

K. Susanna S. Hall

## Do nine-primaried passerines have nine or ten primary feathers? The evolution of a concept

Received: 1 September 2004 / Revised: 23 October 2004 / Accepted: 13 December 2004 / Published online: 3 March 2005  
© Dt. Ornithologen-Gesellschaft e.V. 2005

**Abstract** The number of primary feathers in a bird's wing has been used as a systematic character since the first half of the nineteenth century. During the years, though, the definition of which feathers to count as a primary has changed and today the species historically denoted as having only nine primaries are instead said to have, for example, nine 'functional' primaries. In this study, I investigated the borderline between 'nine-primaried' and 'ten-primaried' birds to search for a proper definition of the term 'nine-primaried'. A total of 161 specimens of 104 bird species, mainly passerines, were examined. All species examined had ten primaries although the 'nine-primaried' species had primary ten more or less concealed under primary covert nine. The number of primary coverts has decreased over time, with ten primary coverts as the ancestral state within Passeriformes and nine primary coverts among most oscine species. In conclusion, a proper definition of 'nine-primaried' might be "with primary ten concealed by primary covert nine". This definition includes all taxa historically denoted 'nine-primaried', i.e. systematically it is a definition of a paraphyletic group. The term 'nine-primaried' is thus too inclusive to be of more than very limited systemic value and, consequently, the New World nine-primaried oscines group might gain from a new denotation.

**Keywords** Fringillidae · Nine-primaried · Passeriformes · Primary covert · Remicle

**Electronic Supplementary Material** Supplementary material is available for this article at <http://dx.doi.org/10.1007/s10336-004-0070-5>

Communicated by A.J. Helbig

K. S. S. Hall  
Swedish Museum of Natural History, Bird Ringing Centre,  
50007, 10405 Stockholm, Sweden  
E-mail: susanna.hall@nrm.se  
Tel.: +46-8-51954050

### Introduction

The development of biological systematic science, from taxonomy in the mid-eighteenth century to the phylogenetic systematic approach of today, has changed the view of morphological characters as tools for determining historical relationships. Similar morphological characters were considered as indicators of close relationship in the nineteenth century, but are nowadays analysed in the light of phylogenetic relationships (based on independent evidence) before conclusions are drawn of whether the similarity between the characters in question are due to common ancestry or to convergent evolution (Schuh 2000). During the nineteenth century, the number of primary feathers in a passerine bird's wing was considered a useful taxonomic character, good enough to name one group of passerine birds, the 'nine-primaried' passerines. Today, the term 'nine-primaried' is still widely used. The present study investigates the character state 'nine-primary-feathers', from its first appearance in the literature in 1840 until today, and searches for a definition of the term that might explain the difference between 'nine-' and 'ten-primaried' passerine birds.

### History of the number of primary feathers as a systematic character

The earliest record, to my knowledge, of the number of primary feathers in a passerine bird's wing was presented by Nitzsch (1840, in translation by Sclater 1867). In his *System der Pterylographie*, he stated that among the Passerinae both nine and ten primaries occur. In 1872, Sundevall published his thesis on bird systematics (in translation by Nicholson 1889), in which he used the Latin terms equivalent to 'nine-primaried' (novempennatae) and 'ten-primaried' (decempennatae) as systematic group names, among others. Wallace (1874) followed up on this idea and divided the passerines into four groups based on the length and occurrence of the

