

Department of Evolutionary Biology, Czechoslovak Academy of Sciences, Praha,  
and Department of Paleontology, Faculty of Natural Sciences, Charles University,  
Praha

## REVIEW OF THE TERTIARY WATERFOWL (AVES: ANSERIDAE) OF ASIA

Jiří MLÍKOVSKÝ and Petr ŠVEC

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**Abstract.** The types of 10 waterfowl species described from the Tertiary of Asia were restudied. The following systematic changes are proposed: *Anas oligocaena* becomes *Dendrochen oligocaena*, *Cygnus pristinus* is synonym of *Cygnus olor*, *Anser liskunae* becomes *Olor liskunae*, *Heterochen vicinus* becomes *Anser vicinus* (species status uncertain), *Anas soporata* becomes *Dendrocygna soporata*. Two species were excluded from Anseridae: *Cygnopterus lambrechtii* is synonym of *Agnopterus turgaiensis* (Phoenicopteridae), and *Limicorallus saiensis* becomes *Phalacrocorax saiensis* (Phalacrocoracidae).

In addition, *Sinanas diatomas* from the Miocene of China, the type of which we could not examine, was found to be a meaningless name until redescription.

### INTRODUCTION

More than 160 nominal fossil species of the waterfowl (order Anseriformes Brisson 1760, family Anseridae Vigors 1825) have been described so far (see Mlíkovský 1983 for their review), and they begin slowly to build a good factual basis for the reconstruction of the waterfowl phylogeny. However, but a small fraction of those nominal species represent species which have really occurred in nature and which may be used in the respective phylogenetic reconstruction. The uncertainty which nominal species represents a real one and which does not makes it necessary to write and to publish papers which are considered destructive, not constructive, by many paleontologists, i. e. papers which contain only revisions of formerly described species and no, or nearly no, descriptions of new material. However, there are only these papers which make the so-called fossil evidence really valuable to science in general and to evolutionary biology and systematics in particular.

In the present paper we continue the modern revision of fossil waterfowl species started independently by Olson (1977a, b, Olson and Feduccia 1980), Van Tets and Rich (1980), Mlíkovský (1982a, b, 1983), and Cheneval (1983). We selected for this purpose the waterfowl species described from the Cenozoic of Asia, in view of the fact that the Cenozoic Asia still belongs to the least known areas in which the waterfowl evolution occurred.

Only 11 fossil waterfowl (or supposedly waterfowl) species were described from the Cenozoic of Asia so far, all of them from the Tertiary. They include 4 species from the Oligocene of Kazakhstan (*Anas oligocaena* Tugarinov 1940, *Cygnavus formosus* Kuročkin 1968, *Cygnopterus lambrechtii* Kuročkin 1968, and *Limicorallus saiensis* Kuročkin 1968), one species from the Miocene of

China (*Sinanas diatomas* Yeh 1980), and 6 species from the Pliocene of Mongolia (*Cygnus pristinus* Kuročkin 1971, *Anser devjatkini* Kuročkin 1971, *Anser liskunae* Kuročkin 1976, *Heterochen vicinus* Kuročkin 1976, *Anas soporata* Kuročkin 1976, and *Aythya spatiosa* Kuročkin 1976). We were able to see and to revise the types of all of them but *Sinanas diatomas* Yeh 1980.

In addition, 8 waterfowl species and subspecies were described from Oligocene to late Pleistocene deposits of Azerbaidzhan and Gruzia in the Causasus region, including *Guguschia nailiae* Aslanova and Burčak-Abramovič 1968, *Anser eldaricus* Burčak-Abramovič and Gadžiev 1978, *Anser udabnensis* Burčak-Abramovič 1957, *Anas apscheronica* Burčak-Abramovič 1958, *Anser azerbaidshanicus* Serebrovskij 1940, *Cygnus olor bergmanni* Serebrovskij 1941, *Anas platyrhynchos palaeoboschas* Serebrovskij 1941, and *Aythya marila asphaltica* Serebrovskij 1941. Although this region is included in Asia by contemporary geographers, Caucasus lays at the border between Europe and Asia and it seems appropriate to treat Caucasian fossils separately from proper Asiatic forms.

In the following we present our critical revision of the waterfowl species described from the Asia proper. The species are arranged according to their systematic position they acquired after our revision. The classification follows Delacour (1954, 1956, 1959) and Woolfenden (1961).

We are deeply indebted to Dr. Evgenij N. Kuročkin (Institute of Paleontology, Academy of Sciences of the USSR, Moscow; PIN AN SSSR) for his kind permission to examine the fossil specimens under his care and to use his comparative collection of Recent birds. We are also very grateful to Aleksandr A. Karkhu (PIN AN SSSR, Moscow) for providing valuable assistance during our visits in Moscow in August 1982 (Jiří Mlíkovský, Petr Švec) and March/April 1983 (Petr Švec). For comparisons we used especially the rich osteological collection of the waterfowl in the PIN AN SSSR in Moscow, which contains representatives of nearly all Recent waterfowl genera. In addition, Jiří Mlíkovský profited during the preparation of this paper from his studies of both Recent and fossil waterfowl skeletons in the collections of the Institute of Zoology, Martin Luther University, Halle (Saale), GDR (R. Piechocki), Museum of Zoology, Humboldt University, Berlin, GDR (K. Fischer, G. Mauersberger, B. Stephan), Institute of Zoology, Academy of Sciences of the USSR, Leningrad, USSR (L. V. Firsova, V. M. Loskot, S. V. Vinter), Anthropos Institute, Moravian Museum, Brno, Czechoslovakia (J. Jelínek, L. Seitzl), and Natural History Museum, Budapest, Hungary (D. Jánossy). He appreciates the help of all of the named persons.

