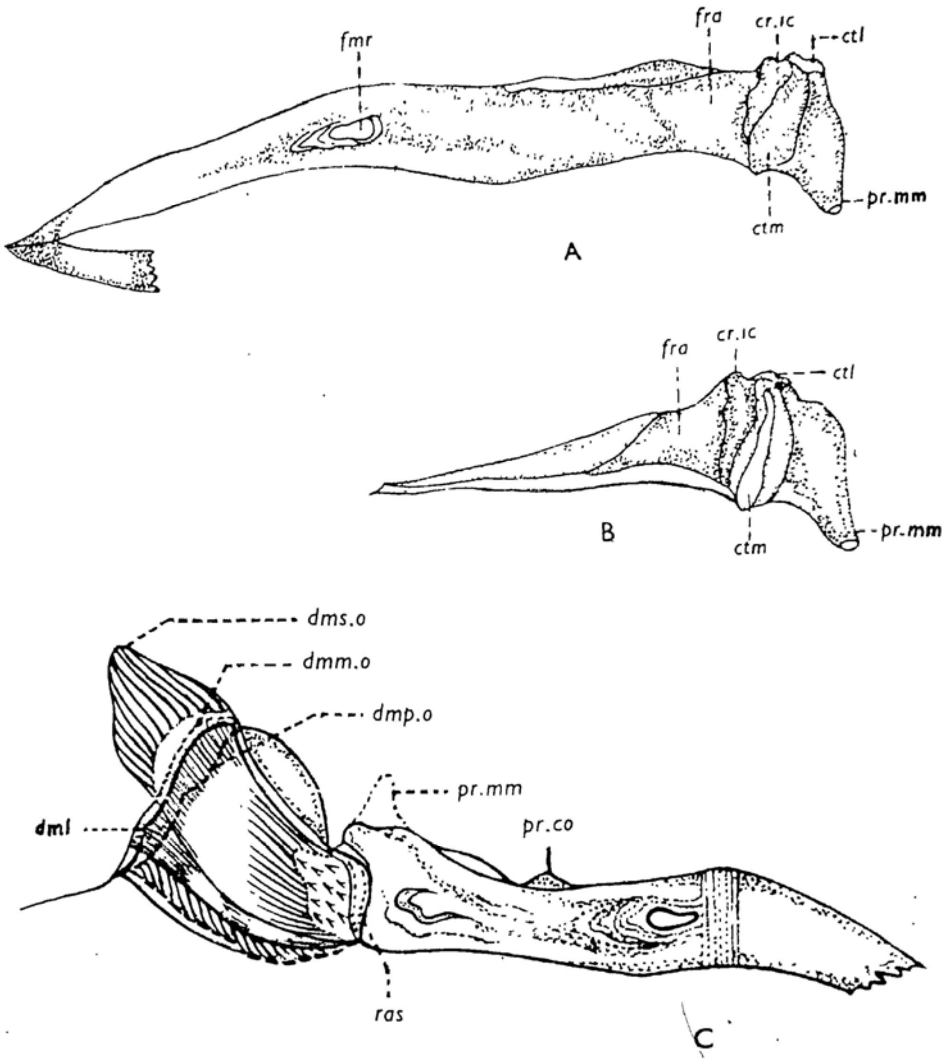

Figure 2. *Ducula aenea nicobarica.* (**A**) Inner medial view of the right mandibular ramus. **(B)** Enlarged medio-dorsal view of the same (part). (**C**) Outer lateral view of the same (part) showing the retroarticular surface and attachments of the M. depressor mandibulae.

3.4a *Adaptive modifications of the jaw muscles:* The jaw muscle patterns in *Columba* and *Streptopelia,* which feed primarily on grains and seeds pecked from the ground, are almost similar, except that the protractor, depressor and the adductor mandibulae muscles in *Streptopelia* are comparatively better developed than in *Columba.* In *Streptopelia,* the caudal insertion-aponeurosis of the M. pseudotemporalis superficialis merges with the central insertion-tendon of the M. adductor mandibulae externus superficialis near its mandibular insertion (figure 3). On the other hand, *Treron* and *Ducula,* being exclusively frugivorous, have their jaw muscle pattern closely similar, but not exactly the same. Both of them possess a very well