tenth primary. Based on the data from Sundevall's thesis (1872, in translation by Nicholson 1889), Wallace (1874) divided the passerines (his Order Passeres) into the following four groups: (1) with ten primaries, the outermost well developed; (2) with ten primaries, the outermost reduced in size; (3) with ten primaries, the outermost rudimentary; and (4) with nine primaries. Wallace (1874) included ten families in the group with nine primaries, i.e. Motacillidae, Mniotiltidae (=Parulidae), Coerebidae, Drepanididae, Dicaeidae, Ampelidae (=Bombycillidae), Hirundinidae, Tanagridae (=Thraupidae), Fringillidae and Icteridae. The groups defined by Wallace were based on morphological similarities, and modern phylogenetic techniques have shown that this was a paraphyletic grouping. However, six of Wallace's 'nine-primaried' families are today included in the "New World nine-primaried oscine" group, i.e. Mniotiltidae (=Parulidae), Coerebidae, Drepanididae, Tanagridae (=Thraupidae), Fringillidae and Icteridae (Raikow 1978). This is the same grouping as the clade Fringillidae sensu Sibley and Ahlquist (1990). Ericson et al. (2000) found two insertions in exon 3 of the *c-myc* gene, one shared by the entire passerine parvorder Passerida (Fig. 1, Electronic Appendix 1) and a second shared only between Motacillidae and Fringillidae (sensu Sibley and Ahlquist 1990; see Electronic Appendix 1). The *c-myc* gene is involved in cell proliferation and apoptosis (Ericson et al. 2000) and it is possible that it at least partly determines the lengths of the different primary feathers. Dicaeidae and Bombycillidae are today not considered close relatives to this clade. Besides the taxa mentioned above, Sundevall (1872) noted that the numbers of primaries varied between nine and ten in the vireos (his Vireoninae) and, accordingly, Vireonidae has sometimes been considered a 'nine-primaried' family (Raikow 1978). Additionally, Raikow (1978) noted the occurrence of a vestigial tenth primary among several families that he did not include in the 'nine-primaried' assemblage (Zosteropidae, Hirundinidae, Alaudidae and Motacillidae).

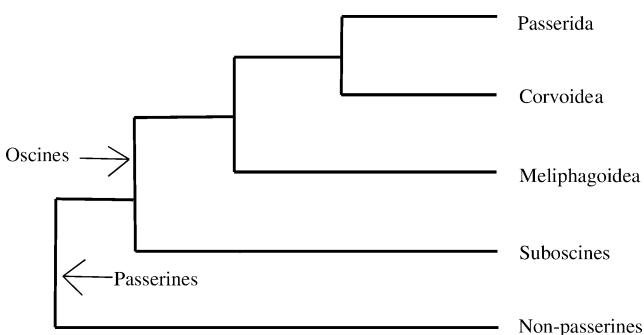
In recent systematic literature, the term 'nine-primaried' oscines (i.e. with nine primary feathers in the wing) is widely used (Winkler and Leisler 1992; Groth 1998; Klicka et al. 2000; Raikow and Bledsoe 2000; Yuri and

Mindell 2002) although some authors mention that the 'nine-primaried' birds do actually have ten primaries (Groth 1998; Raikow and Bledsoe 2000). A modern bird ringer's guide states that passerines may have either nine or ten primaries (Pyle et al. 1987), but in the updated version the 'nine-primaried' birds are described as having nine 'visible' primaries (Pyle 1997). Other authors state that passerines possess ten primaries (Stresemann 1927–1934; Mead 1974), may have nine primaries (Beecher 1953; Pettingill 1956; Gill 1990), or that all passerines have ten primaries, but the outermost, the tenth, may be very short (Gadow 1888; Ashmole et al. 1961; Stresemann and Stresemann 1966; Spencer 1972; van Tyne and Berger 1976; Raikow 1978; Svensson 1992). Stegmann (1962) presented a comprehensive study on the occurrence of a reduced or rudimentary outer primary at the wing margin. He denoted this feather separately as a rudimentary, but considered it to be a primary of varying reduction in lengths.

The term 'nine-primaried' is used by some authors in the meaning of nine 'functional' primaries (van Tyne and Berger 1976; Raikow 1978; Klicka et al. 2000; Yuri and Mindell 2002), although no studies on the functionality of the minute tenth primary have been done. 'Effectively' nine-primaried (Ericson et al. 2000), nine 'obvious' primaries (Witherby et al. 1938–1941) as well as nine 'visible' primaries (Pyle 1997) are other definitions used. Ashmole et al. (1961) wrote that primary ten might be "so small that only nine primaries can easily be seen". Actually, Coues (1890) had already changed the definition of the term 'nine-primaried' when he explained that an outer primary of less than one-third in length compared to the next was not to be counted, and Jeffries (1881) acknowledged the existence of a rudimentary tenth primary, but denoted it as 'absent' in his wing formulas.

