Cottrell) pp. 390-409. Mus. Comp. Zool. Harvard. Cambridge, Mass.

Nei, M. (1978). Estimation of average heterozygosity and genetic distance from a small number of individuals. *Genetics* **89**, 583-590.

Reader's Digest (1976) *Complete Book of Australian Birds.* 1st edn. Reader's Digest Services, Sydney.

Schodde, R. (1982a). *The Fairy-wrens.* Illustrated by R. Weatherly. Lansdowne Editions, Melbourne.

Schodde, R. (1982b). Origin, adaptation and evolution of birds in arid Australia. In: *Evolution of the Flora and Fauna of Arid Australia.* (eds W.R. Barker & P.J.M. Greenslade) pp. 191-224. Peacock Press, Adelaide.

Twidale, C.R. (1972). Evolution of sand dunes in the Simpson Desert, Central Australia. *Trans. Inst. Brit. Geogr.* **56**, 77-109.

Veevers J.J. & Rundle, A.S. (1979). Channel Country fluvial sand and associated facies of central-eastern Australia: modern analogues of Mesozoic desert sands of South America. *Palaeogeog., Palaeoclim., Palaeoecol.* **26**, 1-16.

Wasson, R.J. (1982). Landform development in Australia. In: *Evolution of the Flora and Fauna of Arid Australia.* (eds W.R. Barker & P.J.M. Greenslade) pp. 23-33. Peacock Press, Adelaide.

Wasson, R.J. (1983). The Cainozoic history of the Strzelecki and Simpson dunefields (Australia), and the origin of the desert dunes. *Z. Geomorph. Suppl.* **45**, 85-115.

Wopfner, H. (1974). Post-Eocene history and stratigraphy of northeastern South Australia. *Trans. Roy. Soc. S. Aust.* **98**, 1-12.

The Unusual Syrinx Morphology of Australian Treecreepers *Climacteris*

PETER L. AMES

Harza Engineering Company, 150 South Wacker Drive, Chicago, Illinois 60606 U.S.A.

Received 21 August 1986, accepted 8 March 1987

The six species of Australian treecreepers constitute a fairly homogeneous group usually now considered to constitute a distinct family Climacteridae. The group has given considerable difficulty to taxonomists, who disagree on whether the treecreepers evolved within a general bark-foraging assemblage that includes the holarctic creepers (*Certhia*), nuthatches (*Sitta*) and sittellas (*Daphoenositta*), among others, or within an Australo-Papuan oscine radiation. The latter view, which appears to be gaining prevalence, has been expounded by Sibley *et al.* (1984), who provide an excellent taxonomic history of the genus *Climacteris*. They provide evidence from DNA-DNA hybridisation that the treecreepers represent an ancient diversion from the evolutionary line that produced the rest of the Australo-Papuan oscines. Parker (1982), in a paper arguing for a relationship between the treecreepers and the honeyeaters (Meliphagidae), also summarises the taxonomic history of the treecreepers. In this paper, I provide evidence from the syringeal morphology supporting the view that the treecreepers diverged from the oscine line long ago.

In a broad survey of the passerine syrinx (Ames 1971, 1975), I studied the syrinx in four specimens, representing three of the six species of treecreepers: *Climacteris rufa* (two specimens), *C. affinis*, and *C. melanura*. I found in all three species a striking departure from the basic muscle pattern that prevails throughout the rest of the oscines. Unfortunately, the uniqueness of the syrinx in the treecreepers has so far prevented its use in determining their nearest relatives.

I removed the syrinx from the preserved whole bird or skinned 'carcass' essentially as described by Ames (1971). Following the recording of muscle patterns on a layer-by-layer basis, the muscles of one side were removed so as to note the structure of the underlying bony and cartilaginous elements.

The nomenclature of syringeal muscles employed here is that of Owen (1866), modified slightly (for synonymy, see Ames 1971; George & Berger 1966; or Baumel *et al.* 1979). There are two pairs of extrinsic muscles, *M. tracheolateralis* and *M. sternotrachealis*, and four pairs of intrinsic ones *M. bronchotrachealis posticus, M. bronchotrachealis anticus, M. bronchialis posticus* and *M. bronchialis anticus.* The last of these usually comprises two parts, *pars medialis* and *pars lateralis*, which may be quite distinct or may be one continuous muscle sheet.