Anatomical terminology used in this paper follows Baumel et al. (1979).

## RESULTS AND DISCUSSION

Family: Anseridae Vigors, 1825

Subfamily: incertae sedis

Genus: *Sinanas* Yeh, 1980

*Sinanas diatomas* Yeh, 1980

*Sinanas diatomas* Yeh, 1980: 116, pl. 1

Holotype: incomplete skeleton, location unknown (? Shandong Museum), probably without number.

Age: middle Miocene, Shanwan series

Locality: China, Shandong Province, Linqu

Discussion: We were not able to study the holotype of *Sinanas diatomas*, but we include a brief discussion of it in our review of the Tertiary

waterfowl of Asia for it is complete. Yeh (1980: 124) restricted his diagnosis and description of this species to an assurance that *Sinanas diatomas* is similar to the genus *Anas* Linné, 1758, but differs from it "by its stoutness appearing in bones of limbs". However, robustness of limb bones is typical especially for Cairinini and partly for Aythyini among the waterfowl (Woolfenden 1961; pers. obs.), i. e. for tribes with which Yeh (1980) compared his *Sinanas diatomas* not at all. Other characters listed by Yeh (1980) are of no importance for the identification of *Sinanas diatomas*. For example, he writes "Tarsometatarsus short, only 40 mm in length". Only in central Europe, 13 waterfowl species are living today which have equally short, or even shorter tarsometatarsi (cf. data in Woelfle 1967).

Hence, only the figure saves *Sinanas diatomas* from being nomen nudum. In any case, however, it is a meaningless name until its holotype is located and restudied.

Subfamily: Anserinae Vigors, 1825

Tribus: Dendrocygnini Reichenbach, 1852

Genus: *Dendrochen* Miller, 1944

*Dendrochen oligocaena* (Tugarinov, 1940), combinatio nova

*Anas oligocaena* Tugarinov, 1940b: 314, Fig. 1

Lectotype: distal end of right humerus, PIN 210—745 (here selected; see below). Paralectotypes: distal end of right ulna, PIN 210—746; fragmentary right radius, PIN 210—744; proximal end of left carpometacarpus, PIN 210—747.

Age: late Oligocene, Lake Aral beds

Locality: western Kazakhstan, Agispe

Discussion: Because it cannot be sure that Tugarinov's (1940b) syntypes of *Anas oligocaena* belong all to the same species, or even individual, we select here the distal end of right humerus, PIN 210—745, which is most diagnostic among the syntypes, as the lectotype of *Anas oligocaena* Tugarinov, 1940.

The lectotype humerus fragment differs markedly from the same element of Anatini in having the width of the space between condylus dorsalis and insertio ligamenti collaterale ventrale in relation to this insertio's width narrower. Because this character is exclusive for Dendrocygnini among the Anseriformes (cf. Woolfenden 1961), we transfer "*Anas*" *oligocaena* from Anatini to the latter tribe. This conclusion is supported also by the morphology of the paralectotype carpometacarpus which differs from Anatini and agrees with Dendrocygnini in having: (1) lower portion of the external rim of trochlea carpalis slightly notched, and (2) fovea origini m. extensoris confined to the tip of the processus extensorius.

Three genera are commonly recognized within Dendrocygnini: *Dendrocygna* Swainson, 1837, *Dendrochen* Miller, 1944, and more recently also *Thalassornis* Eyton, 1838 (cf. Kear 1967, Johnsgard 1967, Raikow 1971, Brush 1976). We compared "*Anas*" *oligocaena* with two Recent representatives of the genus *Dendrocygna*, viz. *D. javanica* (Horsfield, 1821) and *D. bicolor* (Vieillot, 1816), from which it differs in having the fossa m. brachialis broader and the internal ridge bordering it consequently narrower. In both these characters "*Anas*" *oligocaena* agrees with the fossil dendrocygnine genus *Dendrochen* (see Miller 1944 for its description). No skeleton of *Thalassor-*

*nis leuconotus* Eyton, 1838, the only living member of the last known genus of Dendrocygnini, was available for comparison, but because *Thalassornis* differs from *Dendrochen* in many respects (J. Cheneval, in litt.), it seems highly improbable that "*Anas*" *oligocaena* can be included in *Thalassornis*. In addition, because "*Anas*" *blanchardi* Milne-Edwards, 1863, "*Anas*" *nator* Milne-Edwards, 1867, and "*Anas*" *consobrina* Milne-Edwards, 1867, all from the Aquitanian of France, are closely related species which belong in Dendrocygnini (Cheneval 1983, Mlíkovský 1983), we compared "*Anas*" *oligocaena* with these species, too (materials from the Museum of Zoology, Humboldt University, Berlin, GDR), although their generic status within Dendrocygnini remains uncertain (Mlíkovský unpubl.). They differ clearly from "*Anas*" *oligocaena* in having the space between the condylus dorsalis and the insertio ligamenti collaterale ventrale in relation to this insertio's width broader.

Hence, it is evident from these comparisons that *Anas oligocaena* should be best transferred in the genus *Dendrochen*, which was known only from the early Miocene of South Dakota so far (Miller 1944). That also the three waterfowl species from the French Aquitanian belong in *Dendrochen* as suggested by Cheneval (1983) is improbable (Mlíkovský, unpubl.).