In 1887, Wray designated the small outermost primary of a duck's wing a 'remicle', i.e. a little remex, and compared it to the rudimentary tenth primary of many Passerines. There has been some confusion around the term 'remicle' and opinions differ as to what it denotes (Ginn and Melville 1983). The 'remicle' has been described as a rudimentary primary (Wray 1887), as a specific kind of primary different from the longer ones used for forward movement (Stephan 1970a), as a tiny and stiff feather in front of the distal primary (Stresemann and Stephan 1968), as a feather (not a primary) whose function it is to protect the outermost tenth primary (Stephan 1997), and as a covert of a claw (Stresemann 1963). Stephan (1970b) suggested that the remicle was already smaller than the following primaries in the ancestral condition, i.e. that it is not the terminal point of an evolutionary reduction in length of a previously longer primary. In the present study, it is not an aim to solve this confusion.

Modern authors thus do acknowledge that 'nine-primaried' birds do have ten primary feathers in the wing, but the number of primaries is still considered a useful character in oscine systematics (Groth 1998) and



**Fig. 1** Simplified phylogeny of the Passeriformes based on Ericson et al. (2002)

the frequent distinction between ‘nine-primaried’ and ‘ten-primaried’ birds indicates an important difference between these groups. To enhance the understanding of this grouping criterion, I investigated the borderline between these groups by examining museum specimens at the Swedish Museum of Natural History.

## Methods

### Definition of primary feather and primary covert

The feathers of a bird’s wing are of two kinds, the stiff remiges used for flight and the softer coverts with the main purpose to protect the wing. The remiges, in turn, are divided into primaries and secondaries with the division line at the skeletal carpal joint. The secondaries are the remiges closest to the body and the primaries those closest to, and constituting, the wing tip (Ginn and Melville 1983). Most authors define primary feathers as the remiges that grow upon the hand (manus) (Pettingill 1956; van Tyne and Berger 1976; Ginn and Melville 1983; Campbell and Lack 1985; Jenni and Winkler 1994) and do not define them in relation to the feathers that a tiny primary would most easily be confounded with, i.e. the primary coverts and the coverts on the outer lining of the wing. Other authors define the primaries with relative criteria, so the dividing line between a dwarfed primary and a covert of similar size (or larger) is not easily drawn. For example, Nitzsch (1840, in translation by Sclater 1867) stated that “The most perfect contour-feathers, or those in which the pennaceous vane is largest and the downy part smallest, are the remiges of the wings and the rectrices of the tail” and Sundevall (1886, the original article 1843) wrote “Remiges primores, which are seated upon the hand, constitute the most important part of the organ of flight, and exceed all others in size, firmness, the size of the quill tube, and the shortness and elasticity of the vane.” In this study, the definition of a primary follows Lucas and Stettenheim (1972, pp. 83–84), according to whom remiges are the feathers growing from the feather buds on the edge of the postpatagium (i.e. the forearm, wrist and hand parts of the wing) during embryonic development of the wing. In contrast, feathers arising from the surface of the wing are considered coverts. Primary coverts arise on the distal side of the primary with the same number (Jenni and Winkler 1994), i.e. primary covert nine arises at the base of primary nine, but covers the base of primary ten.

### Museum specimens

The relation of the primaries to the bones in the hand was carefully checked through dissection of ten species of passerine birds including three species considered to be ‘nine-primaried’ (Electronic Appendix 1, for an illustration of the insertion of feathers to the skeletal bones see Stegmann 1962). In addition, 151 specimens

were examined without dissection for occurrence of a potential primary feather distally to primary nine (counted from the carpal joint outwards towards the wing tip). In total, 161 bird specimens of 104 species (Electronic Appendix 1), both fresh and alcohol preserved, were examined. Primary feathers and primary coverts were counted and primaries eight to ten and primary coverts eight and nine were measured to the nearest half millimetre using a strip of millimetre-paper inserted between the feathers on the proximal side of each feather, i.e. on the side nearest to the bird’s body. Coverts were measured by inserting the millimetre-paper between the feather and the body, i.e. ‘behind’ the feather vane. The distances between the tip of primary ten and the tip of primary coverts eight, nine and the longest primary covert were also measured.