The oscine syrinx

In all oscines described before this paper, about 800 species from warblers to ravens, including all of the purported

0158-4197/87/03192 + 4 $2.00

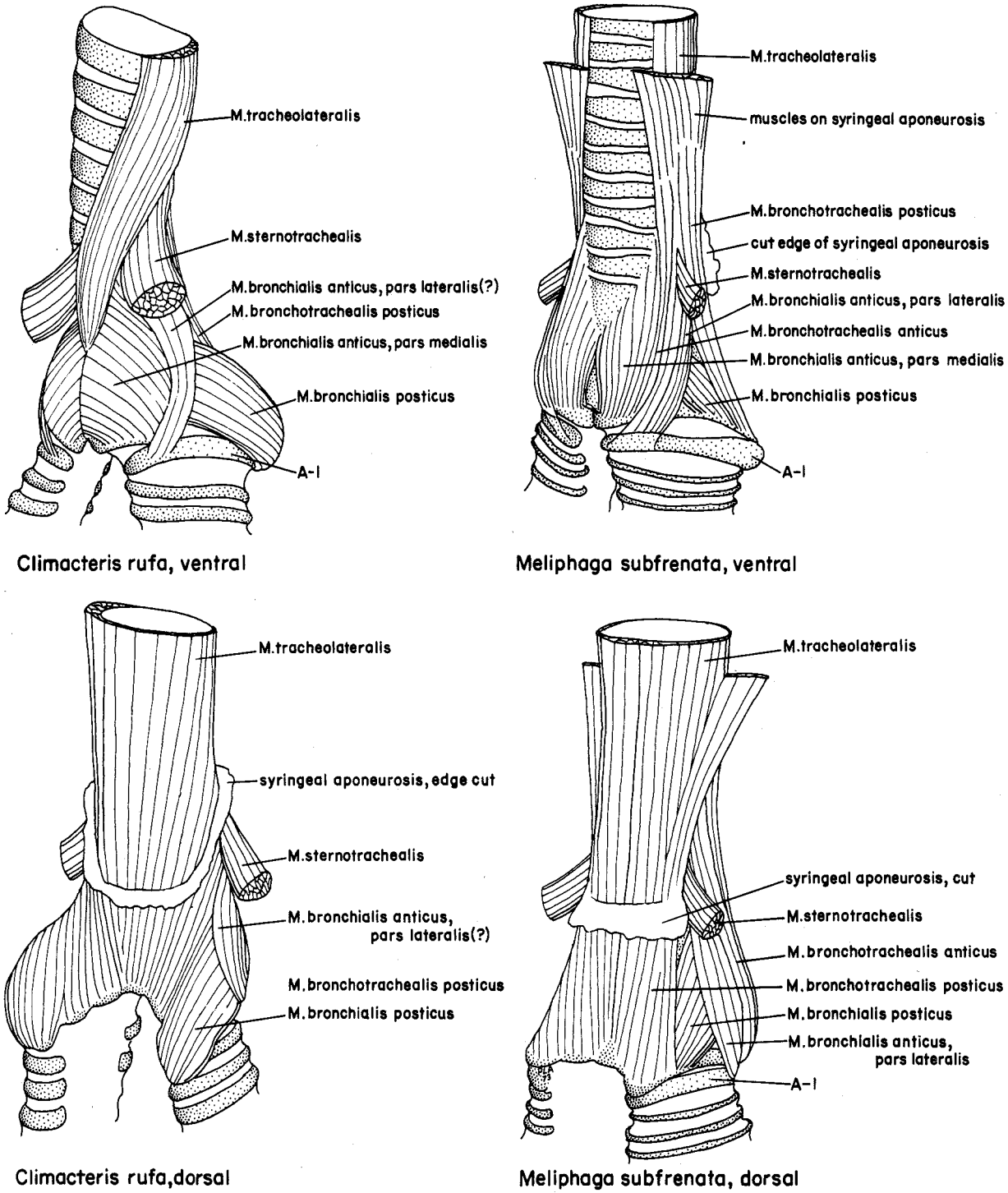

FIGURE 1 Syrinx of *Climacteris rufa* compared with that of a typical oscine, the honeyeater *Meliphaga subfrenata*. Above, left ventro-lateral views; below, right dorso-lateral views.

relatives of the treecreepers, the syrinx contains six basic muscle pairs, two extrinsic and four intrinsic. These invariably show the overall pattern found in *Meliphaga* (Fig. 1). Other examples of this pattern have been described by many authors (e.g. Shufeldt 1890; Miskimen 1951; Baumel *et al.* 1979) Most have based their studies on the Corvidae, but *Galerida, Sylvia, Muscicapa* and *Pellorneum* (Ames 1975) all exhibit the same pattern. Distinctive syringeal patterns do occur in some groups, such as the larks (lacking the bony pessulus at the bronchial junction), thrushes and muscicapine flycatchers (a dorso-posterior extension or 'turdine thumb') and helmet shrikes (a spiral asymmetry of the long ventral muscles). But in each case the over-riding oscine pattern is easily recognisable.

