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The morphology of the syrinx in the Charadriiformes (Aves): Possible phylogenetic implications

Catherine Brown & David Ward

Abstract. The avian vocal structure, the syrinx, is used in a single-character examination of phylogeny in the shorebirds (Charadriiformes). The two major trends evident are the reduction in the number of parts constituting the pessulus and an increase in the ossification of the tracheobronchial region. The patterns of variation in syrinx structure are largely consistent with recent phylogenetic analyses using skeletal and biochemical characters (Strauch 1978, Sibley & Ahlquist 1985). However, considerable variation was found in the structure of the syrinx of coursers (Cursoriinae), which is inconsistent with the most recent classification of this group (Urban et al. 1986). In addition, the similarity of syrinx structure of the plovers *Vanellus* and coursers *Rhinoptilus*, which is supported by behavioural data on agonistic displays, suggests that these two groups may be closely related and not just convergently similar as was previously thought (Snow 1978). The syrinx structure of the sandgrouse (Pteroclididae) is unlike that of the doves (Columbiformes) or the plovers (Charadriiformes), groups with which this family is usually associated (Wetmore 1960, Maclean 1967, Sibley & Ahlquist 1985).

Key words. Syrinx, shorebirds, Charadriiformes.

Introduction

The order Charadriiformes (shorebirds) includes limicoline (plovers and sandpipers), aerial-littoral (gulls and pratincoles) and natatorial (alcids) forms. These groups, together with several other less familiar groups, constitute the order Charadriiformes of Wetmore (1960). This study was conducted with the intention of helping to resolve the following questions:

- a) Are sandgrouse (Pteroclididae) members of the order Charadriiformes or the order Columbiformes?
- b) What are the relationships between the Burhinidae (stone curlews) and the rest of the Charadriiformes?
- c) Is the family Glareolidae (coursers and pratincoles) descended from the larine (Laridae — gulls and terns) or pluvialine (Charadriidae — plovers) branch of charadriiform evolution?
- d) Do the Scolopacidae (sandpipers) and Charadriidae (plovers) constitute a monophyletic lineage within the order?

Syrinx structure

Syringeal morphology was first applied to the classification of birds by Nitzsch (1829), who described the syringes of many European passerine and non-passerine birds. Subsequently, there have been a number of detailed studies of syringeal anatomy (e. g. Ames 1971, Warner 1972, Cannell 1986).

The avian syrinx was first described by Herissant (1753) who recognized it as the

source of voice in the domestic duck. The syrinx is a specialized structure in the respiratory pathway situated at the junction between the trachea and the bronchi. It lies within the interclavicular air-sac which is the only unpaired air-sac of the avian lung/air-sac system (Nottebohm 1975).

Traditionally, syringes are classified by position: tracheal (a modification of the lower end of the trachea), bronchial (a modification of the bronchi), or, as in most birds, tracheobronchial (involving both the trachea and the bronchi). The syrinx is associated with a number of muscles, of which there are two basic types:

(a) the paired extrinsic muscles, which originate away from the syrinx and insert on it. There are two types of extrinsic muscles, the tracheolateralis and sternotrachealis muscles. The former originate at the lateral surface of the cricoid cartilage of the larynx and extend down the lateral surface of the trachea to insert on the ventral and/or lateral surface of one or more elements of the syringeal region. The sternotrachealis muscles originate on the internal surface of the coracoid or the costal process of the sternum, or on the internal surface of one or more of the ribs and insert on the lateral and/or ventral surface of the trachea, or on tissues surrounding the trachea.

(b) intrinsic muscles, which originate and insert on the syrinx. Charadriiformes birds do not possess intrinsic muscles (pers. obs.).

The vibratile elements of the syrinx are the paired tympaniform membranes. Syringeal membranes vary in thickness and flexibility, sometimes blending into a sheet of cartilage, and are of two kinds. The pair of internal tympaniform membranes comprise most of the internal surface of the bronchi and are supported at the edges by tracheal rings and bronchial semi-rings. The external tympaniform membranes are the largest of the membranes on the lateral side of the syrinx. Between the two bronchial openings a small septum extends forward into the trachea. The free margin of this septum is a crescent-shaped membrane known as the semi-lunar membrane. It is supported by a small ridge, the pessulus, a bony or cartilaginous rod lying in the mid-sagittal plane of the trachea at the junction of the internal tympaniform membranes. The internal and external tympaniform membranes may each bear a lip near the semi-lunar membrane, known as the internal and external labia.