### Systematic grouping

The *c-myc* gene is known to affect cell-division (Ericson et al. 2000) and might be involved in determining the length of feathers. Investigating the systematic relationships within passerines, Ericson et al. (2000) found two insertions in the *c-myc* gene, and Ericson and Johansson (2003) showed that at least one of these was correlated with the length of primary ten. Since this indicates a possible phylogenetic explanation to the length of primary ten, I used the number of insertions to investigate the relative length of primary ten to primary nine and primary covert nine in a phylogenetic perspective. This criteria resulted in three groups: 0, with no insertions (non-passerines, Suboscines, Meliphagoidea and Corvoidea, 11 species); 1, with one insertion (most Passerida, 56 species); and 2, with two insertions (clade Fringillidae sensu Sibley and Ahlquist (1990) plus Motacillidae, 37 species; Electronic Appendix 1; Fig. 1). The group with two insertions thus included most but not all of the ‘nine-primaried’ species.

## Results

### Number of primaries and primary coverts

All birds examined had a feather in the position of the tenth primary. In almost all birds traditionally considered to be ‘nine-primaried’, the tenth primary was concealed by the ninth primary covert and, in these cases, primary ten could be discovered only if primary covert nine was carefully lifted upwards. Thus, the ‘nine-primaried’ species only had nine ‘obvious’ primaries and primary ten was in a position where it probably did not have any effect on the morphology of the outer wing margin. In no case among the ‘nine-primaried’ species was primary ten more than 2 mm longer than primary covert nine. There were ten primary coverts in the examined non-passerines and suboscines, but only nine in most oscines, although it was sometimes uncertain

whether a specific feather was to be considered a primary covert or a covert of the outer margin of the wing. Also, some specimens were poorly prepared and it was then unclear whether a tiny feather at the wing margin might be missing (Electronic Appendix 1).

### Correlation of length and relative length of primary ten

The length of primary nine was correlated to the length of primary ten (Spearman rank  $R_s=0.41$ ,  $n=104$ ,  $P<0.01$ ), but the strength of the correlation differed between groups (Table 1). There was a significant difference in the median relative length of primary ten to primary nine between the groups based on the number of *c-myc* insertions (Kruskal-Wallis test:  $H_3=55.0$ ,  $P<0.01$ ). The relative length of primary ten to primary nine decreased with an increasing number of insertions in the *c-myc* gene (Fig. 2) and the three groups differed significantly from each other (Mann-Whitney  $U$ -test:  $U_{0-1}=28.5$ ,  $P<0.05$ ;  $U_{0-2}=0.00$ ,  $P<0.05$ ;  $U_{1-2}=148.0$ ,  $P<0.05$ ;  $n_0=11$ ,  $n_1=56$ ,  $n_2=37$ ; Bonferroni correction, Dunn-Šidák method; Sokal and Rohlf 1995).

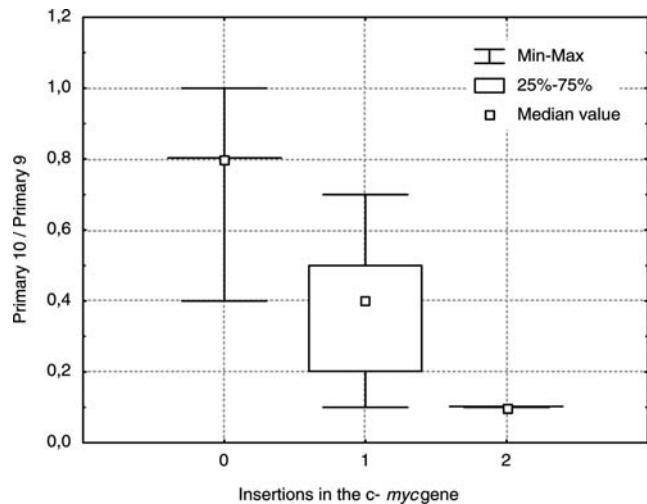
The length of primary ten and primary covert nine were also correlated (Spearman rank  $R_s=0.64$ ,  $n=104$ ,  $P<0.01$ ), but the strength of the correlation again differed between groups (Table 1). The median relative length of primary ten to primary covert nine differed between the groups based on the number of *c-myc* insertions (Kruskal-Wallis test:  $H_3=60.1$ ,  $P<0.01$ ). The relative length of primary ten to primary covert nine decreased with an increasing number of insertions in the *c-myc* gene (Fig. 3) and the three groups differed