The syringeal muscles insert (and the intrinsic muscles originate) on modified cartilages of the tracheobronchial region. These exhibit varying degrees of ossification. The medial surfaces of the bronchi consist of membranes whose tension is controlled by the muscles, acting on the modified cartilages (intermediary bars). In all oscines so far studied, the posterior four or five complete tracheal elements are fused into a rigid cylinder, called the drum.

Climacteris versus other oscines

The trachea of oscines lies on the right side of the neck, next to the esophagus, but curves back to the ventral midline to enter the thoracic cavity loosely attached to the oesophagus. This twisting of the trachea tends to induce a certain amount of asymmetry, usually limited to inequality in muscle size or area of attachment between the right and left members of a muscle pair. In *Climacteris* there is not only gross asymmetry of the extrinsic muscles, but some unusual aspects of fibre direction, as will be seen in the following muscle-by-muscle comparison with *Meliphaga.*

M. tracheolateralis. The members of this pair originate on the lateral surfaces of the cricoid cartilage of the larynx and extend posteriad on both sides of the trachea to insert on the anterior region of the drum and on the syringeal aponeurosis. Usually the members of the pair converge to cover the dorsal surface of the trachea, but remain separate ventrally.

In *Climacteris* the situation is quite unusual. The left member of this pair is much thicker than the right, but narrower. It lies on the lateral surface of the trachea posteriad to about tracheal ring A-10, where it begins an abrupt spiral to a mid-ventral position. The trachea, in passing from the right side of the neck to the mid-ventral entrance of the thoracic cavity, spirals in the opposite direction from the muscle. The left tracheolateral muscle inserts in a narrow mid-ventral region of the anterior edge of the drum.

The right *M. tracheolateralis* also spirals somewhat but spreads out into a thin sheet of muscle that covers the dorsal surface of the trachea, meeting the left muscle inseparably. From fibre direction, it appears that the dorsal muscle sheet is entirely derived from the right muscle, while the entire left muscle passes on the ventral side of *M. sternotrachalis.* The right muscle is interrupted by the syringeal aponeurosis, on which it inserts, with the deeper fibres attached to the anterior region of the drum and to adjacent connective tissue. It lies entirely on the dorsal side of *M. sternotrachealis.*

M. sternotrachealis. This paired muscle orginates on the inner surface of the sternum (or on connective tissue) and extends through the interclavicular air sac to insert on the lateral surface of the syrinx. It is present in all passerines and in nearly all other bird groups. In songbirds *M. sternotrachealis* varies in thickness from about one-twentieth to about one-quarter the long diameter of the trachea.

In all of my specimens of *Climacteris,* this muscle originates and inserts normally but is exceptionally robust, being about a third the long diameter of the trachea.

M. bronchotrachealis anticus. This long ventral muscle normally originates on the ventral surface of the syringeal aponeurosis and on the lateral surface of the trachea and extends posteriad to insert on one or two of the intermediary bars (A-1 and/or A-2) and often on the connective tissue between them. There rarely is as much muscle tissue on the syringeal aponeurosis as is found in *Meliphaga subfrenata.*

In *Climacteris,* the syringeal aponeurosis is quite weak and supports no muscle fibres ventrally. *M. bronchotrachealis anticus* cannot be distinguished with certainty but there is a discrete band of muscle on each side of the trachea that may correspond to the *M. bronchotrachealis anticus* of other oscines or to the *pars lateralis* of *M. bronchialis anticus.* Whatever its homology, it originates immediately posterior to the *M. sternotrachealis* and is continuous with the origin of the aberrant *M. bronchialis anticus.* It extends as a narrow band to insert near the ventral end of A-1. The members of this muscle pair are essentially alike.

M. bronchotrachealis posticus. This pair of long dorsal and dorso-lateral muscles originates on the syringeal aponeurosis, the tracheal elements and their connective tissue, and the anterior edge of the drum. The members of the pair nearly always meet mid-dorsally. Each extends posteriad to insert on the dorsal ends of the intermediary bars (A-1, A-2 and A-3) and sometimes even on the drum. *Meliphaga subfrenata* is typical, except that the area of insertion on A-1 is somewhat greater than usual.

Climacteris is nearly normal with regard to this muscle,

except that the breadth of the muscle is reduced and the insertion on A-1 is lacking. The entire dorso-lateral muscle mass, which covers the end of A-1, consists of the *M. bronchialis posticus.*

M. bronchialis anticus. This muscle typically originates on the dorsal edge of the drum and on adjacent tracheal rings and extends parallel to the tracheal axis to insert on the ventral ends of all three intermediary bars (A-1, A-2 and A-3). It usually consists of a nearly continuous sheet of nearly parallel fibres, some of which are covered by *M. bronchotrachealis anticus.* Often the more lateral fibres form a distinct slip, the *pars lateralis.* At the ventral midline, the members usually are in parallel contact, but a space is not uncommon. The type of space found in *Meliphaga subfrenata*, a separation only at the posterior end of the muscles, is characteristic of honeyeaters and vireos.