Some disputed aspects of the phylogeny of the Charadriiformes

a) Pteroclididae: Sandgrouse are seed-eating, desert birds with cryptic coloration, long, pointed wings and a short bill typical of granivorous birds. Behaviourally they are similar to several other arid-adapted charadriiforms (Maclean 1967). Their young, like those of the Charadriiformes, are downy and precocial. The Pteroclididae have traditionally been included with the Columbiformes (doves) on the basis of morphological and ecological similarities (Wetmore 1960). This classification has been the cause of much dispute and there is a growing body of evidence to suggest that the sandgrouse belong with the Charadriiformes. Maclean (1967) presented evidence for the inclusion of the sandgrouse in the Charadriiformes based on similarities of breeding biology, behaviour, some morphology and pterylosis. Fjeldsa (1976) made an extensive cladistic study of the orders Charadriiformes and Columbiformes in which he concluded that the doves are an early side branch from the charadriiform line. The doves then became arboreal,

adopted perching habits and underwent a complete change in breeding biology. He suggested that the sandgrouse diverged later from the glareolid line (coursers and pratincoles) and advocated that both the doves and the sandgrouse be included in the Charadriiformes as the sub-order Columbae. Based on comparisons of DNA material of charadriiforms and sandgrouse, Sibley & Ahlquist (1985) placed the Pteroclididae with the charadriiforms and suggested that the infraorder Pterocletes is a sister group of the infraorder Charadrii.

b) Burhinidae: Like the sandgrouse, many of the burhinids (stone curlews) are arid-adapted. The stone curlews are birds of crepuscular and nocturnal habit. Their plumage is cryptic, the bill stout and their legs have swollen tibiotarsal joints. The chicks are downy and precocial. The Burhinidae were placed nearest the Otididae (Gruiformes) by Lowe (1931) on account of certain skeletal similarities of these two groups, but their charadriine affinities are indicated by protein evidence (Ahlquist 1974), as well as by chick plumages (Jehl 1968). Jehl (1968) suggested that the Burhinidae were allied to the Haematopodidae (oystercatchers) and Recurvirostridae (stilts and avocets). Ahlquist (1974) found the IFPA patterns of *Burhinus* to resemble those of *Haematopus* and *Recurvirostra* and some sandpipers more than those of the bustards (Otididae) and suggested that the Burhinidae may be the most primitive group in the Charadriiformes.

c) Glareolidae: Coursers and pratincoles are fairly small birds with grey or brown upperparts, white underparts and bold facial markings. The wings are long and pointed in pratincoles (Glareolinae) and shorter and more rounded in coursers (Cursoriinae). The bill has a slight downward curve. Lowe (1931b) considered the Glareolidae to be closely allied to the Chionididae (sheathbills) and Dromadidae (crab plover). Bock (1964) found that the differences between the Glareolidae and Charadriidae are minor and suggested that the two families may be closely related. Jehl (1968), in a study of the downy plumage of charadriiform young, suggested that any affinity between the Glareolidae and Charadriidae should be found in the Cursoriinae rather than in the more specialized Glareolinae. Jehl (1968) agreed with Bock (1964) that the Glareolidae and Charadriidae were closely related and suggested that the superfamily Glareoloidea was superfluous and that the Charadriidae and Glareolidae be placed in the super-family Charadrioidae.

d) Scolopacidae and Charadriidae: The relationship between the Scolopacidae and the Charadriidae, and the question of whether they constitute a monophyletic lineage, has been the cause of much debate. Earlier workers have assumed either that all waders represent a monophyletic group (Jehl 1968) or, that the Charadriidae and Scolopacidae form one monophyletic group, and the Lari (gulls and terns) and the remaining shorebirds a second such group (Wetmore 1960). Fjeldsa (1977) suggested that the lapwing form (*Vanellus* — Charadriidae) gave rise not only to the typical plovers but also to the coursers and the more primitive Scolopacidae. Sibley & Ahlquist (1972) found the patterns of egg-white proteins of the scolopacine waders to differ from the main charadriiform pattern and suggested that the Scolopacidae may be more different from the Charadriidae than originally thought. In a later paper, using comparisons of DNA material, Sibley & Ahlquist (1985) showed that the oldest division of the Charadriiformes was between the Scolopacidae and the Charadriidae. Strauch (1978), using skeletal characters, divided the Charadriiformes into three

phyletic lines, namely the Scolopaci, Charadrii and the Alcae (auks). Strauch (1978) included the Lari in the Charadrii line, along with the Recurvirostridae, Glareolidae, Haematopodidae, Ibisornithidae and Dromadidae.

Material and Methods

Whole syringes (fresh or preserved in alcohol) were dehydrated and set in paraplast (a commercial plastic wax). Sections (7 µm thick) were cut and stained with Mallory's Triple stain as described by Drury & Wallington (1980). The optimal time for staining was found to be 4.5 min. Fifteen species from five families (Charadriidae, Scolopacidae, Pteroclididae, Laridae and Glareolidae) were examined. Five specimens of each of the following species were examined: *Vanellus coronatus*, *V. melanopterus*, *V. lugubris*, *V. senegallus* and *V. armatus* (Charadriidae). Since there was no intraspecific variation in any of the five *Vanellus* species, and because there was no sexual dimorphism in vocalizations of any of the other species, only one specimen of each of the other species was examined. All specimens were adult and were collected by us (*Vanellus* spp.) or obtained from the Transvaal Museum, Pretoria, South Africa.