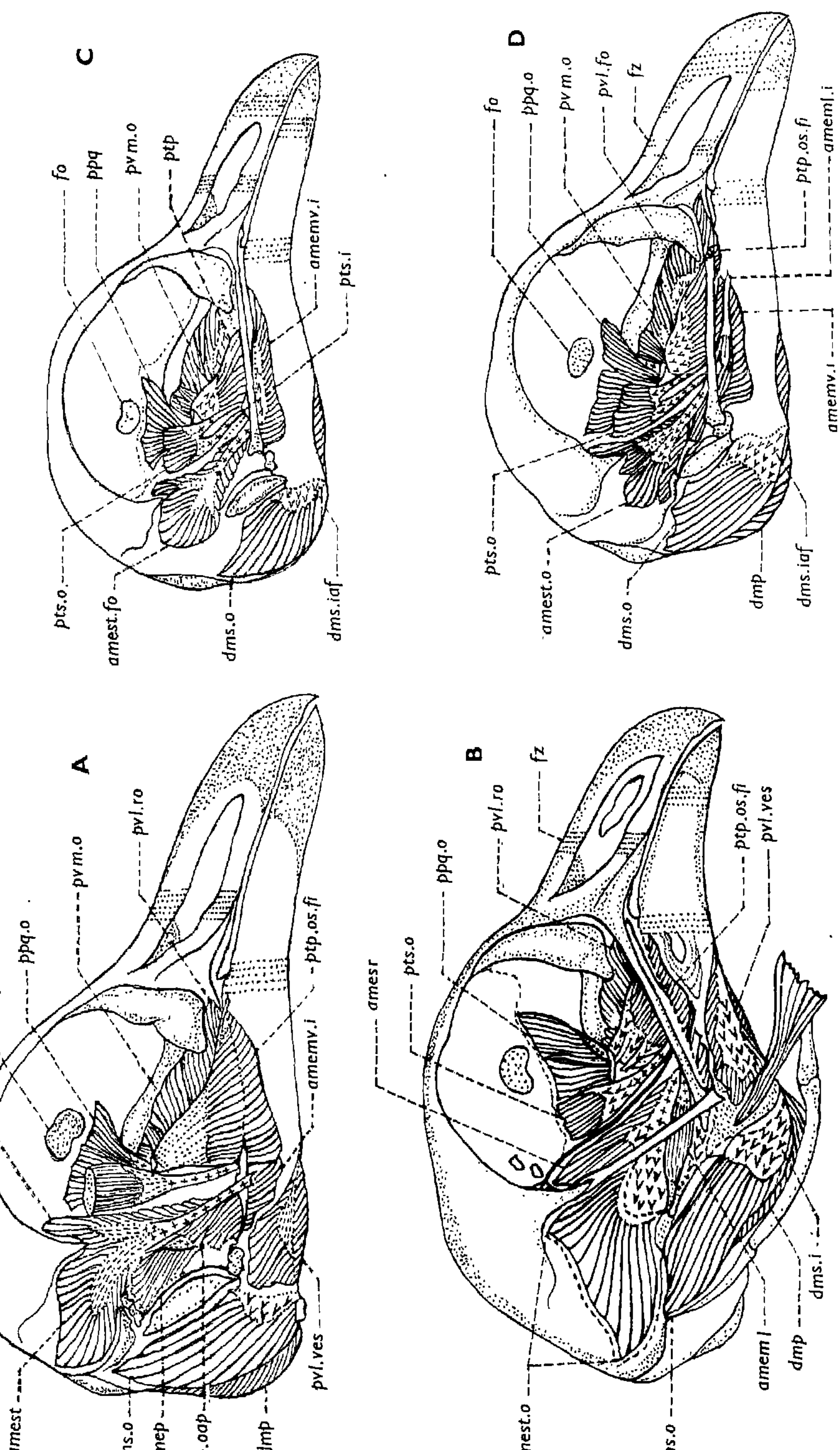

Figure 3. Lateral view of skulls showing jaw muscle patterns *in situ*. **(A)** *Ducula*. **(B)** *Treron*. **(C)** *Columba*. **(D)** *Streptopelia*.

developed M. adductor mandibulae externus superficialis with an extensive 'temporalis' part, the massive M. protractor pterygoidei et quadrati and M. pseudotemporalis profundus and a thick and broad M. pterygoideus ventralis (both 'lateralis' and 'medialis' parts) with the remarkable development of a 'venter externus' slip from its lateralis part. This slip inserts compactly and fleshly on the outer articular and angular mandible (figures 3-5). In both *Treron* and *Ducula,* the forceful closure of the bill and grasping over the fruit become possible due to pronounced development of the adductor and adductor-cum-retractor groups of the jaw muscles.