In *Climacteris* the short ventral muscles have a peculiarity of fibre direction so far not found in other oscines. The members of the pair originate on opposite sides of the ventral midline of the drum and on connective tissue between it and the anterior intermediary bar (A-3). The anterior fibres originate on several tracheal elements anterior to the drum. The fibres of each muscle are directed latero-posteriad to insert on the ventral half of the second intermediary bar (A-2) and in the mid-lateral region of A-3.

M. bronchialis posticus. This dorso-lateral muscle originates on the anterior lateral surface of the drum, almost invariably hidden by *M. bronchotrachealis anticus* and *M. bronchialis anticus, pars lateralis*, and inserts near the dorsal end of A-2. As in most syringeal muscles, some fibres insert on connective tissue between the intermediary bars. The condition shown in *Meliphaga* is typical. Notable variants include the 'turdine thumb' condition (Ames 1975), found in thrushes and muscicapine flycatchers. In this condition the dorsal end of A-1 bends posteriad and is enveloped by *M. bronchialis posticus* and *M. bronchotrachealis posticus*, forming a thumb-like extension roughly parallel to the tracheal axis.

In *Climacteris, M. bronchialis posticus* is strongly developed, occupying the lateral and dorsal areas usually dominated by *M. brochotrachealis posticus.* It originates, as in other oscines, on the lateral surface of the drum, where it is overlain by the narrow band of muscle that above I have called *M. bronchotrachealis anticus.* It extends dorsad and somewhat posteriad to wrap around the enlarged dorsal end of A-1, on which most of it inserts. The medial fibres also insert on the dorsal end of A-2.

Phylogenetic implications

The unusual syrinx of the treecreepers does nothing to reveal their closest relatives among the oscines, because no other group has been found with this muscle pattern. Considering the relative uniformity of the syrinx among the other oscines and their great radiation in other morphological and vocal characteristics, the treecreeper syrinx suggests long separation from the main stem of oscine evolution or a high selective pressure for this type of syrinx.

Sibley & Ahlquist (1985) conclude, on the basis of biochemical evidence, that the treecreepers diverged very early from the main evolutionary line of the Australo-Papuan oscines, even before the lyrebirds (*Menura*) and scrub-birds (*Atrichornis*). The syringeal evidence supports their conclusion but too little is known at present about the adaptive value of syringeal specialisations to allow one to draw further conclusions about the relationships of the treecreepers.

Acknowledgements

Specimens that formed the broad basis for this study were borrowed from eight museums. Appreciation has been expressed to these institutions and their curators in my earlier paper (Ames 1971). Additional specimens of *Climacteris* were provided to me by G.F. Mees, whose special interest in this genus has stimulated the work. I thank Dr Philip Burton for providing access to *Climacteris* specimens in the spirit collection at the British Museum (Natural History), and Charles G. Sibley, Shane Parker and C.J.O. Harrison who have shared their research findings with me in advance of publication.

References

Ames, P.L. (1971). The morphology of the syrinx in passerine birds. *Peabody Mus. Nat. Hist. Yale Univ. Bull.* **37**.

Ames, P.L. (1975). The application of syringeal morphology to the classification of the Old World Insect Eaters (Muscicapidae). *Bonn. zool. Beitr.* **26**, 107-134.

Baumel, J.J., King, A.S., Lucas, A.M., Breazile, J.E. & Evans, H.E. (1979). *Nomina Anatomica Avium.* Academic Press, London.

George, J.C. & Berger, A.J. (1966). *Avian Myology.* Academic Press, N.Y.

Miskimen, M. (1951). Sound production in passerine birds. *Auk* **68**, 493-504.

Owen, R. (1866). *Anatomy of Vertebrates*, Vol. 2. Longman, Green & Co., London.

Parker, S.A. (1982). The relationships of the Australo-Papuan treecreepers and sittellas. *South Aust. Ornithol.* **28**, 197-200.

Shufeldt, R.W. 1890. *The Myology of the Raven (Corvus corax sinuatus).* MacMillan & Co., London.

Sibley, C.G., Schodde, R. & Ahlquist, J.E. (1984). The relationships of the Australo-Papuan treecreepers Climacteridae as indicated by DNA-DNA hybridization. *Emu* **84**, 236-241.

Sibley, C.G. & Ahlquist, J.E. (1985). The phylogeny and classification of the Australo-Papuan passerine birds. *Emu* **85**, 1-14.