

attention to this order of branching as the Columbiformes is the first order listed in it.

In the NJ tree (Fig. 8.59A) columbiforms are the sister of the passerine clade. Association of columbiforms with passerines is marked by the loss of the fibrous or amorphous sheath (a change which we could alternatively envisage as homoplastic). The mutual presence of an elongate midpiece maps as a homoplasy. Homoplastic elongation of the midpiece is acceptable as detailed ultrastructure of the midpiece (not computed) in columbiforms differs from that of passerines.

If the Metaves were a valid grouping loss of the amorphous sheath in Columbiformes would be homoplastic with taxa in the Coronaves. Nevertheless, the location of columbiforms by Sibley and Ahlquist (1990) in a clade which would now be attributable to the Coronaves is not contraindicated by spermatozoal ultrastructure. The phylogenetic position of the Columbiformes and the validity of the Metaves are far from settled. The molecular consensus of Harshman (Chapter 1, Fig. 1.1) places Columbiformes in the Metaves far removed from the Passeriformes.

**Coronaves.** Orders of the Coronaves that have been investigated for spermatozoal ultrastructure (see accounts in previous sections) are: Piciformes, Cuculiformes, Psittaciformes, Gruiformes, Charadriiformes, Falconiformes and Passeriformes. As usual in avian studies, the passerines have received the most attention in terms of numbers of taxa investigated. The grouping Coronaves is not supported by sperm ultrastructure.

**Psittaciformes.** In the molecular analyses of Sibley *et al.* (1988) and Sibley and Ahlquist (1990), the psittaciforms are preceded hierarchically only by the Coliiformes and Cuculiformes at the base of the Passerae. Psittaciforms have a highly unresolved position in the Coronaves in the consensus phylogenies of Harshman (Chapter 1, Fig. 1.2).

In the NJ tree psittaciforms lie in the same unresolved assemblage (containing both Metaves and Coronaves) as *Caprimulgus*. They share with columbiforms a homoplastic reduction in the size of the dense periaxonemal fibers. Psittaciforms show a homoplastic loss of the amorphous sheath, a loss shared with cuculiforms and passeriforms though this character did not map unambiguously on the NJ tree.

The distinctive feature, and autapomorphy, of psittaciform sperm compared all other Aves is the condition of the nuclear-acrosomal junction (see section 8.10.5) though, as an autapomorphy, this does not clarify their relationship with other orders. The unique acrosome-nuclear disjunction was not scored in the matrix but has been added to the tree, thus uniting *Melopsittacus* and *Nymphicus*.

In the portion of a 50% majority rule (MR), maximum parsimony tree shown in Fig. 8.59B Psittaciformes have a sister group relationship with *Grus+Falco* and successively more basal sister groups are *Caprimulgus* and *Apus*.

**Piciformes.** The Piciformes were placed by Sibley *et al.* (1988) and Sibley and Ahlquist (1990) at the base of the Neoaves (ignoring the questionably placed

Turniciformes), i.e. as the sister group of all other Neoaves, a view supported, again from DNA-DNA hybridization, by Bleiweiss *et al.* (1994). In the NJ tree (Fig. 8.59A) *Melanerpes* has an unresolved position as part of a polytomy consisting also of a charadriiform (*Jacana*), a cuculiform (*Crotophaga*), Columbiformes+Passeriformes. This clade is united by loss of the perforatorium, and endonuclear canal, a feature which could, alternatively, have occurred homoplastically.

Features of piciforms differing from oscines and shared with other non-passerines (asterisks indicate characters that were not computed) are the small acrosome: nucleus ratio, the acrosome being shorter than the elongate nucleus whereas it longer in at least the higher passerines; absence of an helical membrane; distribution of mitochondria in a cirlet around the axoneme of the principal piece, as seen in transverse section; the presence (so far as can be deduced from a micrograph, Fig. 8.26) of an amorphous sheath around the principal piece; the stated absence of dense axonemal fibers; and the irregular distribution\* of spermatozoa in the testes (a difference from Passerida but possibly not from corvids). On the other hand, there is no mention of presence of a perforatorium seen in Galloanserae and most other non-passerines, nor of the elongate distal centriole seen in paleognaths, *Apus* and, with some shortening, in Galloanserae. Absence of outer dense axonemal fibers requires confirmation.