As regards pinnateness of jaw muscles, both unipinnate and bipinnate arrangements of fibres are observed in *Columba* and *Streptopelia.* In *Treron* and *Ducula,* complex

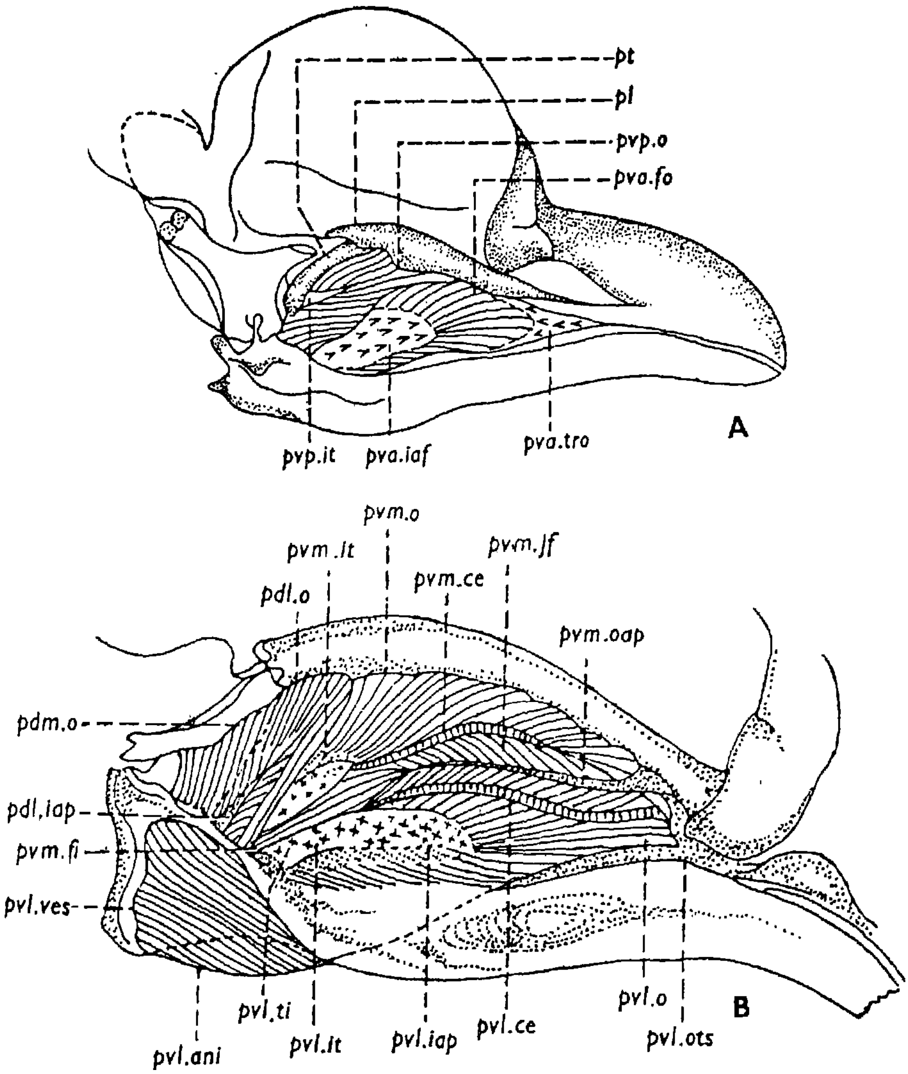

Figure 4. Lateral view of the M. pterygoideus. (**A**) *Columba,* **(B)** *Ducula.*