**Table 1** Summary of data by group: average lengths of primaries nine and ten and primary covert nine. Mean and median relative length of primary ten (p10) compared to primary nine (p9) and primary covert nine (pc9), respectively. Spearman rank correlation coefficients for the relative lengths of primary ten compared to primary nine and primary covert nine (mean  $\pm$  standard deviation). Groups are defined by the number of insertions in the *c-myc* gene as reported by Ericson et al. (2000): 0, with no insertions (non-passernines, Suboscines, Meliphagoidea and Corvoidea, 11 species); 1, with one insertion (most Passerida, 56 species); and 2, with two insertions (clade Fringillidae sensu Sibley and Ahlquist 1990, plus Motacillidae, 37 species)

Group	No insertion	One insertion	Two insertions
Group code	0	1	2
Sample size	11	56	37
Mean length primary 9	$69.3 \pm 17.3$	$59.5 \pm 24.5$	$60.4 \pm 12.0$
Mean length primary 10	$54.2 \pm 18.4$	$24.4 \pm 20.0$	$5.9 \pm 1.6$
Mean length primary covert 9	$13.4 \pm 3.6$	$9.4 \pm 6.1$	$7.5 \pm 1.7$
Mean p10/p9 relationship	$0.79 \pm 0.2$	$0.38 \pm 0.2$	$0.1 \pm 0.0$
Median p10/p9	0.80	0.40	0.1
Mean p10/pc9 relationship	$4.1 \pm 0.8$	$2.5 \pm 1.1$	$0.79 \pm 0.1$
Median p10/pc9	4.1	2.7	0.8
Spearman rank corr. p10/p9	0.67*	0.39**	0.73**
Spearman rank corr. p10/pc9	0.75**	0.70**	0.80**

\* $P \leq 0.05$

\*\* $P < 0.01$

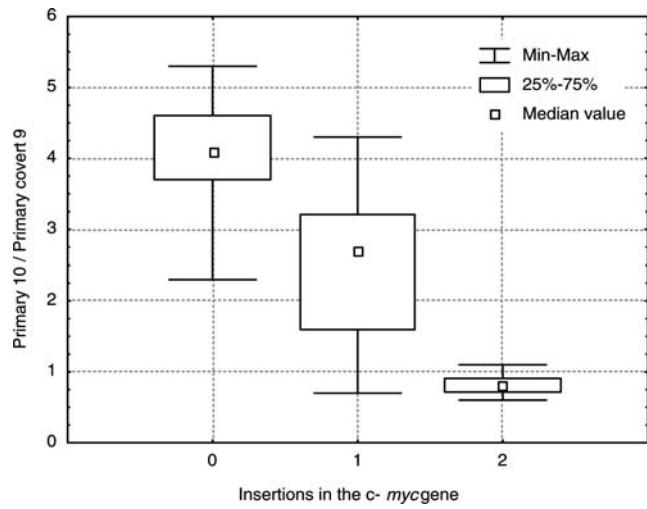


**Fig. 2** Relative length of primary ten to primary nine by group. Groups are defined by number of insertions in the *c-myc* gene as reported by Ericson et al. (2000): 0, no insertions (non-passernines, Suboscines, Meliphagoidea and Corvoidea, 11 species); 1, one insertion (most Passerida, 56 species); and 2, two insertions (clade Fringillidae sensu Sibley and Ahlquist 1990, plus Motacillidae, 37 species)

significantly from each other (Mann-Whitney  $U$ -test:  $U_{0-1}=71.5$ ,  $P<0.05$ ;  $U_{0-2}=0.00$ ,  $P<0.05$ ;  $U_{1-2}=92.5$ ,  $P<0.05$ ;  $n_0=11$ ,  $n_1=56$ ,  $n_2=37$ ; Bonferroni correction, Dunn-Šidák method; Sokal and Rohlf 1995).