This uncertainty as to the position of the Piciformes is reflected in the molecular consensus (Harshman, Chapter 1, Fig. 1.2) in which a clade containing the Piciformes has an unresolved position in the Coronaves.

**Cuculiformes.** The sperm of *Crotophaga ani* as described by Saita *et al.* (1982b) and in this study, has the following characteristics: acrosome conical, shorter than the nucleus; perforatorium and endonuclear canal absent; short distal centriole, short midpiece with several mitochondria in transverse section, helical membrane absent, central axonemal singlets absent from the centriole, amorphous sheath present; and presence of an annulus. It is thus a distinctly non-passerine sperm.

In the molecular consensus of Harshman (Chapter 1, Fig. 1.2) cuculiforms are part of a huge polytomy in the Coronaves. In the NJ tree (Fig. 8.59A) *Crotophaga* is part of a large polytomy, other members of which are *Melanerpes*, *Jacana*, the columbiform+passeriform clade and *Apus*. Determination of the phylogenetic position of the Cuculiformes thus still requires morphological and molecular clarification.

**Passerimorphae.** The Passerimorphae (*sensu* Sibley *et al.* 1988; Sibley and Ahlquist 1990) contains the orders Columbiformes, Gruiformes, the greatly expanded order 'Ciconiiformes' and the Passeriformes. Passerimorphae cannot be said to be supported in the spermatozoal analyses. There is, similarly, no equivalent of the Passerimorphae in the consensus phylogenies of Harshman (Chapter 1) as the constituent families (or orders) lie in the Metaves (Columbiformes) and Coronaves (Gruiformes, orders of the former Ciconiiformes and the Passeriformes).

**Charadriiformes, Gruiformes and Falconiformes.** Charadriiformes, subsumed in the Ciconiiformes by Sibley *et al.* (1988) and Sibley and Ahlquist (1990), are represented for sperm ultrastructure only by *Jacana jacana*. As shown in section 8.10.7.2, a button-like acrosome characterizes this species and many other charadriiform species examined by light microscopy whereas the Scolopacidae have elongate, spiral sperm. The button-like acrosome fails to group *Jacana* with *Grus* and *Falco*, all of which are ciconiiforms *sensu* Sibley and Ahlquist, in the NJ and MR trees (Fig. 8.59A, B). *Grus* and *Falco* have an unlikely sister-group relationship on the basis of the shared button-like acrosome and midpiece consisting of a small group of mitochondria. It is uncertain how much credence can be placed on this grouping as the possibility exists that this acrosomal form and midpiece morphology are homoplastic. This must indeed be the case in the passeridan Eurasian bullfinch in the sperm of which Birkhead *et al.* (2006) have demonstrated a button-like acrosome (and, we may add, a falconiform-like external sperm morphology), the only known exception for passerines. Furthermore, *Jacana* has only an unresolved relationship with *Grus* + *Falco* in the MR tree (not illustrated). With regard to the spiral sperm of scolopacids it is pertinent that molecular analyses place them firmly in a charadriiform clade (Paton *et al.* 2003). *Falco* has an unresolved position, though also in the Coronaves in the molecular consensus (Harshman, Chapter 1, Fig. 1.2).

**Suboscines.** The sperm of suboscines (Tyranni), represented in the trees only by *Tyrannus tyrannus*, are poorly known. Nevertheless, they occupy their traditional place at the base of the Passeriformes in the NJ tree (Fig. 8.59A) in a passeriform clade. Monophyly of passeriforms and the basal position in these of suboscines is endorsed by molecular studies (Sibley *et al.* 1988; Sibley and Ahlquist 1990; Harshman, Chapter 1, Fig. 1.4). In the NJ tree (Fig. 8.59A) the only unambiguous synapomorphy for the Passeriformes is the presence of the 'helical membrane' (but see below). Computation of unambiguous changes (not shown) on the MR tree gave none for *Tyrannus* but grouped all oscines by enlargement of the periaxonemal dense fibers.