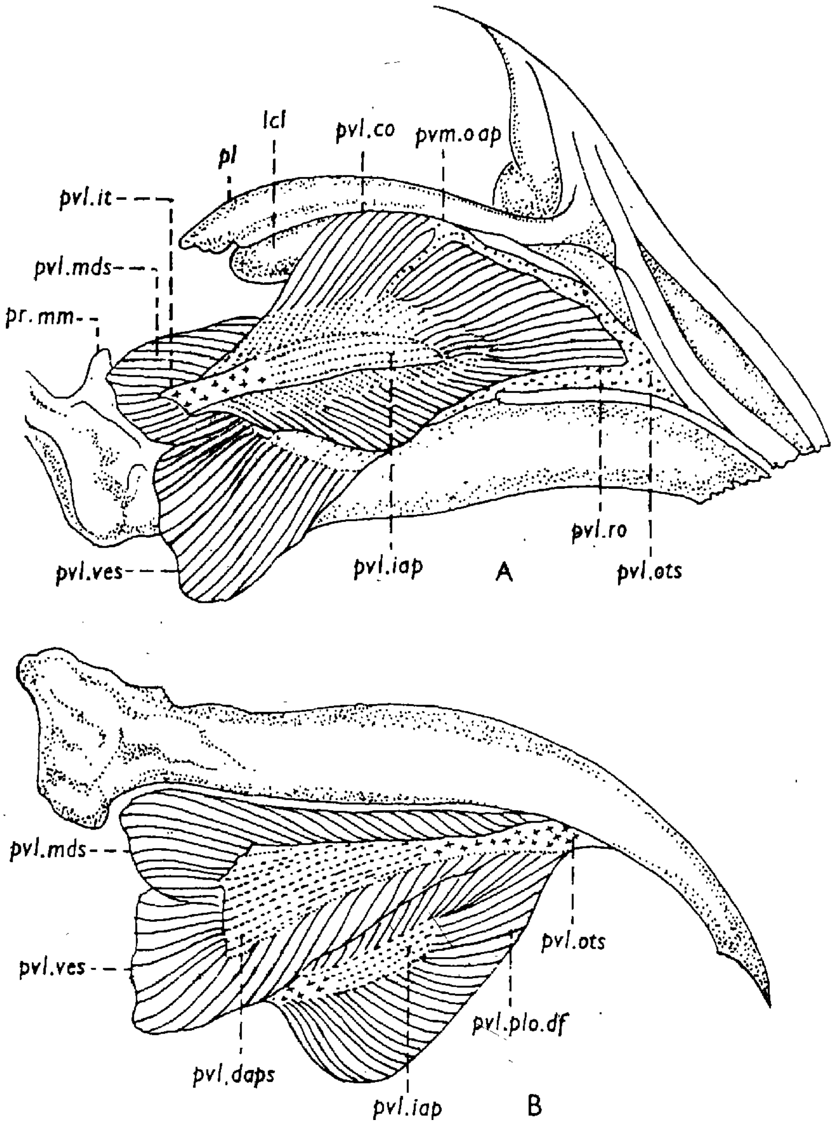

Figure 5. *Ducula badia insignis.* **(A)** Lateral view of the M. pterygoideus ventralis lateralis with its main insertion-tendon and insertion of 'venter externus' slip detached. **(B)** Dorso-lateral view of the M. pterygoideus ventralis lateralis.

bipinnate and multipinnate arrangements of fibers along thick and strong tendons and aponeuroses indicate large numbers of muscle fibres and appreciably greater force production by their jaw muscles.

3.4b *Adaptive modifications of the tongue apparatus:* The tongue features (figure 6) are no less adaptive in the diversity of feeding adaptations in birds than the bone-muscle complexes of the jaw apparatus. The tongues in the columbid birds