Genus: *Dendrocygna* Swainson, 1837

*Dendrocygna saporata* (Kuročkin, 1976), combinatio nova

*Anas saporata* Kuročkin, 1976: 61, Fig. 8

Holotype: proximal end of right coracoid, PIN 2614—95

Age: middle Pliocene, Chirgiz-Nur Formation

Locality: western Mongolia, Šargain-Gobi

Discussion: The proximal end of coracoid on which *Anas saporata* has been based differs according to our observations on the same element of several Recent representatives of this genus from *Anas* Linné, 1758 in having: (1) notch in the facies articularis clavicularis nearly absent, (2) medial margin of this facies sharp and extended over the canalis triosseus, (3) medial margin of the head deeply undercut by sulcus m. supracoracoidei, and (4) ventromedial margin of this sulcus sharp. Such a character complex is quite typical for Dendrocygnini (see also Woolfenden 1961), indicating thus that "*Anas*" *saporata* should be transferred in that tribe.

Within Dendrocygnini, we were unfortunately not able to compare the coracoid fragment under discussion with the same element of *Dendrochen* (where it is unknown so far) and *Thalassornis*, but until this comparison will be possible we suggest that "*Anas*" *saporata* should be best placed in the genus *Dendrocygna* (sensu lato). The tentative exclusion of *Dendrochen* is based on its stratigraphic occurrence (Oligocene through early Miocene; Mlíkovský 1983), and that of *Thalassornis* on its biogeographic occurrence (Recently only in the Afrotropical region; Brown et al. 1982).

Tribus: Anserini Brisson, 1760

Genus: *Cygnavus* Lambrecht, 1931

*Cygnavus formosus* Kuročkin, 1968

*Cygnavus formosus* Kuročkin, 1968: 95, Fig. 2

Holotype: distal end of right tibiotarsus, PIN 2432—36

Age: early Oligocene, Aksyriskian Formation

Locality: eastern Kazakhstan, Žongiz-Šoki

Discussion: Our reexamination of the holotype tibiotarsus fragment confirmed wholly the description given by Kuročkin (1968: 94—96). An additional difference between *Cygnavus* on the one hand and *Cygnus* Bechstein, 1803 and *Olor* Wagler, 1832 on the other one can be noted, namely that incisura intercondylaris is markedly narrower in *Cygnavus*. Hence, we agree with Kuročkin's (1968) opinion that *Cygnavus formosus* is a primitive anserid closely resembling Recent swans (*Cygnus* and *Olor*) in its morphology, and that it is quite probably congeneric with *Cygnavus senckenbergi* Lam-brecht, 1931, the only previously known representative of the genus *Cygnavus*.

Genus: *Olor* Wagler, 1832

Note: We include here substantiation of the separation of the genera *Olor* Wagler, 1832 and *Cygnus* Bechstein, 1803, because they are repeatedly lumped in the common genus *Cygnus* by some recent authors (e. g., von Boetticher 1952, Delacour 1954, Johnsgard 1978, 1979, Kolbe 1984). However, all of these authors based their classification on external characters only, and although they were certainly aware of some other differences between *Olor* and *Cygnus*, they ignored them simply in this case. On the other hand, authors studying internal morphology of swans (e. g., Berndt 1938, Howard 1946, Wetmore 1951, Woolfenden 1961), their behavior (Johnsgard 1960, Petzold 1964), and external morphology of downy cygnets (Nelson 1976) found significant differences between *Olor* and *Cygnus* and suggested then usually that *Olor* should be established as a valid unit. We consider the latter approach correct (cf. also Mlíkovský 1983) and follow it, hence, throughout the present paper.

*Olor liskunae* (Kuročkin, 1976), combinatio nova

*Anser liskunae* Kuročkin, 1976: 59, Fig. 6

Holotype: distal end of left humerus, PIN 2614—105

Age: middle Pliocene, Chirgiz-Nur Formation

Locality: western Mongolia, Dzabchan

Discussion: According to our comparison of *Anser liskunae* with the Recent representatives of the genera *Anser* Brisson, 1760, *Branta* Scopoli, 1769, *Cygnus* Bechstein, 1803, and *Olor* Wagler, 1832, its holotype humerus fragment shows clear differences from the humeri of both *Anser* and *Branta* as follows: (1) fossa olecrani not divided from the shaft by a conspicuous rim, (2) fossa olecrani more shallow and wide, (3) foramina pneumatica in the fossa olecrani present, and (4) the whole extremitas distalis more robust in shape. In all of these characters *Anser liskunae* agrees with Recent swans (*Cygnus* and *Olor*). However, in having the distance between the insertio ligamenti collaterale ventrale and condylus dorsalis small, it differs from *Cygnus* and agrees with *Olor*.

Within the genus *Olor*, *Olor liskunae* seems to be smaller than *Olor bewickii* (Yarrell, 1830), the hitherto smallest known representative of the genus: width of the distal end of humerus is 28.2 mm (holotype; not 27.2 mm as printed in Kuročkin 1976: 59) and 26.6 mm (referred specimen), respectively, in *Olor liskunae*, while it is 28.8—36.6 mm in 31 adult males and females of the Recent *Olor bewickii* (Bacher 1967). We suggest, thus, that "*Anser*"

*liskunae* represents a small, distinct *Olor* species, *Olor liskunae* (Kuročkin 1976).

### Genus *Cygnus* Bechstein, 1803

#### *Cygnus olor* (Gmelin, 1789)

*Cygnus pristinus* Kuročkin, 1971: 60, Fig. 2 = *Anas* (= *Cygnus*) *olor* Gmelin, 1789, syn. nov.

**Holotype** (of *Cygnus pristinus*): distal fragment of left radius, PIN 2614—25

**Age**: middle Pliocene, Chirgiz-Nur Formation

**Locality**: western Mongolia, Chung-Kure

**Discussion**: Kuročkin (1971) considered his *Cygnus pristinus* to represent an intermediate form between *Cygnus* Bechstein, 1803 and *Olor* Wagler, 1832, which he held for congeneric (cf. our above comments on this problem). Although the distal part of radius on which *Cygnus pristinus* is based is not a very diagnostic element in the waterfowl (and in birds in general), the radii of *Cygnus* differ from those of *Olor* in having: (1) the dorsal margin of extremitas distalis very narrow and rather sharp (this margin is more rounded in *Olor*), and (2) the most distal point of the dorsal margin building a blunt tip (this tip is more pointed in *Olor*). *Cygnus pristinus* agrees with *Cygnus* (sensu stricto) in both these characters, indicating thus that it is a true member of this genus (sensu stricto) and not a link between *Cygnus* and *Olor* as suggested by Kuročkin (1971).