### Discussion

Based on the material in the present study, ten primaries and ten primary coverts seem to be the ancestral condition within Passeriformes. Ten primary coverts were found in all specimens investigated belonging to the non-passernines and the suboscines. Among the oscines, both



**Fig. 3** Relative length of primary ten to primary covert nine by group. Group definitions as in Fig. 2

ten and nine primary coverts occurred, but nine was the most common state. The number of primary coverts is likely to influence the wing margin and is probably related to the number, and maybe the length of, the primary feathers. However, the ecological significance of this reduction, from ten to nine primary coverts in most oscine species remains to be investigated.

All passerines investigated had ten primaries, including the ‘nine-primaried’ species which, in light of the many re-definitions of the term ‘nine-primaried’ (‘functional’, ‘visible’, ‘obvious’ and so on), was expected. In fact, this was already concluded with convincing evidence in the nineteenth century (Jeffries 1881; Gadow 1888). Primary ten is short in many oscine families (Gadow 1888; Stegmann 1962; Raikow 1978; Svensson 1992), and Raikow (1978) and Groth (1998) suggested that the condition with a vestigial tenth primary is a derived state that has evolved several times. The present study can only corroborate this.

All species with two insertions in the *c-myc* gene had a primary ten short enough to be concealed by primary covert nine, but this was also the case for a few species with only one insertion in this gene as well as for some vireos lacking both insertions. The relative length of primary ten is thus of very limited systematic value.

The relative length of primary ten to primary nine does not differ very much between the ‘nine-primaried’ genus *Fringilla* (10%) and the ‘ten-primaried’ genus *Sylvia* (20–30%) (Electronic Appendix 1). The major difference between them is that *Fringilla* has primary ten hidden under primary covert nine whereas primary ten is readily discovered in *Sylvia*. Based on the present study, the term ‘nine-primaried’ might be interpreted as “with primary ten (more or less) concealed by primary covert nine”. This definition defines the character and includes all taxa historically denoted ‘nine-primaried’, but the term ‘nine-primaried’, by this definition, is too inclusive to be of more than very limited systematic value. To avoid confusion, the ‘New World nine-primaried oscines’ would gain from a new denotation.

Winkler and Leisler (1992) showed that a more pronounced length difference between primaries nine and ten was correlated with a longer migration distance for 25 sylviid species. Most of the ‘nine-primaried’ species are not considered long-distance migrants and migratory habits seems to vary more within this group (Cramp and Perrins 1994a, b) than the relative length of primary ten. Within the family Vireonidae, though, the relative length of primary ten to primary nine varied from 9–63% in this study ( $n=3$ ; Electronic Appendix 1; Pyle 1997) and a closer look at this group might reveal interesting selection pressures acting on wing morphology. The group shows heterogeneous migration patterns with both resident and long distance migrating species (Mountjoy and Leger 2001). If migration distance is an important evolutionary factor favouring a reduction of primary ten to a rudimentary state this might be possible to detect in the Vireonidae. This investigation, though,

has to await a comprehensive phylogeny of the family Vireonidae.

In conclusion, the term ‘nine-primaried’ has survived for over 160 years by changing value over time as well as changing the group of birds denoted. All passerines investigated had ten primary feathers and ten or nine primary coverts, ten primary coverts being the ancestral state. The taxa denoted ‘nine-primaried’ shared the character of having primary ten reduced in size to the degree that it is more or less concealed by primary covert nine. Today, ‘nine-primaried’ is a character state of very limited systematic value. The state is shared by taxa that are not each others’ closest relatives. With the growth of ecological phylogenetic studies (Brooks and McLennan 1991), the need for a terminology relevant to both systematic and ecological bird research will increase and the use of a term with such limited systematic value will reasonably fade away. Although two insertions in the *c-myc* gene do correlate with the length of primary feather ten, these insertions do not explain the distribution of the ‘nine-primaried’ state in a phylogenetic perspective.