Results

With the exception of the Double-banded Courser *Rhinoptilus africanus* (Glareolidae) (Fig. 1), all the other species examined had upper tracheal rings (above the tympanum) which were laterally flattened in transverse section and had ridges on their cranial and caudal surfaces. These ridges were composed of hyaline cartilage. The Bronzewing Courser *Rhinoptilus chalcopterus* (Fig. 2), Crowned Plover *Vanellus coronatus* (Fig. 3), Blackwinged Plover *V. melanopterus* (Fig. 4), Lesser Blackwinged Plover *V. lugubris*, African Wattled Plover *V. senegallus* and Blacksmith Plover *V. armatus* had upper tracheal rings that were ossified around most of their circumference, with a cartilaginous cavity in the centre of each tracheal ring.

The shape of the upper tracheal rings of all the species examined, with the exception of *Rhinoptilus africanus*, was such that the rings overlapped with one another to form a close-knit tracheal wall. In *Rhinoptilus chalcopterus* and all five *Vanellus* species, the tracheal rings were ossified and fused at the tympanum. The first two bronchial semirings were also ossified. A number of the other species examined also had ossified, but not fused, tracheal rings in the tympanic region. These species were the Redwinged Pratincole *Glareola pratincola* (Glareolidae — tracheal rings (Tr) 1–3 and bronchial ring (Br) 1 (counting from the tracheobronchial junction) (Fig. 5), Curlew Sandpiper *Calidris ferruginea* (Scolopacidae — Tr 1–5 and Br 1–2) (Fig. 6), Ethiopian Snipe *Gallinago nigripennis* (Scolopacidae — Tr 1–4) (Fig. 7), and the Ruff *Philomachus pugnax* (Scolopacidae — Tr 1–5 and Br 1–4) (Fig. 8).

The first bronchial ring of the Wood Sandpiper *Tringa glareola* (Scolopacidae) was modified in that it was far larger than the other bronchial rings (Fig. 9). In this species, the bronchial walls were greatly thickened by loose connective tissue and protruded into the lumen, forming a distinct external labium. The first four bronchial rings of the Spotted Dikkop *Burhinus capensis* (Burhinidae) were similarly enlarged and well supported by connective tissue (Fig. 10). In both these species, the syringeal area showed no sign of ossification, the rings being cartilaginous. In all the species examined, with the exception of the Namaqua Sandgrouse *Pterocles namaqua* (Pteroclididae — Fig. 11), the tracheal rings surrounding the syringeal area were

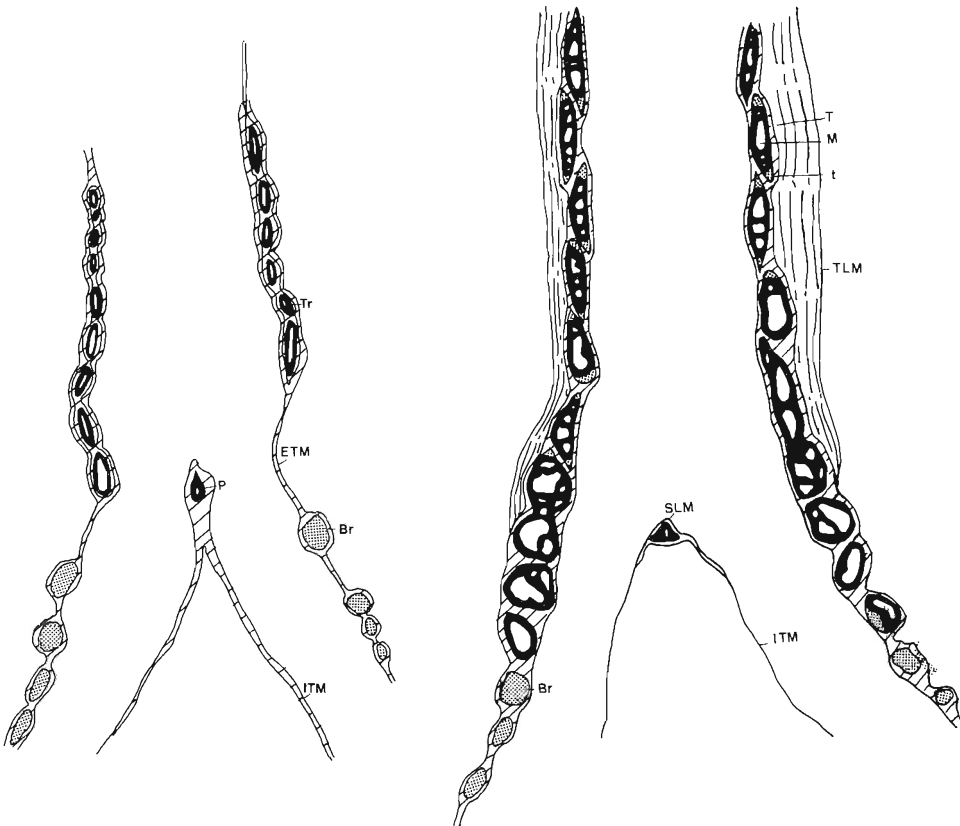


Fig. 1 (left): Longitudinal section of the syrinx of the Doublebanded Courser *Rhinoptilus africanus*. Br = bronchial semiring; ETM = external tympaniform membrane; ITM = internal tympaniform membrane; M = marrow cavity; P = Pessulus; SLM = semilunar membrane; Tr = tracheal ring. Tissue types are shaded as follows: cartilage = dotted; connective tissue = hatched; bone = black.