Within the genus *Cygnus*, Kuročkin (1971) calls only one difference between *Cygnus pristinus* and *Cygnus olor*, namely the presence of a broad sulcus on the margo dorsalis extremittatis distalis radii in *Cygnus pristinus*. This structure is, however, well known in some specimens of *Cygnus olor*, too (Bacher 1967, Mlíkovský pers. obs.), and is therefore evidently assignable to individual variability. There are also no biometrical differences between *Cygnus pristinus* and *Cygnus olor*: dorsoventral width of the extremitas distalis radii measures 16.5 mm in *Cygnus pristinus* (holotype; pers. obs.) and 14.2—17.6 mm in 50 adult males and females of the Recent *Cygnus olor* (Bacher 1967). Hence, we propose to synonymize *Cygnus pristinus* Kuročkin, 1971 with the Recent *Cygnus olor* (Gmelin, 1789), which is the only known Recent or fossil representative of the genus *Cygnus* sensu stricto in Palearctic (cf. Vaurie 1965, Hilprecht 1970, Ogilvie 1972, Johnsgard 1978, Kolbe 1984), which still locally occurs in Mongolia (Vaurie 1964, Piechocki 1968, Piechocki et al. 1981), and which is a common breeder in the nearby Kazakhstan (Dolgušin 1960, Krivonosov 1981).

### Genus: *Anser* Brisson, 1760

#### *Anser devjatkini* Kuročkin, 1971

*Anser devjatkini* Kuročkin, 1971: 64, Fig. 3

**Holotype**: distal end of left tibiotarsus, PIN 2614—28

**Age**: middle Pliocene, Chirgiz-Nur Formation

**Locality**: western Mongolia, Chirgiz-Nur-2

**Discussion**: The results of our reexamination of the holotype tibiotarsus fragment are in full agreement with Kuročkin's (1971) original description.

*Anser vicinus* (Kuročkin, 1976), combinatio nova

*Heterochen vicinus* Kuročkin, 1976: 60, Fig. 7

Holotype: proximal part of right tarsometatarsus, PIN 2614—110

Age: middle Pliocene, Chirgiz-Nur Formation

Locality: western Mongolia, Chirgiz-Nur-2

Discussion: The holotype tarsometatarsus fragment of *Heterochen vicinus* differs from the same element of *Heterochen pratensis* Short, 1970, the type species of the genus *Heterochen* Short, 1970 and its only formerly known representative, in having: (1) fossa infracotylaris dorsalis deep, and (2) crista medialis hypotarsi with a small, but distinct, distad oriented tip (see Short 1970 for the description of *Heterochen pratensis*). In its robustness and a relatively very short hypotarsus, *Heterochen vicinus* most closely resembles the Recent *Anser fabalis* (Latham, 1787), sensu lato, while it differs from other Anserini just by this combination of characters.

We are, hence, convinced that "*Heterochen*" *vicinus* is actually a goose from the *Anser fabalis* complex. We are, however, not able to decide at present with any certainty the exact taxonomic relation between *Anser vicinus* and *Anser fabalis* for the following reasons: First, the systematics of the Recent *Anser fabalis* complex is far from understood (cf., e. g., Alferaki 1904, 1907, Buturlin 1907, 1908, 1934, Peters 1931, Grote 1934, Dement'ev 1936, Tugarinov 1941: 144—150, Hachler 1944a, b, Johansen 1945, Coombes 1947a, b, 1951, Delacour 1951, 1954, Vaurie 1965, Bauer and Glutz von Blotzheim 1968, C. S. Rose-laar in Cramp and Simmons 1977, Johnsgard 1979, Van Impe 1980, 1981). Second, we compared *Anser vicinus* with only two specimens of *Anser fabalis* from the Kuročkin's collection in Moscow, and we found two differences between these two tarsometatarsi and the holotype tarsometatarsus of *Anser vicinus*, namely greater robustness and larger foramina vascularia proximalia in *Anser vicinus*. However, both these differences could be well assigned to individual or other intraspecific variability, when larger series of *Anser fabalis* could be compared. Third, there are still serious conceptual difficulties in recognizing fossil species (e. g., Tintant 1980, Mlíkovský et al. 1985). Fourth, it is possible that *Anser vicinus* is actually a valid species, but then it may be synonymous with *Anser devjatkini* Kuročkin, 1971 which was described from the same horizon and the same locality as *Anser vicinus*, and whose systematic position within the genus *Anser* remains uncertain, but which could not be compared with *Anser vicinus* due to the lack of knowledge of comparable elements representing these two species.

Hence, until a complete revision of waterfowl materials from the middle Pliocene of Mongolia is made, and until taxonomic problems with the Recent *Anser fabalis* are satisfactorily solved and its osteological peculiarities studied, we preliminarily leave *Anser vicinus* (Kuročkin, 1976) as a valid species in the *Anser fabalis* complex of the genus *Anser* Brisson, 1760.