## Zusammenfassung

Neun oder zehn Handschwingen bei Singvögeln? Die Evolution eines Konzeptes

Seit der ersten Hälfte des 19. Jahrhunderts wurde die Anzahl der Handschwingen im Vogelflügel als systematisches Merkmal verwendet. Im Lauf der Zeit änderte sich jedoch die Definition dessen, was als Handschwinge bezeichnet wurde. Die früher als Singvögel mit neun Handschwingen (Ammernverwandtschaft i.w.S.) bezeichneten Arten werden heute (korrekt) als Arten mit neun *funktionalen* Handschwingen bezeichnet. Ich untersuchte anhand von Museumsmaterial (104 Arten, 161 Individuen) die Grenze zwischen den Gruppen mit neun bzw. zehn funktionalen Handschwingen, um eine möglichst klare Trennung zu definieren und den systematischen Wert dieses Merkmals zu untersuchen. Alle Arten hatten 10 Handschwingen, doch war bei den Ammern- und Finkenverwandten (Fringillidae sensu Sibley and Ahlquist 1990) die 10. Handschwinge meist so stark reduziert, dass sie von der 9. Handdecke mehr oder weniger verdeckt war. Sperlingsvögel haben ursprünglich 10 Handdecken, doch wurde die Zahl bei den meisten Singvögeln auf 9 reduziert. Die korrekte Definition der historisch als “Singvögel mit neun Handschwingen” bezeichneten Artengruppe sollte lauten “Singvögel, deren 10. Handschwinge (weitgehend) von Handdecke 9 verdeckt wird”. Diese Artengruppe ist nicht monophyletisch, so dass dieses Merkmal von geringem systemischen Wert ist.

**Acknowledgements** The majority of the birds examined came from the Swedish Museum of Natural History, Stockholm but some birds were provided by Tovetorp Zoological Research Station, Stockholm University. I am grateful to Michael Diemer, Thord Fransson and Rinse Wassenaar for help with translation of the

German sources, and to Peter Mortensen, Ingrid Cederholm, Anders Hansson, Erik Åhlander and Olavi Grönwall for help with practical matters during my work in the bird collection at the National Museum of Natural History. I am also indebted to Per Ericson, Thord Fransson, Birgitta Tullberg and Walter Bock for valuable comments and support during the process of writing this manuscript. Finally, I would like to thank Ulf Johansson for several years of discussions around this topic.