Fig. 2 (right): Longitudinal section of the syrinx of the Bronzewinged Courser *Rhinoptilus chalcopterus*. Br = bronchial semiring; C = connective tissue (dense); ITM = internal tympaniform membrane; M = marrow cavity; P = pessulus; SLM = semilunar membrane; Tr = ridge on the posterior and anterior edges of the laterally-flattened tracheal rings. Shading as for Fig. 1.

rounded or only slightly flattened in transverse section. The unmodified bronchial rings were cartilaginous and rounded.

There was considerable interspecific variation in the structure of the semilunar membrane and pessulus of the species examined, with a number of trends evident. The burhinids, larids and pteroclidids all had a large septum with a pessulus consisting of a number of pieces of cartilage. The pessulus of the Kelp Gull *Larus dominicanus* (Laridae — Fig. 12) also consisted of a number of cartilage pieces, although it was not possible to discriminate other features of this species' syrinx because of the dif-

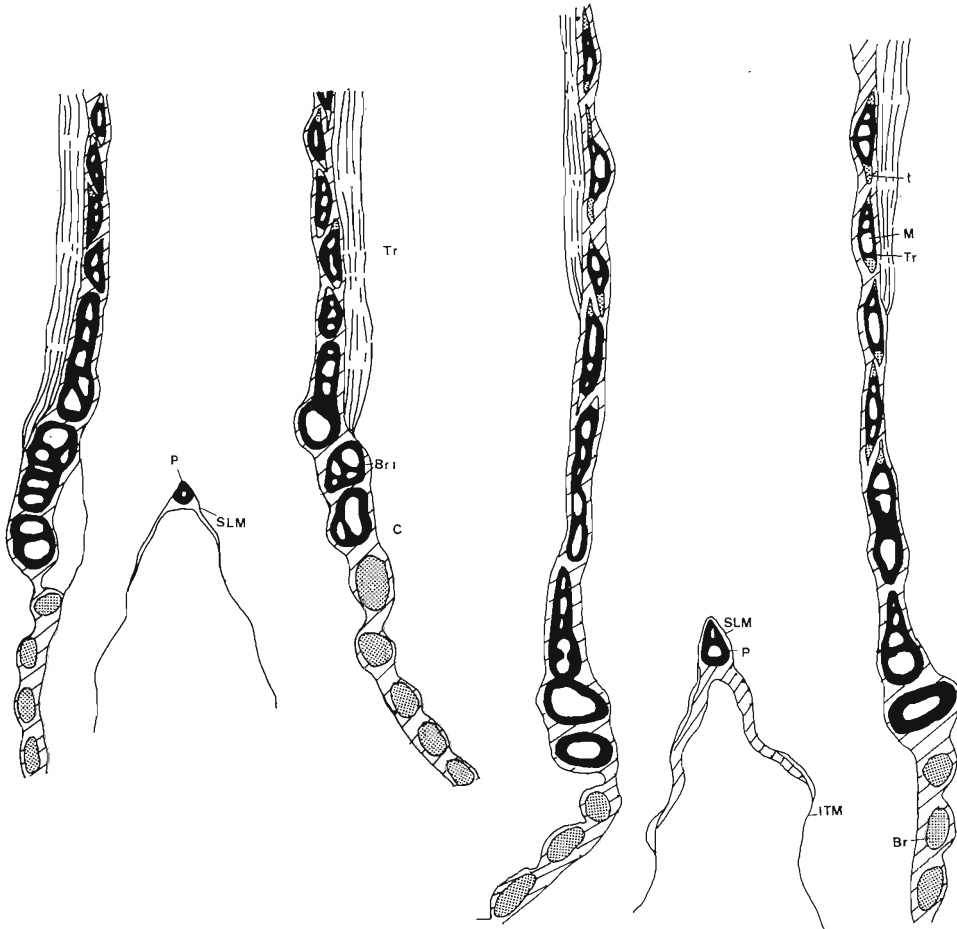


Fig. 3 (left): Longitudinal section of the syrinx of the Crowned Plover *Vanellus coronatus*. Br1 = first bronchial semiring; Br = bronchial semiring; ITM = internal tympaniform membrane; M = marrow cavity; SLM = semilunar membrane; TLM = tracheolateralis muscle; T = tracheal ring; t = ridge or tail on posterior and anterior edges of the laterally-flattened tracheal rings. Shading as for Fig. 1.

Fig. 4 (right): Longitudinal section of the syrinx of the Blackwinged Plover *Vanellus melanopterus*. Br = bronchial semiring; ITM = internal tympaniform membrane; M = marrow cavity; P = pessulus; SLM = semilunar membrane; Tr = tracheal ring; t = ridge or tail on posterior and anterior edges of the laterally-flattened tracheal rings. Shading as for Fig. 1.

difficulty experienced in sectioning (owing to the large size and high degree of ossification). *Tringa glareola* (Scolopacidae) had a similar septum and pessulus (Fig. 9) to those of the specimens from the above three families (Burhinidae, Laridae and Pteroclididae), with three cartilaginous pieces making up the pessulus. Among the Scolopacidae, there appeared to be considerable variation in pessulus structure.