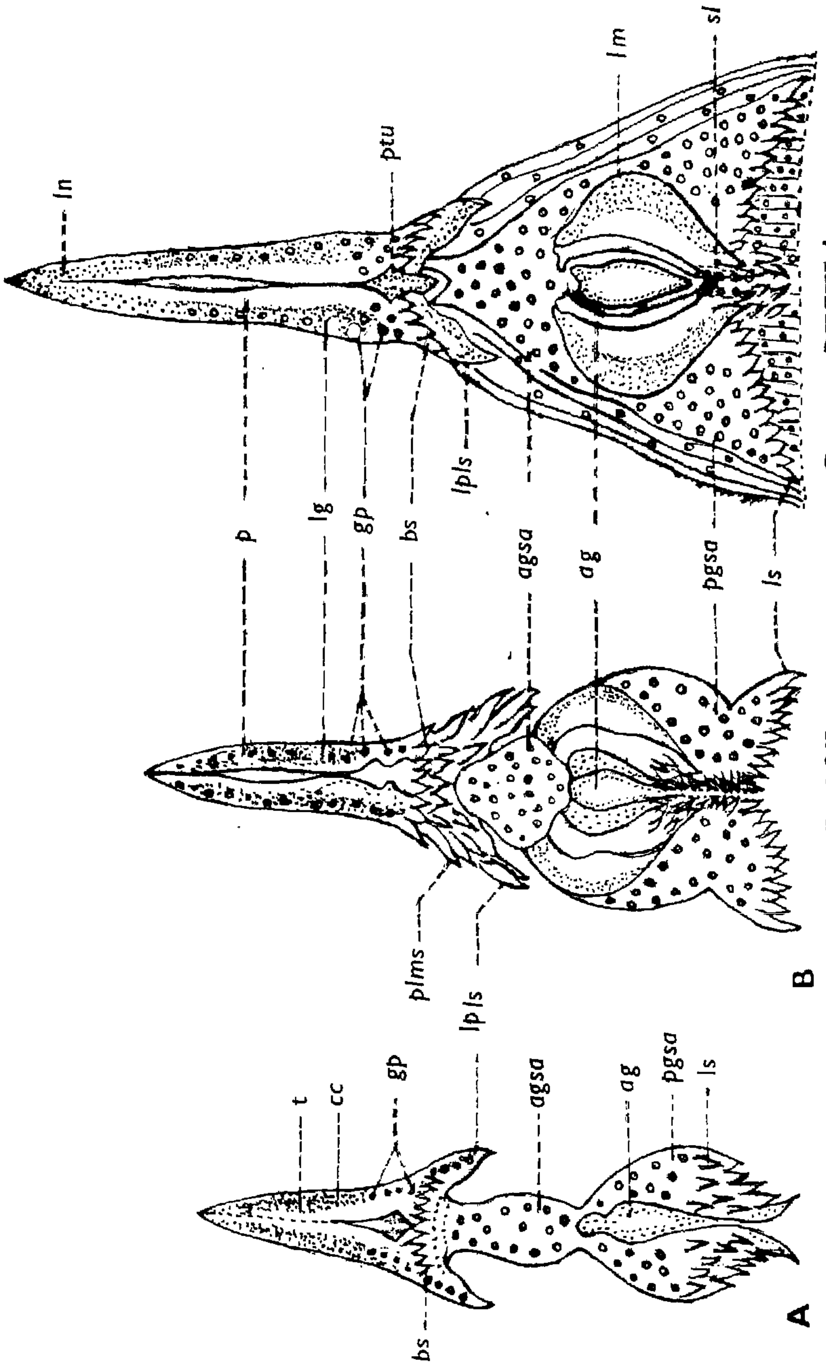

Figure 6. Dorsal view of the tongue in a few columbid birds. (A) *Columba*. (B) *Treron*. (C) *Ducula*.

studied share certain common features such as, the absence of apical hyaline margins, cuticular hairs or any incision at the tongue tip. The tongues in *Treron* and *Ducula* are comparatively much longer (longest in *Ducula;* 24 mm- against 12 mm in *Columba*), so that in fruit-eating adaptation of these birds. the tongue can be protracted far forward up to nearly the ventral limit of the mandibular symphysis. The tongues in *Treron* and *Ducula* are invested by a thick and cornified epithelium and the glandulo-sensory pits are profusely distributed at the base and margins of the tongue.

