

Phylogenetic Relationships in the Hierofalco Complex (Saker-, Gyr-, Lanner-, Laggar Falcon)

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ABSTRACT

Saker, Gyr, Lanner and Laggar represent large falcons that belong to the Hierofalco complex. We have amplified and sequenced the mitochondrial cytochrome b gene of all representatives of this clade, including several hundreds of Sakers from Kazakhstan and Mongolia. DNA data show that these taxa are very closely related. Within the Saker falcons 3 genetic lineages can be detected. No evidence could be obtained that the Altai falcon or the other Saker subspecies can be recognised at the DNA level. Within the Lanner falcon two lineages are evident that correspond to the subspecies *F. b. biarmicus* or *F. b. feldeggii*. The Australian *F. subniger* appears to be associated with the Hierofalco complex.

INTRODUCTION

Although Gyr, Lanner and Saker falcons are apparently closely related, they show a high degree of plumage polymorphism and have puzzled taxonomists for some time. O. Kleinschmidt (1901, 1958) and Meinertzhagen (1954) had placed them in a single species, *Falco hierofalco*, and distinguished *F. h. islandus* Brünn, *F. h. norvegicus* Schleg., *F. h. cherrug* Gray and *F. h. feldeggi* Schleg. *F. hierofalco* has been split since and today some authorities include *F. rusticolus*, *F. cherrug*, *F. biarmicus*, *F. jugger* and *F. mexicanus* in the subgenus Hierofalco and consider them as a superspecies (Amadon & Bull 1988; del Hoyo *et al.* 1994; Sibley & Monroe 1990; Cramp 1980). Within the species some subdivision, mostly concerning geographical forms or even morphs, has been considered (Niethammer 1938; Dementiev 1960; Weick 1980; Amadon & Bull 1988; del Hoyo *et al.* 1994; Sibley & Monroe 1990):

- *F. rusticolus* L.: Several subspecies; *F. r. rusticolus* (Scandinavia and northern Russia); *F. r. uralensis* Menzbier (Russia east of Petschora); *F. r. islandus* Brünnich (on Iceland); *F. r. candicans* Gmelin (on Greenland)
- *F. cherrug*: Several subspecies; *F. c. cherrug* Gray (E Europe, Russia to Altai mountains and Yenisey) and *F. c. milvipes* Jerdon (Siberia, Mongolia, China) (del Hoyo et al., 1994). Weick (1980) distinguishes: *F. c. cherrug*, *F. c. cyanopus* Thiemann (Bohemia to Wolga River), *F. c. saceroides* (Bianchy) (Kirghiz steppe Saja, Altai, Tarbatagai, NW Mongolia), *F. c. coatsi* Dementiev (Tian Shan west to NE Iran), *F. c. hendersoni* Hume (Pamir, Himalayas to Kansu), *F. c. milvipes* Jerdon (Mongolia, Manchuria). Weick includes *F. c. altaicus* in *F. c. milvipes* and also concludes that *F. c. saceroides*, *F. c. coatsi* and *F. c. hendersoni* could be colour morphs and would then be treated as *F. c. milvipes*.
- *F. altaicus* Menzbier: a dark coloured falcon of central Asia (Altai region, NW Mongolia, W China); treated also as a morph, either closer to *F. rusticolus* or *F. cherrug*. Ellis (1995) provided arguments that *F. altaicus* is a good species.
- *F. biarmicus*: 5 geographically defined subspecies; *F. b. biarmicus* Temminck (southern Africa), *F. b. abyssinicus* Neumann (western, central and eastern Africa), *F. b. tanypterus* (northern Africa, Israel, Iraq), *F. b. erlangeri* Kleinschmidt (NW Africa), *F. b. feldeggii* Schleg. (southern Italy, E to Armenia and Azerbaijan)
- *F. jugger* : monotypic (Indian subcontinent)
- *F. mexicanus*: (North America)

We have started to use molecular genetic techniques to elucidate the complex relationships in the Hierofalco complex. We mainly rely on nucleotide sequences of the mitochondrial cytochrome b gene that shows a good resolution on genus and even species level. Nucleotide sequences of the mitochondrial cytochrome b gene have already been employed to study the systematics and evolution of diurnal raptors (Griffiths 1997; Mindell 1997; from our laboratory: Groombridge *et al.* 2002, Kruckenhauser *et al.* 2003; Riesing *et al.* 2003; Seibold *et al.* 1993, 1996; Seibold & Helbig 1995, 1996; Helbig *et al.* 1994; Wink 1995, 1998, 2000; Wink & Seibold 1996; Wink & Sauer-Gürth 2000; Wink *et al.* 1996, 1998a,b;).