Fig. 5 (left): Longitudinal section of the syrinx of the Redwinged Pratincole *Glareola pratincola*. Br = bronchial semiring; ITM = internal tympaniform membrane; M = marrow cavity; P = pessulus; SLM = semilunar membrane; Tr = tracheal ring; TLM = tracheolateralis muscle; t = ridge on posterior and anterior edges of the laterally-flattened tracheal rings. Shading as for Fig. 1.

Fig. 6 (right): Longitudinal section of the syrinx of the Curlew Sandpiper *Calidris ferruginea*. Br = bronchial semiring; EL = external labium; ITM = internal tympaniform membrane; M = marrow cavity; P = pessulus; SLM = semilunar membrane; Tr = tracheal ring; TLM = tracheolateralis muscle. Shading as for Fig. 1.

Philomachus pugnax had an ossified, elongate pessulus (Fig. 8), while *Calidris ferruginea* had a similar pessulus but with little cartilage. *Tringa glareola* had an intermediate condition between these two species, having more cartilage than *C. ferruginea* and no bone. *Gallinago nigripennis* had no pessulus and the septum consisted of only dense, regular connective tissue (Fig. 7). The pessulus was a vertically elongate structure in *Rhinoptilus africanus* (Glareolidae). In the *Vanellus* spp. (Charadriidae), there was a crescent-shaped semilunar membrane and a pessulus consisting of a single, large bone with a cartilaginous cavity.

The morphology of the syrinx of *Pterocles namaqua* (Pteroclididae) was considerably different from that of the other species studied. The tracheal rings at the tracheobronchial junction were highly modified. The first three tracheal rings were

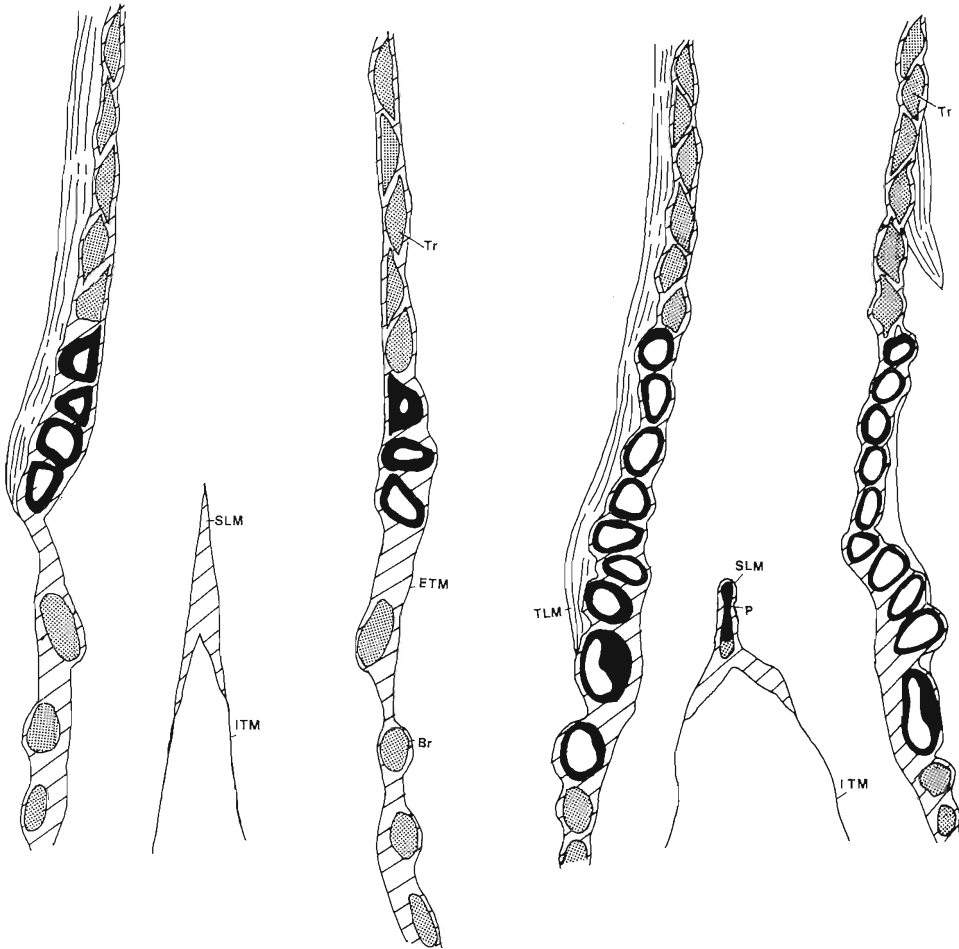


Fig. 7 (left): Longitudinal section of the syrinx of the Ethiopian Snipe *Gallinago nigripennis*. Br = brachial semiring; ETM = external tympaniform membrane; ITM = internal tympaniform membrane; SLM = semilunar membrane; Tr = tracheal ring. Shading as for Fig. 1.