Subfamily: Anatinae Vigors, 1825

Tribus: Aythyini Delacour and Mayr, 1945

Genus: *Aythya* Boie, 1822

*Aythya spatiosa* Kuročkin, 1976

*Aythya spatiosa* Kuročkin, 1976: 62, Fig. 9

Holotype: distal end of right femur, PIN 2614—81

Age : middle Pliocene, Chirgiz-Nur Formation

Locality : western Mongolia, Čono-Chariach

Discussion : Although a deep fossa poplitea on which Kuročkin (1976) based his tribal determination of the species under discussion is characteristic not only for Aythyini, but also for, e. g., Dendrocygnini or Somateriini (pers. obs.), we agree that *Aythya spatiosa* is a member of Aythyini because of the lateral position of its trochlea fibularis. We are, however, not quite sure about the position of *Aythya spatiosa* within Aythyini, but because it more closely resembles *Aythya* Boie, 1822 than *Netta* Kaup, 1829 in its general shape, we have no reason to doubt Kuročkin's (1976) original allocation of *Aythya spatiosa* in the genus *Aythya*.

We are also presently not able to discuss with a sufficient insight the validity and position of this species within the genus *Aythya*. Hence, until a detailed osteological revision of the genus *Aythya*, or even better of the whole tribus Aythyini, is made, we suggest to leave *Aythya spatiosa* as a valid species in this genus.

#### Species non-Anseriformes

"*Agnopterus*" *turgaiensis* Tugarinov, 1940

*Cygnopterus lambrechtii* Kuročkin, 1968: 93, Fig. 1 = *Agnopterus turgaiensis* Tugarinov, 1940b, syn. nov.

Holotype (of *Cygnopterus lambrechtii*): distal end of left humerus, PIN 1399—123

Age : middle Oligocene, Indricotherium beds

Locality : central Kazakhstan, Kur-Saj

Discussion : The genus *Cygnopterus* in which Kuročkin (1968) placed his new species under discussion was originally erected by Lambrecht (1931: 1) for *Sula affinis* Van Beneden, 1883 from the Rupelian (middle Oligocene) of Flanders, Belge. In the same paper Lambrecht (1931) suggested that *Cygnopterus* has anseriform affinities. Mlíkovský (1983) revised Lambrecht's (1931) redescription of this species and excluded it from Anseriformes leaving it preliminarily in Aves incertae sedis. A similar fate has *Cygnopterus lambrechtii*. Its holotype humerus fragment lays in many characters well out of the range of morphological variability of the Anseriformes (cf. Woolfenden 1961; pers. obs.) and is decidedly not anseriform. It differs from Anseriformes and agrees with Phoenicopteridae (pers. obs. on the genus *Phoenicopterus* Linné, 1758) in having: (1) impressio m. brachialis located in the length axis of the shaft, (2) tuberculum supracondylare ventrale absent, (3) cranial surface of the distal end immediately proximally to the condylus ventralis conspicuously deepened, (4) condylus ventralis oval in shape, and (5) epicondylus dorsalis located more proximally.

The only representative of the Phoenicopteridae known so far from the Paleogene of Asia is *Agnopterus turgaiensis* Tugarinov, 1940 which was described from the same horizon as *Cygnopterus lambrechtii* and from a locality which is only about 10 km distant from the Kur-Saj gorge, the type locality of *Cygnopterus lambrechtii* (A. A. Karkhu, pers. comm.). *Agnopterus turgaiensis* was described on the basis of a distal part of tibiotarsus, so that it is not directly comparable with *Cygnopterus lambrechtii*. However, as judged from the proportions of Recent flamingos (pers. obs.), both *Cygnopterus lambrechtii* and *Agnopterus turgaiensis* were birds of approximately the same size. Because we consider the co-occurrence of two similar-sized flamingo species rather



improbable, we tentatively synonymize here *Cygnopterus lambrechtii* Kuročkin, 1968 with *Agnopterus turgaiensis* Tugarinov, 1940.

A problem poses the generic name of this species. *Agnopterus* was based upon *Agnopterus laurillardii* Milne-Edwards, 1868 from the late Eocene of France, which was recently found to be non-phoenicopterid by Olson and Feduccia (1980). They concluded at the same time that *Agnopterus turgaiensis* represents a true flamingo species, a point of view with which we agree. Hence, *Agnopterus turgaiensis* cannot be included in the genus *Agnopterus*, and it should be either included in another flamingo genus known so far, or placed in a new, own genus. Currently, at least 6 fossil and Recent flamingo genera are recognized, including *Juncitarsus* Olson and Feduccia, 1980, *Leakeyornis* Rich and Walker, 1983, *Palaelodus* Milne-Edwards, 1863 (incl. *Megapalaelodus* Miller, 1944), *Phoeniconotius* Miller, 1963, *Ocyplanus* DeVis, 1906, *Xenorhynchopsis* DeVis, 1906, and *Phoenicopterus* Linné, 1758. We were not able to study the problem of the systematic position of "*Agnopterus*" *turgaiensis* within Phoenicopteridae (sensu lato) in any detail, and we leave, thus, the problem of its generic allocation open.

*Phalacrocorax saiensis* (Kuročkin, 1968), combinatio nova

*Limicorallus saiensis* Kuročkin, 1968: 99, Fig. 4

Holotype: distal end of left humerus, PIN 1442—262

Age: middle Oligocene, Indricotherium beds

Locality: central Kazakhstan, Myn-Saj

Discussion: This species was originally described by Kuročkin (1968) as a member of Rallidae, but Cracraft (1973: 39) suggested after examining Kuročkin's original figure of its holotype the re-allocation of *Limicorallus saiensis* in Anseridae. The figure of the holotype published in Kuročkin (1968: 100, Fig. 4) is, indeed, very suggestive of Anseridae, but our re-examination of the actual holotype revealed that the figure is not very accurate and that *Limicorallus saiensis* belongs neither in Rallidae nor in Anseridae.