The diversity of food-habit is also reflected in the musculature of the tongue. Corresponding to two different food-habits of columbid birds studied, close similarities are observed between the tongue muscles of *Columba* and *Streptopelia* on one hand and between *Treron* and *Ducula* on the other. In *Columba* and *Streptopelia,* the protractor (M. branchiomandibularis, M. genioglossus), the depressor (M. ceratoglossus) and the retractor (M. tracheohyoideus, M. tracheolateralis) muscles of the tongue are just moderately developed whereas, in *Treron* and *Ducula,* all these muscles are especially well developed, being composed of longer, thicker and broader bands. In these two birds (more particularly in *Ducula),* the M. branchiomandibularis posterior has an additional slip possessing its origin from the lateral surface of the mandibular ramus, the well-formed M. hypoglossus anterior and the long, thick and broad M. ceratoglossus have one (*Ducula*) or two (*Treron*) tendons of insertion (figure 7). The tongue movements in these birds become more diversified and stronger (than in *Columba* and *Streptopelia*) in agreement with the nature of food ingested. The larger fruits and nuts eaten by the fruit pigeons require greater strength of the tongue to carry these larger food particles into the mouth.

4. Discussion

The functional morphological study of .these 6 species of columbid birds reveals certain interesting correlations between the structural modifications of their skeleto-muscular and connective tissue components of the feeding apparatus and the divergence in their food-habits. *Columba* and *Streptopelia,* primarily feeding on grains and seeds pecked from the ground, do not require any massive or elongated bill for pecking and grasping their food-grain. Both of them, however, quite often invade other food-niches for which their jaw and tongue muscles have been suitably modified. Of the two, *Streptopelia* shows greater divergence of food-habit which accounts for the better development of their adductor mandibulae externus, protractor and depressor muscles of the jaws. At the species level, *S. decaocto* shows slightly better development of its jaw and tongue muscles, which may be correlated with greater diversity of food explored by this species.

In the fruit-eating pigeons, *Treron* and *Ducula,* diversity occurs in the nature of fruits ingested, In both genera, the bill is massive with the thick epidermal coating and the bill-tip hooked for plucking and/or grasping the fruit more efficiently. In both these birds, the lower jaw depressor and adductors, as well as, the palatine and quadrate retractors have not only acquired a larger mass and more complex fibre-arrangements, but the aponeuroses, tendons and ligaments have become more extensive and diversified. In fact the pinnateness of fibres had reached much greater complexity than that observed in *Columba* and *Streptopelia*. Among the tongue