Fig. 8 (right): Longitudinal section of the syrinx of the Ruff *Philomachus pugnax*. Br = brachial semiring; ITM = internal tympaniform membrane; SLM = semilunar membrane; Tr = tracheal ring; M = marrow cavity; TLM = tracheolateralis muscle; P = pessulus. Shading as for Fig. 1.

laterally flattened in transverse section and the caudal ends were more rounded than the cranial ends. These rings lay facing inwards at about 45° . The tracheal rings were cartilaginous. Tracheal rings 4–6 were rounded, although irregularly so, and were cartilaginous. The upper tracheal rings resembled those of other members of the Charadriiformes. The first brachial ring was laterally flattened and cartilaginous but, unlike the tracheal rings, lay in a vertical position directly opposite the pessulus.

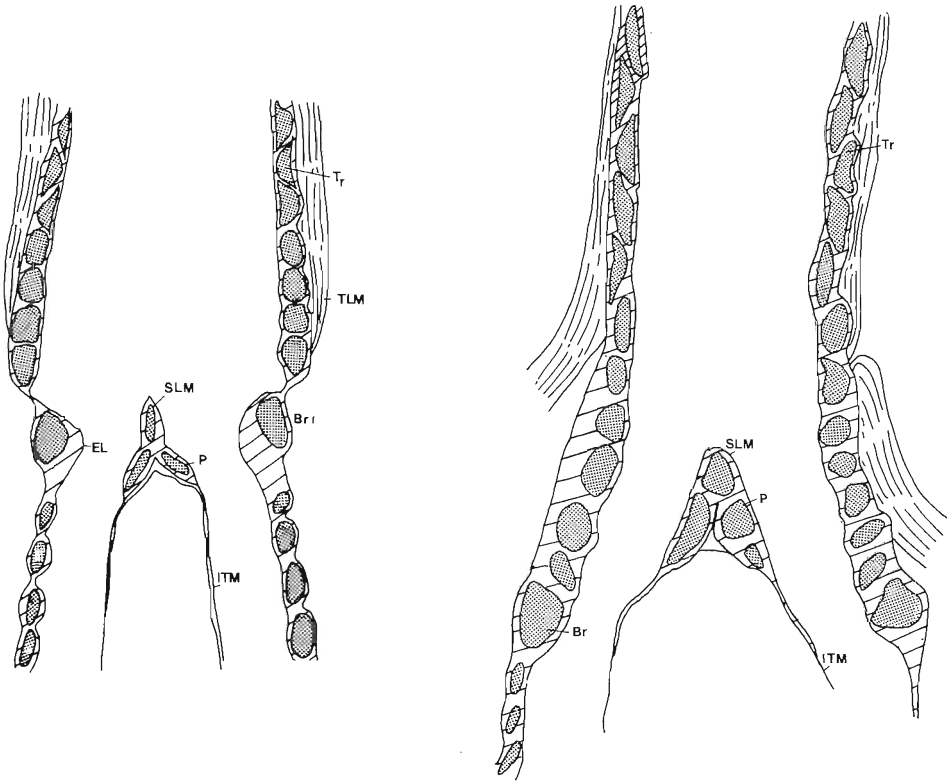


Fig. 9 (left): Longitudinal section of the syrinx of the Wood sandpiper *Tringa glareola*. Br1 = first bronchial semiring; Br = bronchial semiring; ITM = internal tympaniform membrane; SLM = semilunar membrane; Tr = tracheal ring; TLM = tracheolateralis muscle; P = pessulus; EL = external labium; ETM = external tympaniform membrane. Shading as for Fig. 1.

Fig. 10 (right): Longitudinal section of the syrinx of the Spotted Dikkop *Burhinus capensis*. Br = bronchial semiring; ITM = internal tympaniform membrane; SLM = semilunar membrane; Tr = tracheal ring; P = pessulus. Shading as for Fig. 1.

The other bronchial rings were ossified around most of their perimeter and had a marrow cavity in the centre. Some bronchial rings were joined by a layer of cartilage.

Discussion

Several trends were evident in the syringeal structure of the charadriiform species examined. The syringes of the Burhinidae and Pteroclididae are assumed to be primitive because the pessulus was large, cartilaginous and consisted of many pieces. In addition, the syrinx lacked ossification. There appeared to be a divergence in syrinx structure between the Scolopacidae and the Charadrii (of Strauch 1978). The scolopacids showed a retention of the cartilaginous syringeal components, while the