In its general shape, the holotype humerus fragment agrees closely with the same element of small representatives of the family Phalacrocoracidae (cf. Ono 1980). Particularly it differs from Anseridae and agrees with Phalacrocoracidae in having: (1) tuberculum supracondylare ventrale oval, proximally pointed and ventrally inclined, (2) fossa m. brachialis very long and relatively narrow, and (3) a distinct fossa located proximally to the condylus ventralis and condylus dorsalis present.

All true cormorants (Phalacrocoracidae) are usually united in one genus only, *Phalacrocorax* Brisson, 1760 (e. g., Peters 1931; cf. also Brodkorb 1963). We agree with this opinion, and synonymize here consequently the genus *Limicorallus* Kuročkin, 1968 (type species: *L. saiensis* Kuročkin, 1968) with *Phalacrocorax* Brisson, 1760. *Actiornis* Lydekker, 1891, another genus listed by Brodkorb (1963) in Phalacrocoracidae is actually no cormorant, although its relationships remain unclear (Harrison and Walker 1976, Olson 1981), and *Pliocarbo* Tugarinov, 1940a, the last cormorant genus recognized by Brodkorb (1963) is known only from a tarsometatarsus and needs re-examination before it can be used in future systematic work.

Within the genus *Phalacrocorax*, *Phalacrocorax saiensis* seems to represent a valid species. Among other Oligocene and early Miocene cormorant species, *P. marinavis* Shufeldt, 1915 from the early Miocene of Oregon, *P. littoralis*

Milne-Edwards, 1863 from the Aquitanian of France (see also Paris 1912) and West Germany (Lambrecht 1933), and *P. subvolans* Brodkorb, 1956 from the early Miocene of Oregon are all much larger than *Phalacrocorax saiensis*, and also *P. miocaenus* Milne-Edwards, 1867 from the Aquitanian of France and Czechoslovakia (Švec, unpubl.), which was recently transferred in its own genus *Nectornis* by Cheneval (1984), and *P. anatolicus* Mourer-Chauviré, 1978 from the early or middle Miocene of Turkey, although smaller than the previously listed cormorant species, are still sufficiently larger than *Phalacrocorax saiensis* to leave no doubt on its species identity: width of the distal end of humerus is 11.0 mm in *Phalacrocorax miocaenus* (Milne-Edwards, 1867), while it is only 8.6 mm in *Phalacrocorax saiensis* (Kuročkin, 1968). *Phalacrocorax anatolicus* is said to be somewhat larger than *Phalacrocorax miocaenus* (Mourer-Chauviré 1978).

We are presently not able to discuss, or even to solve, the question of the relationships of *Phalacrocorax saiensis* within the genus *Phalacrocorax*. If one would divide the genus *Phalacrocorax* in two or more smaller genera as suggested for the Recent cormorants by, e. g., Wolters (1975—1982) and Van Tets (1976), and for fossil ones by Lambrecht (1933) (but see Wetmore 1935 and Brodkorb 1963 for his critics), it would perhaps be advisable to retain a separate genus, *Limicorallus* Kuročkin, 1968, for *Phalacrocorax saiensis*.

#### SUMMARY

Eleven waterfowl species from the Tertiary of Asia were revised, based on personal re-examination of type materials (10 species), or on the re-examination of the original description and figure (1 species). The following results were achieved:

(1) The taxonomic status of *Cygnavus formosus* Kuročkin, 1968, *Anser devjatkini* Kuročkin, 1971, and *Aythya spatiosa* Kuročkin, 1976 was confirmed, although with some restrictions for the latter two species.

(2) *Cygnopterus lambrechtii* Kuročkin, 1968 was excluded from Anseriformes and synonymized with *Agnopterus turgaiensis* Tugarinov, 1940 from Phoenicopteridae.

(3) *Limicorallus saiensis* Kuročkin, 1968 was excluded from Anseriformes and included in the genus *Phalacrocorax* (Phalacrocoracidae) as a valid species *Phalacrocorax saiensis* (Kuročkin, 1968), combinatio nova.

(4) *Anas oligocaena* Tugarinov, 1940 was transferred from *Anas* in *Dendrochen* (Dendrocygnini), where it represents a valid species *Dendrochen oligocaena* (Tugarinov, 1940), combinatio nova.

(5) *Cygnus pristinus* Kuročkin, 1971 was synonymized with the Recent *Cygnus olor* (Gmelin, 1789).

(6) *Anser liskunae* Kuročkin, 1976 was transferred from *Anser* in *Olor* (Anserini), where it represents a valid species, *Olor liskunae* (Kuročkin, 1976), combinatio nova.

(7) *Heterochen vicinus* Kuročkin, 1976 was transferred from *Heterochen* in *Anser* (Anserini), where it belongs in the *Anser fabalis* complex. Whether or not it is a valid species cannot be decided until the systematics of this species complex is elaborated.

(8) *Anas soporata* Kuročkin, 1976 was transferred from *Anas* in *Dendrocygna* (Dendrocygnini), where it represents a valid species *Dendrocygna soporata* (Kuročkin, 1976), combinatio nova.

(9) *Sinanas diatomas* Yeh, 1980 was found to be a meaningless name until a re-description.