It is uncertain whether in suboscines the mitochondrial component is unilateral, as it is in Passerida, and there appears to be more than one mitochondrion; the dense outer axonemal fibers have either not been illustrated or, in *Tyrannus*, are smaller than those of oscines; absence of a nuclear rostrum requires confirmation; and accounts are contradictory as to whether there is an helical membrane, though where described for Tyranni this differs in structure from that of oscines. As noted, an apomorphy (not computed) shared with oscines is the helical nucleus. A plesiomorphic feature not seen in oscines is the (constant?) presence of two centrioles.

**Passeri (oscines).** The Corvida are represented by *Corvus splendens* but with some reference to the light microscopy of Ballowitz (1888) and Retzius (1911, 1912) and the account of Birkhead *et al.* (2006). In the NJ tree they were not resolved by any unambiguous character state from *Tyrannus*. However, they are shown as the plesiomorph sister group of the Passerida in Fig. 8.59A as

one can confidently add two Corvida+Passerida synapomorphies: loss of the proximal centriole and enlargement of the dense fibers. *Tyrannus* has both centrioles and small dense fibers. These features require confirmation in most suboscines. Corvida have the oscine synapomorphy of a true helical membrane (imperfectly known but at least present as a microtubular bundle in the spermatid) but remain plesiomorphic in the short acrosome and midpiece, relative to the length of the nucleus. However, some exceptions to the typical acrosome: nuclear ratios, below unity in Corvida and above in Passerida are noted in section 8.10.10.1 and Table 8.6.

**Passerida.** Two synapomorphies for the Passerida are well established from the large number of light microscope descriptions reviewed in this chapter and from new information, notably for *Myrmecocichla formicivora* and *Philetairus socius*. The most distinctive synapomorphy is the very long spiral midpiece differing from that of the other group with a long midpiece, the columbiforms (and possibly *Coturnix japonica*), in consisting of a single, spiral mitochondrial strand. The second is the elongation of the acrosome relative to the nucleus, though exceptionally, as recorded in Table 8.6, it remains shorter than the nucleus as in the suboscines and most Corvida.

A more discriminating analysis should be attempted when a greater knowledge of sperm ultrastructure in a much larger range of species accrues. For instance, a detail of the mitochondrial helix, the presence of a fibrous helix, might well diagnose the Muscicapoidae and presence of a granular helix may have taxonomic value.

## 8.12 CONCLUSION

The author has attempted in this chapter to review works on the ultrastructure of avian spermatozoa, with some reference to light microscopical studies, with a view to demonstrating the diversity which exists in sperm structure in birds and phylogenetic patterns which may be discerned. A very preliminary phylogenetic analysis using PAUP has been presented. It is uncertain, when a more complete matrix for all groups is obtained, whether the considerable homoplasy which exists in avian sperm characters will permit the production of highly resolved trees. Nevertheless, the taxonomic and phylogenetic value of sperm characters is indisputable. Thus we have seen that even the highly peculiar, 'neotenus' sperm of the Eurasian bullfinch yielded up its identity as a passerine sperm when closely examined.

Spermatozoal characters of paleognaths have confirmed crocodyloid and basal amniote relationships. They also allow confident identification of a spermatozoon with its ordinal or subordinal grouping in many cases and increasing discernment will presumably become possible as descriptions are improved. Thus it is already possible to recognize a distinctive sperm type for each of the groups Struthioniformes, Galloanserae, Galliformes, Anseriformes, Psittaciformes, Apodiformes, Columbiformes, Passeriformes, Corvida and Passerida.

It is hoped that this compendium will prove a stimulus and aid to other researchers on avian spermatozoal morphology and will provide a background for those interested in sperm function and general biology.

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