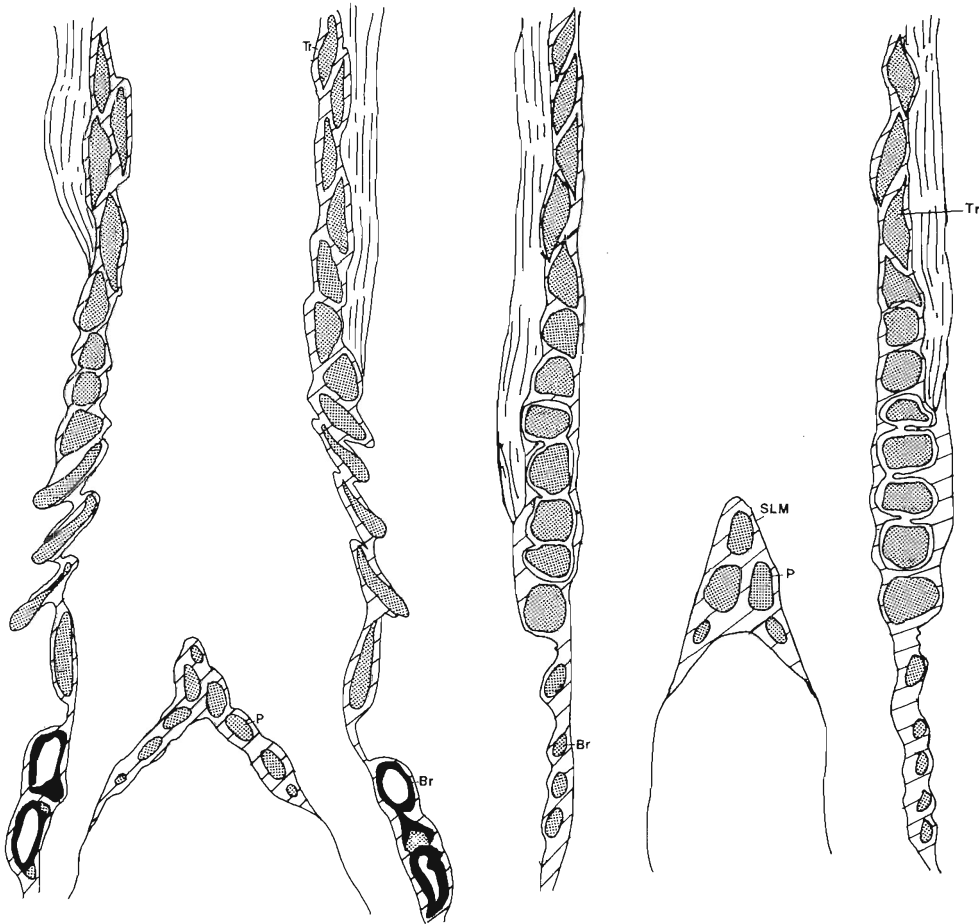


Fig. 11 (left): Longitudinal section of the syrinx of the Namaqua Sandgrouse *Pterocles namaqua*. Br1 = first bronchial semiring; ITM = internal tympaniform membrane; SLM = semilunar membrane; Tr1 = first tracheal ring; P = pessulus; TLM = tracheolateralis muscle; t = tail. shading as for Fig. 1.

Fig. 12 (right): Longitudinal section of the syrinx of the Kelp Gull *Larus dominicanus*. Br = bronchial semiring; ITM = internal tympaniform membrane; SLM = semilunar membrane; Tr = tracheal ring; P = pessulus. Shading as for Fig. 1.

Charadrii had highly ossified tracheal rings which were fused at the tympanum and they had a bony pessulus. The divergence of these two groups agrees with the evidence of Strauch (1978) and Sibley & Ahlquist (1985), using skeletal and biochemical characters, respectively. Of the scolopacids examined, the only species with a bony pessulus was *Philomachus pugnax*. We suggest that there is a trend in the Scolopacidae of a reduction in the pessulus with *Gallinago nigripennis* most recently evolved, since it has no pessulus at all. Within the scolopacids, only *Tringa glareola* lacked ossification in the tympanic region of the trachea.

The glareolid syringes were very similar to the charadriid syringes. The syrinx of *Rhinoptilus chalcopterus* (Glareolidae) was almost identical to those of the five *Vanellus* species examined, suggesting that the two groups are very closely related. This is supported by field observations of the behaviour of these six species (Ward 1987, pers. obs.) since all six species exhibit a double-wing flick in agonistic display, a display not exhibited by other charadriiform birds. The plumage similarity of *Vanellus coronatus* and *R. chalcopterus* was previously considered to be a case of convergent evolution (Snow 1978), but this may indeed be the result of a shared dived character. The syringeal structure of *Rhinoptilus africanus* was very different from *R. chalcopterus* and from all other species examined. *R. africanus* lacked the ridges on the upper tracheal rings characteristic of the other species of Charadriidae and Glareolidae examined. In addition, the pessulus and semilunar membrane of *R. africanus* was elongated rather than rounded as was the case in the other species of the Glareolidae and Charadriidae. Therefore, *R. africanus* showed no syringeal affinities (apart from ossified tracheal rings) with the other members of these two families. Behaviourally, *R. africanus* differs from *R. chalcopterus* in lacking the double-wing flick agonistic display (pers. obs.) and does not "pump" its body up and down while holding its head still in agonistic display, as do *Cursorius temmincki* (pers. obs.) and *C. cursor* (Cramp & Simmons 1983). The genera *Cursorius* and *Rhinoptilus* have been lumped into a single genus *Cursorius* in the most recent taxonomic treatment of the group (Urban et al. 1986, but see Wolters 1975–1982). The considerable variation in syringeal morphology and behaviour in this group suggests that the genus *Rhinoptilus* should be reinstated and *R. africanus* may not be a member of either this genus or *Cursorius*. A parsimonious solution is to reinstate *R. africanus* to its former position in the monotypic genus *Smutsornis* (Roberts 1940, see also Wolters 1975–1982).