#### REFERENCES

- Alferaki, S. N., 1904: Gusi Rossii (The geese of Russia). Moskva: Kušnerev, 189 pp + 24 pls.
- Alferaki, S. N., 1907: A few words in reply to Mr. E. W. Oates' paper on the species of bean-geese. *J. Bombay nat. Hist. Soc.*, 17: 598—602.
- Aslanova, S. M., N. I. Burčak-Abramovič, 1968: A fossil swan from the Maykopian series of Azerbaydzhan. *Acta zool. cracov.*, 13: 325—338.
- Bacher, A., 1967: Vergleichend morphologische Untersuchungen an Einzelknochen des postkranialen Skeletts in Mitteleuropa vorkommender Schwäne und Gänse. Diss., Ludwig-Maximilian-Universität München, 109 pp.
- Bauer, K. M., U. N. Glutz von Blotzheim, 1968: Handbuch der Vögel Mitteleuropas. Vol. II. Anseriformes 1. Frankfurt (Main): Akademische Verlagsgesellschaft.
- Baumel, J. J., A. S. King, A. M. Lucas, J. E. Breazile, H. E. Evans, eds., 1979: Nomina anatomica avium. London: Academic Press, 637 pp.
- Bechstein, J. M.: 1803: Ornithologisches Taschenbuch von und für Deutschland. Vol. II. Leipzig.
- Berndt, R., 1938: Intrasternale Trachealschlingen bei Vögeln. *Morphol. Jb.*, 82: 27—118.
- Boetticher, H. von, 1952: Gänse- und Entenvögel aus aller Welt. Leipzig: Geest & Portig, 95 pp.
- Boie, F., 1822: Tagebuch, gehalten auf einer Reise durch Norwegen im Jahre 1816. Schleswig: Taubstummen-Institut.
- Brisson, M. J., 1760: Ornithologia. Vol. VI. Paris: Bauche, 543 + xlvii + 146 + xxiii pp.
- Brodkorb, P., 1956: Two new birds from the Miocene of Florida. *Condor*, 58: 367—370.
- Brodkorb, P., 1963: Catalogue of fossil birds: Part 1 (Archaeopterygiformes through Ardeiformes). *Bull. Florida State Mus., Biol. Sci.*, 7: 179—293.
- Brown, L. H., E. K. Urban, K. Newman, 1982: The birds of Africa. Vol. I. London: Academic Press, 536 pp.
- Brush, A. H., 1976: Waterfowl feather proteins: analysis of use in taxonomic studies. *J. Zool.*, 179: 467—498.
- Burčak-Abramovič, N. I., 1957: Iskopaemyj gus' v gipparionovoj faune Udabno (A fossil goose in the Hipparion fauna of Udabno). *Dokl. AN Azerb. SSR*, 13: 655—659.
- Burčak-Abramovič, N. I., 1958: Tretičnyje pticy SSSR (Tertiary birds of the USSR). *Uč. Zap. Azerb. gos. Univ. (Otd. biol.)*, 1: 81—88.
- Burčak-Abramovič, N. I., D. V. Gadžiev, 1978: Anser eldaricus sp. nova from Upper Sarmatian Hipparion fauna of Eldar. *Acta zool. cracov.*, 23: 67—78.
- Buturlin, S. A., 1907: On bean geese. *J. Bombay nat. Hist. Soc.*, 17: 603—607.
- Buturlin, S. A., 1908: Bean-geese of Asia. *J. Bombay nat. Hist. Soc.*, 18: 555—561.
- Buturlin, S. A., 1934: A vetési ludfajták szemléje (Übersicht der Saatgansrassen). *Aquila*, 38—41: 219—226.
- Cheneval, J., 1983: Les Anatidae (Aves, Anseriformes) du gisement aquitanien de Saint-Gérand-le-Puy (Allier, France). In: E. Buffeteaut, J. M. Mazin, E. Salmon, eds., Actes du symposium paléontologique Georges Cuvier: 85—98. Montbéliard.
- Cheneval, J., 1984: Les oiseaux aquatiques (Gaviiformes a Anseriformes) du gisement aquitanien de Saint-Gérand-le-Puy (Allier, France): révision systématique. *Palaeovertebrata*, 14: 33—115.
- Coombes, R. A. H., 1947a: On the races of the bean goose in the Netherlands. *Limosa*, 20: 229—230.
- Coombes, R. A. H., 1947b: On the original description of the bean goose. *Ibis*, 89: 272—275.
- Coombes, R. A. H., 1951: Two races of bean goose in western Europe. In: S. Hörstadius, ed., Proceedings of the Xth International ornithological congress: 185—188. Uppsala: Almqvist and Wiksells.