First and preliminary results have been published already on the phylogenetic relationships of Hierofalcons. The first publications based on the PhD thesis of I. Seibold (Seibold 1994) (Seibold *et al.* 1993; Wink 1995b, 1998; Wink & Seibold 1996; Wink *et al.* 1998) presented a mistaken picture, since nuclear copies of the cytochrome b genes had been sequenced by chance (in Hierofalcons but not for the other falcons), which placed the Hierofalcons at the base of the falcon tree. The mistake was identified when new PCR primers and new sequencing techniques were employed. Later phylogenies unequivocally showed that *F. rusticolus*, *F. biarmicus*, *F. cherrug* and *F. jugger* form a closely related complex that clusters as a sister group to the peregrines (Wink 2000; Wink & Sauer-Gürth 2000). *F. mexicanus* is not a member of this clade but shares ancestry with both peregrines and hierofalcons. A closer relationship with peregrines had been postulated by Schmutz & Oliphant (1987).

We have amplified and sequenced the mitochondrial cytochrome b gene of all representatives of this clade, including several hundreds of Sakers from Kazakhstan and Mongolia. Samples are included that were identified by scientists and falconers as "Altai falcons". Although the present study is still incomplete, since important samples from several populations/subspecies are still missing, a few conclusions can be drawn and a new hypothesis put forward on the phylogeny and taxonomy of this falcon complex.

MATERIAL AND METHODS

We have isolated total DNA from feather, blood or tissue samples (see Wink 2000) which had been kindly supplied by several colleagues (W. Bednarek, J. Bragin, F. Nittinger, A. Gamauf, R. Pfeffer, D. Ristow, J. Penhallurick, M. Heidenreich). The cytochrome b gene was amplified by PCR (primer sequences in Wink & Sauer-Gürth 2000) and sequenced by using AlfExpress (Amersham Pharmacia Biotech) or a capillary sequencer ABI 3100 (Applied Biosystems) instruments. Sequences of 1000 and more base pairs were aligned manually and analysed with the software packages PAUP* (Swofford, 2002) and MEGA2 (Kumar *et al.* 2001) (see Wink 2000; Wink & Sauer-Gürth 2000; Wink *et al.* 2002; Broders *et al.* 2003 for further details).

RESULTS AND DISCUSSION

Figure 1 shows a molecular phylogeny of the Hierofalco complex based on a reconstruction with Maximum Parsimony (NJ and ML lead to similar results; trees are not shown because of limited space). The overall topology shows that:

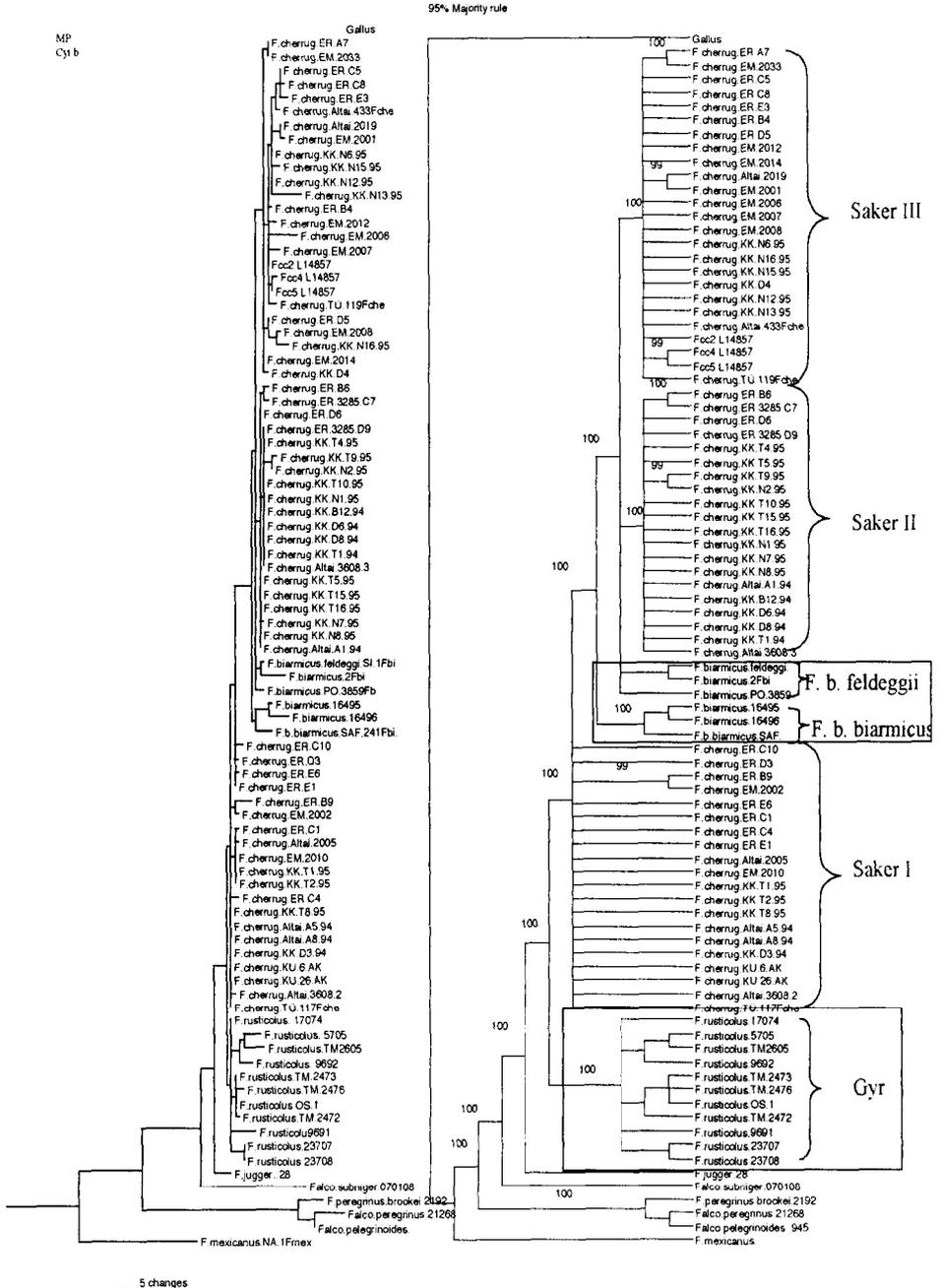
- The peregrines (*F. peregrinus*, *F. pelegrinoides*) form a sister group to the Hierofalcons that include *F. rusticolus*, *F. cherrug*, *F. biarmicus*, *F. jugger* and apparently *F. subniger*.
- *F. mexicanus* is not a member of the Hierofalco group *sensu stricto*; thus Schmutz & Oliphant (1987) were right in their conclusions that *F. mexicanus* is closer to *F. peregrinus* than to *F. rusticolus*.
- *F. subniger* from Australia clusters at the base of the Hierofalco clade; sequences of more birds are needed to corroborate this surprising finding. Since members of the Hierofalco complex were found on all continents except Australia, this finding would make sense.
- Members of the Hierofalco clade are closely related; the interspecific genetic distances between Gyr, Saker and Lanner falcons are in the range of 0.4 to 2.0%, indicating that they have evolved during the last 200,000 to 1 million years (assuming a 2% divergence = 1 million years; Wilson *et al.* 1987; Tarr & Fleischer 1993). This is the divergence range of young species; in some bird families taxa with such small genetic distances would be considered as subspecies. Thus the concept of O. Kleinschmidt (1901) or Meinertzhagen (1954) to lump these taxa into a single species *Falco hierofalco* had some merits and justification.