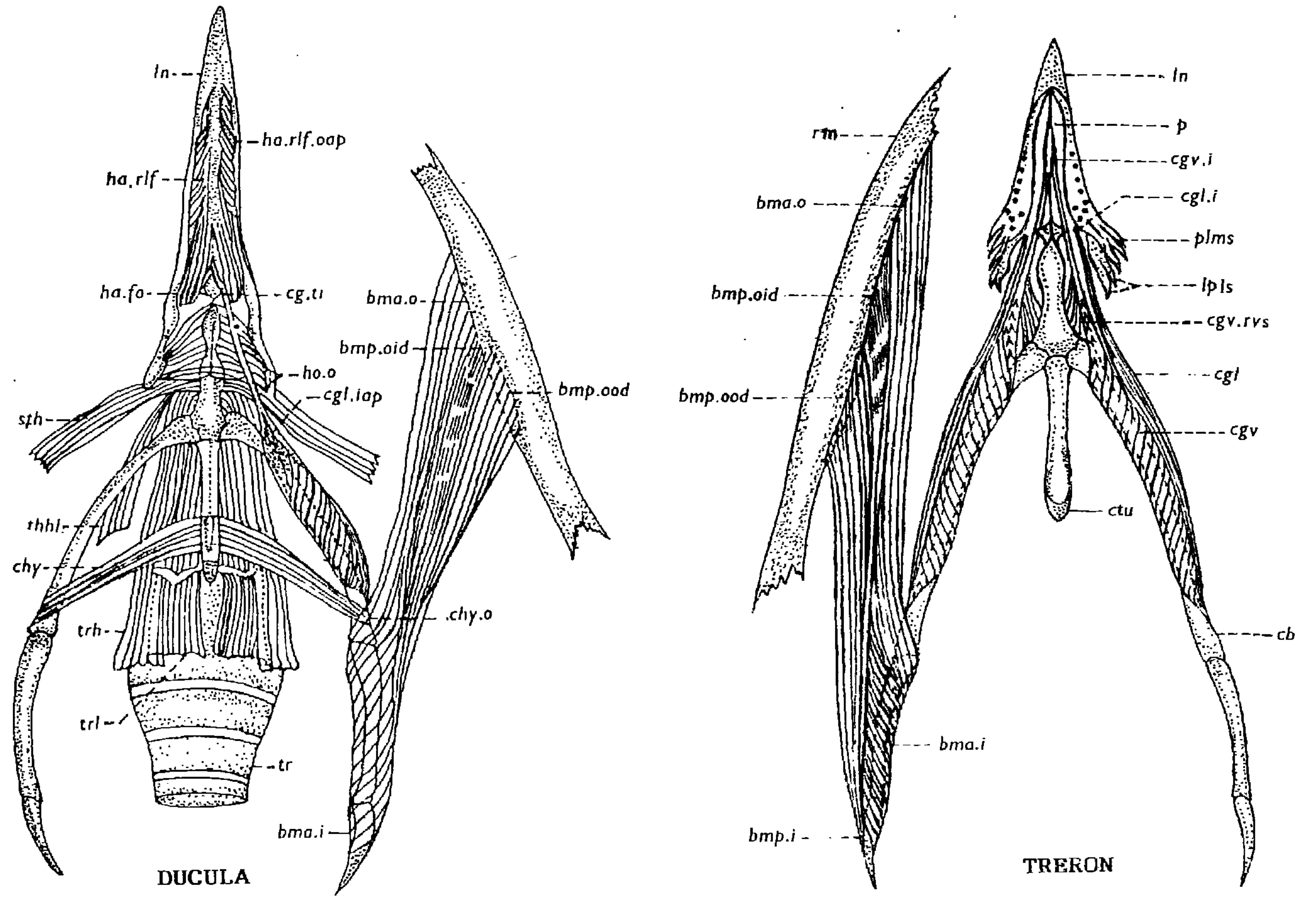

Figure 7. Ventral view of the tongue muscles in **(A)** *Ducula* and **(B)** *Treron* showing origins and insertions of the M. branchiomandibularis posterior and the M. ceratoglossus.

muscles, greater protraction of the tongue becomes possible in *Treron.* and *Ducula* (more so in *Ducula*) due to better development of the Mm. branchiomandibularis and genioglossus. The outer mandibular origin of the M. branchiomandibularis posterior possibly permits greater lateral movement of the tongue in these birds. The M. ceratoglossus, the depressor of the tongue, has two main parts, the 'ventralis' and 'lateralis' parts which have their separate tendinous insertions on the tongue in *Treron,* but in *Ducula,* the aponeuroses from the two parts unite to form a single, long and stout tendon of insertion. In adaptations for gaping, greater depression of the tongue assists in the increase of space within the mouth cavity for manipulating large-sized fruits.

Ecomorphological analysis of the feeding apparatus inquires into the causes, both environmental and mechanistic to explain the feeding adaptations in birds. Birds with divergent feeding adaptations (*e.g., Streptopelia, Ducula*) have their bill-shape, upper jaw kinesis and bone-muscle complexes of the feeding apparatus suitably modified for the purpose. Such modifications, however small, may be reflected even at the species level.

In considering the enormous diversity in the feeding adaptations in birds, the functional morphological study alone may not be adequate to explain all the diversities unless the knowledge of ecology, physiology and behaviour is incorporated.

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[For most of the abbreviations used in figures, refer to earlier publications by the author (Bhattacharyya 1980, 1982, 1989, 1990). A key to some abbreviations, however, is given for ready reference: agsa, anterior glandulo-sensory area; cgl, M. ceratoglossus lateralis; cgl.iap, M. ceratoglossus lateralis, insertion-aponeurosis; cgv, M. ceratoglossus ventralis; cgv.i, M. ceratoglossus ventralis, insertion; cgv.rvs, M. ceratoglossus ventralis, rostro-ventral slip; db, dorsal bar of the upper jaw; fra, Fossa rostralis articularis; gp, Glandular pore; ha.rlf, M. hypoglossus anterior, rostro-lateral fibres; ha.rlf.oap, M. hypoglossus anterior, rostro-lateral fibres, origin aponeurosis; hm, M. hypoglossus medialis; hn, holorhinal nostril; ios, interorbital septum; lb, lateral bar of nasal; Ig, lingual gland; lm, laryngeal mound; ln, lingual nail; n, Os nasale; nis, nasal-interorbital septum; pgsa, posterior glandulo-sensory area; sl, Sulcus laryngealis; vb, ventral bar of upper jaw].