## References

- Ashmole NP, Dorward DF, Stonehouse B (1961) Numbering of primaries. *Ibis* 103a:297–298
- Beecher WJ (1953) A phylogeny of the oscines. *Auk* 70:270–333
- Brooks DR, McLennan DA (1991) Phylogeny, ecology, and behaviour: a research program in comparative biology. University of Chicago Press, Chicago
- Campbell B, Lack E (1985) A dictionary of birds. Poyser, Calton
- Coues E (1890) Field and general ornithology. Macmillan, London
- Cramp S, Perrins CM (1994a) The Birds of the Western Palearctic, vol VIII. Oxford University Press, New York
- Cramp S, Perrins CM (1994b) The birds of the western Palearctic, vol. IX. Oxford University Press, New York
- Ericson PGP, Johansson US (2003) Phylogeny of Passerida (Aves: Passeriformes) based on nuclear and mitochondrial sequence data. *Mol Phyl Evol* 29:126–138
- Ericson PGP, Johansson US, Parsons TJ (2000) Major divisions in oscines revealed by insertions in the nuclear gene c-myc: a novel gene in avian phylogenetics. *Auk* 117:1069–1078
- Ericson PGP, Christidis L, Irestedt M, Norman JA (2002) Systematic affinities of the lyrebirds (Passeriformes: *Menura*), with a novel classification of the major groups of passerine birds. *Mol Phyl Evol* 25:53–62
- Gadow H (1888) Remarks on the numbers and the phylogenetic development of the remiges of birds. *Proc Zool Soc Lond* 1888:655–667
- Gill FB (1990) Ornithology. Freeman, New York
- Ginn HB, Melville DS (1983) Moult in Birds. BTO guide 19. British Trust for Ornithology, Tring
- Groth JG (1998) Molecular phylogenetics of finches and sparrows: consequences of character state removal in cytochrome b sequences. *Mol Phyl Evol* 10:377–390
- Jeffries JA (1881) On the number of primaries in birds. *Bull Nuttall Ornith Club* 6:156–163
- Jenni L, Winkler R (1994) Moult and ageing of European Passerines. Academic, London
- Klicka J, Johnson KP, Lanyon SM (2000) New world nine-primaried oscine relationships: constructing a mitochondrial DNA framework. *Auk* 117:321–336
- Lucas AM, Stettenheim PR (1972) Avian anatomy, integument. Agriculture handbook 362, Washington DC
- Mead C (1974) Bird ringing. BTO guide 16. British Trust for Ornithology, Tring
- Mountjoy DJ, Leger DW (2001) Vireo song repertoires and migratory distance: three sexual selection hypotheses fail to explain the correlation. *Behav Ecol* 12:98–102
- Nicholson F (1889) Sundevall's tentamen. Porter, London
- Nitzsch CL (1840) System der Pterylographie. Halle. (In German, for translation see Sclater 1867).
- Pettingill OS (1956) A laboratory and field manual of ornithology. Burgess, Minneapolis
- Pyle P (1997) Identification guide to North American birds, part I. Slate Creek Press, Bolinas
- Pyle P, Howell SNG, Yunick RP, DeSante DF (1987) Identification guide to North American Passerines. Slate Creek Press, Bolinas
- Raikow RJ (1978) Appendicular myology and relationships of the new world nine-primaried oscines (Aves: Passeriformes). *Bull Carnegie Mus Nat Hist* 7:1–43
- Raikow RJ, Bledsoe AH (2000) Phylogeny and evolution of the Passerine birds. *BioScience* 50:487–499
- Schuh RT (2000) Biological systematics: principles and applications. Cornell University, Ithaca
- Sclater PL (ed) (1867) Nitzsch's Pterylography. Hardwicke, London
- Sibley CG, Ahlquist JE (1990) Phylogeny and classification of birds. Yale University Press, New Haven
- Sibley CG, Monroe BL (1990) Distribution and taxonomy of birds of the world. Yale University Press, New Haven
- Sokal RR, Rohlf FJ (1995) Biometry, 3rd edn. Freeman, New York
- Spencer R (1972) The ringer's manual. British Trust for Ornithology, Tring
- Stegmann B (1962) Die verkümmerte distale Handschwinge des Vogelflügels. *J Ornithol* 103:50–85
- Stephan B (1970a) Über Vorkommen und Funktion des Remicle. *Beitr Vogelkd* 16:372–385
- Stephan B (1970b) Eutaxie, Diastataxie und andere Probleme der Befiederung des Vogelflügels. *Mitt Zool Mus Berlin* 46:339–437
- Stephan B (1997) Reduktion von Fingerkrallen, Phalangen und Handschwingen. *Mitt Zool Mus Berlin* 73(Suppl: Ann Orn 21):45–57
- Stresemann E (1927–1934) Handbuch der Zoologie. de Gruyter, Berlin
- Stresemann E (1963) Variations in the number of primaries. *Condor* 65:449–459
- Stresemann E, Stephan B (1968) Über das Remicle. *J Ornithol* 3:315–322
- Stresemann E, Stresemann V (1966) Die Mauser der Vögel. *J Ornithol* 107:Sonderheft
- Sundevall CJ (1872) Methodi naturalis avium disponendarum tentamem. Samson and Wallin, Stockholm. (In Latin, for translation see Nicholson 1889).
- Sundevall CJ (1886) On the wings of birds. *Ibis* 16: 389–457 (Translated from the original article in Swedish from 1843).
- Svensson L (1992) Identification Guide to European Passerines. Lars Svensson, Stockholm
- Van Tyne J, Berger AJ (1976) Fundamentals of ornithology, 2nd edn. Wiley, New York
- Wallace AR (1874) On the arrangement of the families constituting the Order Passeres. *Ibis* 4:406–416
- Winkler H, Leisler B (1992) On the ecomorphology of migrants. *Ibis* 134(suppl 1):21–28
- Witherby HF, Jourdain FCR, Ticehurst NF, Tucker BW (1938–1941) The handbook of British birds, vol I. Witherby, London
- Wray RS (1887) On some points in the morphology of the wings of birds. *Proc Zool Soc Lond* 1887:343–357
- Yuri T, Mindell D (2002) Molecular phylogenetic analysis of Fringillidae, “New World nine-primaried oscines” (Aves: Passeriformes). *Mol Phyl Evol* 23:229–243