Our data allow some comments on the **intraspecific** genetic variation of *F. rusticolus*, *F. cherrug* and *F. biarmicus*:

- The Gyr falcons appear as a monophyletic group, often clustering at the base of the Gyr/Saker/Lanner assemblage but no birds from Siberia or North America have been studied so far.
- Lanner falcons are represented in our study by two subspecies: *F. b.*

biarmicus from southern Africa and *F. b. feldeggii* from southern Italy. Both groups are genetically divergent and differ by 1.0 to 1.4% (p-distance) indicating that they are genetically separated for almost 500,000 years.

Figure 1. Molecular phylogeny of hierofalcons inferred from nucleotide sequences of the cytochrome b gene
 Reconstruction with maximum parsimony; representation as a phylogram (left) and 95% major consensus cladogram.



The Sakers are most diverse. At least three well-supported clades (termed as Saker I, II & III) are evident, which do not show a good geographical correlation. The Saker III clade, for example, comprises birds from Hungary (i.e. *F. c. cherrug*) and also birds from Kazakhstan and Mongolia (i. e. *F. c. milvipes*). Saker I and Saker II clades also contain birds that would be attributed to either *F. c. cherrug* or *F. c. milvipes*. Thus a clear geographical correlation, as seen in the Lanner, is not evident in the Saker Falcon. Sakers, that were classified as "Altai falcons" because of their dark plumage, are found in all three Saker clades, indicating that they are morphs and not valid subspecies or even species (*F. altaicus*). A similar conclusion can be found already in Sibley & Monroe (1990) or del Hoyo *et al.*, (1994) (but see Ellis 1995).

In most reconstructions, the Saker does not cluster as a monophylum, but rather as a paraphyletic group. As can be seen in Fig. 1, the Lanners cluster as a sister group to Saker II and III.

How to explain the genetic and morphological diversity in Sakers? Since the haplotypes do not correlate with populations we speculate that the clades are the result of old hybridisations (not recent; according to the genetic distances found we have to think in terms of 100,000 to 200,000 years), of an ancient Saker with Gyr and Lanner falcons. The plumage polymorphism seen in Sakers would also be a plausible consequence of such early hybridisations. Other genetic markers, such as microsatellite analyses, are necessary to elucidate and corroborate this hypothesis. Gyr and Saker falcons can be easily hybridised in captivity; since several of these hybrids have already escaped to the wild, the future situation might become even more complicated if these birds start to interbreed with wild birds.

In addition, genomic fingerprinting with ISSR-PCR (results not shown; for the method see Wink *et al.* 2000; Wink 2000), which usually shows significant differences between species, exhibits only few differences between the Saker and Gyr falcons, thus confirming their close relatedness.

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