The relationships of the Burhinidae with the rest of the Charadriiformes remain obscure. The Burhinidae have been allied to the Haematopodidae and Recurvirostridae by Jehl (1968) and Ahlquist (1974). However, since neither of these two families was included in the scope of this study it is not possible to comment on that relationship. The syrinx of *Burhinus capensis* lacked ossification, had a large septum and a multicomponent pessulus. Based on these characteristics, we support Ahlquist's (1974) contention that the Burhinidae is a primitive group in the order Charadriiformes. This is based on the hypothesis that the general trends in the evolution of the charadriiform syrinx are towards a reduction in the size of the pessulus (and the number of components therein) and an increase in the ossification of the tracheal rings at the tracheobronchial junction. Further clarification of the systematic position of the Burhinidae may be obtained by comparison of the syringes of this family with those of the Haematopodidae and Recurvirostridae.

The syrinx of *Pterocles namaqua* (Pteroclididae) differed greatly from that of any other members of the Charadriiformes examined and from the columbiform syrinx (Warner 1972). The pessulus of the sandgrouse is considered primitive, consisting of numerous cartilaginous pieces. If the Pteroclididae are indeed members of the Charadriiformes then, in all likelihood, they split off early from the main charadriiform line. Evidence for the inclusion of the Pteroclididae with the Charadriiformes has been provided by several authors (Maclean 1967, Fjeldsa 1976,

Sibley & Ahlquist 1985). This affinity is not indicated by their syringeal structure. Although *P. namaqua* shares one syringeal feature with *Columba palumbus* (Columbidae), that of asymmetrically-inserted extrinsic tracheal muscles, the other major syringeal features are not shared with those of the doves.

The results obtained for *Larus dominicanus* also suggest that the Laridae constitute a primitive group, because the syringeal components of the single species examined were not ossified and it had a multicomponent pessulus. However, little else can be determined because of the difficulty in sectioning such a large specimen.

Conclusions

The variations in syringeal structure in the order Charadriiformes show a number of trends. These trends appear to have some taxonomic importance since they are correlated with recognized divisions within the order, derived from examination of skeletal and biochemical material. The two major trends are the reduction in the number of components comprising the pessulus and an increase in the ossification of the tracheobronchial region. The results of this study indicate that syringeal morphology may be a useful indicator of phylogeny. Further work will need to encompass more families and more species both within the order and in orders such as the Columbiformes and Gruiformes to determine the extent and importance of syringeal variation in the phylogeny of the Charadriiformes.

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Zusammenfassung

Als Einzelmerkmalsprüfung der Phylogenie der Watvögel (Charadriiformes) wird der Stimmapparat, die Syrinx, benutzt. Die zwei klaren Hauptrichtungen sind die Reduktion der Teile, die den Pessulus bilden, und eine Zunahme der Verknöcherung der Tracheo-Bronchialregion. Das Variationsmuster der Syrinxstruktur ist überwiegend übereinstimmend mit gegenwärtigen phylogenetischen Analysen, bei denen Skelett- und biochemische Merkmale benutzt werden (Strauch 1978, Sibley & Ahlquist 1985). In der vorliegenden Arbeit wurde jedoch eine erhebliche Variation bei der Syrinx der Rennvögel (Cursoriinae) gefunden, die nicht mit der gebräuchlichen Klassifikation dieser Gruppe übereinstimmt (Urban et al. 1986). Zusätzlich deutet die Ähnlichkeit der Syrinxstruktur der Regenpfeifer *Vanellus* und der Rennvögel *Rhinoptilus* — durch verhaltensbiologische Daten an agonistischen Zurschaustellungen gestützt — auf eine nahe Verwandtschaft dieser zwei Gruppen. Der Ähnlichkeit der beiden Familien liegt also nicht nur konvergente Entwicklung zugrunde. Die Syrinxstruktur der Flughühner (Pteroclididae) unterscheidet sich von der der Tauben (Columbiformes) und der der Watvögel (Charadriiformes), zu denen sie normalerweise gezählt werden (Wetmore 1960, Maclean 1967, Sibley & Ahlquist 1985).

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Catherine Brown, Dr. David Ward, Dept. of Zoology & Entomology, University of Natal, P. O. Box 375, Pietermaritzburg 3200, South Africa. Present address of DW and address for correspondence: Mitrani Centre for Desert Ecology, Jacob Blaustein Institute for Desert Research, Ben Gurion University of the Negev, Sede Boqer Campus 84993, Israel.