- Cracraft, J., 1973: Systematics and evolution of the Gruiformes (class Aves). 3. Phylogeny of the suborder Grues. *Bull. amer. Mus. nat. Hist.*, 151: 1—127.
- Cramp, S., K. E. L. Simmons, eds., 1977: The birds of western Palaearctic. Vol. I. Ostrich to ducks. Oxford: Oxford University Press, 722 pp.
- Delacour, J., 1951: Taxonomic notes on the bean geese, *Anser fabalis* Lath. *Ardea*, 39: 135—142.
- Delacour, J., 1954: The waterfowl of the world. Vol. I. London: Country Life, 284 pp.
- Delacour, J., 1956: The waterfowl of the world. Vol. II. London: Country Life, 232 pp.
- Delacour, J., 1959: The waterfowl of the world. Vol. III. London: Country Life, 270 pp.
- Delacour, J., E. Mayr, 1945: The family Anatidae. *Wilson Bull.*, 57: 3—55.
- Dement'ev, G. P., 1936: Essai de revision des formes de l'Oie des Moissons. *Alauda*, 8: 169—193.
- De Vis, C. W., 1906: A contribution to the knowledge of the extinct avifauna of Australia. *Ann. Queensland Mus.*, 6: 3—25.
- Dolgušin, I. G., ed., 1960: Pticy Kazachstana (The birds of Kazakhstan). Vol. I. Alma-Ata: AN Kazach. SSR.
- Eyton, T. C., 1838: A monograph of the Anatidae or duck tribe. London: Longman, Orme, Brown, Green, Longman & Eddowes, 183 pp.
- Gmelin, J. F., 1789: *Systema naturae*. Vol. II. Leipzig, p. 501—1032.
- Grote, H., 1934: A vetési ludfajták ismertető jegyei (Die Kennzeichen der Saatgansrasen. *Aquila*, 38—41: 211—218.
- Hachler, E., 1944a: Über die Farbvarietäten einiger Saatgansformen (*Anser fabalis* Lath.). *Verh. naturforsch. Ver. Brünn*, 75: 157—171.
- Hachler, E., 1944b: Geografické rasy husy pohní (*Anser fabalis* Lath.) a jejich variety (Geographic races of the bean goose (*Anser fabalis* Lath.) and their varieties). *Cs. Ornithol.*, 11: 17—21.
- Harrison, C. J. O., C. A. Walker, 1976: Birds of the British Upper Eocene. *Zool. J. Linn. Soc.*, 59: 323—351.
- Hilprecht, A., 1970: Höckerschwan, Singschwan, Zwergschwan. 2nd rev. ed., Wittenberg Lutherstadt: A. Ziemsen, 184 pp.
- Horsfield, T., 1821: Systematic arrangement and description of birds from the island of Java. *Trans. Linn. Soc. London*, 13: 133 ff.
- Howard, H., 1946: A review of the Pleistocene birds of Fossil Lake, Oregon. *Carnegie Inst. Publ.*, 551: 141—195.
- Johansen, H., 1945: Om racor af Saedgaes (On the races of the bean goose). *Dansk ornithol. Foren. Tidsskr.*, 39: 106—127.
- Johnsgard, P., 1960: Comparative behaviour of the Anatidae and its evolutionary implications. *Wildfowl Trust annu. Rep.*, 11: 31—45.
- Johnsgard, P., 1967: Observations on the behaviour and relationships of the white-backed duck and the stiff-tailed ducks. *Wildfowl Trust annu. Rep.*, 18: 98—107.
- Johnsgard, P., 1978: Ducks, geese and swans of the world. Lincoln: University of Nebraska Press, 409 pp.
- Johnsgard, P., 1979: Order Anseriformes. In: E. Mayr, G. W. Cottrell, eds., Check-list of birds of the world. Vol. I: 425—506. Cambridge: Museum of Comparative Zoology.
- Kaup, J. J., 1829: Skizirte Entwicklungsgeschichte und natürliches System der europäischen Thierwelt. Vol. I. Darmstadt: Leske.
- Kear, J., 1967: Notes on the eggs and downy young of *Thalassornis leuconotus*. *Ostrich*, 38: 227—229.
- Kolbe, H., 1984: Die Entenvögel der Welt. 3rd rev. ed., Radebeul: Neumann, 382 pp.
- Krivososov, G. A., 1981: Skolko lebedej-šipunov v SSSR? (How many mute swans are there in the USSR?). *Ochota ochot. Chozajstvo*, 1981 (7): 18—19.
- Kuročkin, E. N., 1968: Nove oligocenovye pticy Kazachstana (New Oligocene birds of Kazakhstan). *Paleontol. Ž.*, 1968 (1): 92—101.
- Kuročkin, E. N., 1971: K avifaune pliocena Mongolii (On the Pliocene avifauna of Mongolia). In: B. A. Trofimov, ed., Fauna mezozoja i kajnozoja Zapadnoj Mongolii (The fauna of the Mesozoic and Cenozoic of western Mongolia): 58—67. Moskva: Nauka.

- Kuročkin, E. N., 1976: Novye dannye o pticach pliocena zapadnoj Mongolii (New data on the Pliocene birds of western Mongolia). In: Paleontologija i biostratigrafia Mongolii (Paleontology and biostratigraphy of Mongolia): 51—67. Moskva: Nauka.
- Lambrecht, K., 1931: *Cygnopterus* and *Cygnavus*, zwei fossile Schwäne aus dem Tertiär Europas. *Bull. Mus. Hist. nat. Belgique*, 7 (31): 1—6.
- Lambrecht, K., 1933: *Handbuch der Palaeornithologie*. Berlin: Gebr. Borntraeger, 1024 pp.
- Latham, J., 1787: *Supplement to the general synopsis of birds*. London.
- Linné, K. von, 1758: *Systema naturae*. 10th ed., Stockholm: Salvius, 824 pp.
- Lydekker, R., 1891: *Catalogue of the fossil birds in the British Museum (Natural History)*. London: British Museum (Natural History), 368 pp.
- Miler, A. H., 1944: An avifauna from the Lower Miocene of South Dakota. *Univ. California Publ., Bull. Dept. geol. Sci.*, 27: 85—100.
- Miller, A. H., 1963: The fossil flamingos of Australia. *Condor*, 65: 289—299.
- Milne-Edwards, A., 1863: Mémoire sur la distribution géologique des Oiseaux fossiles et description de quelques espèces nouvelles. *Ann. Sci. nat. Paris*, 20: 132—176.
- Milne-Edwards, A., 1867—1868: *Recherches anatomiques et paléontologiques pour servir à l'histoire des Oiseaux fossiles de la France*. Vol. I. Paris: Masson & Fils, 475 pp. + 96 pls.
- Mlíkovský, J., 1982a: Taxonomische Identität der *Anas submajor* Jánossy, 1979 (Aves: Anseriformes) aus dem Oberpliozän Ungarns. *Věst. čs. Společ. zool.*, 46: 199—202.
- Mlíkovský, J., 1982b: Zur systematischen Stellung von *Bucephala angustipes* Jánossy, 1965 und *Somateria gravipes* Harrison, 1979 (Aves: Anseriformes) aus dem Pleistozän Europas. *Z. geol. Wiss.*, 10: 1463—1475.
- Mlíkovský, J., 1983: Fossilní doklady evoluce vrubozobých (Aves: Anseriformes) [Fossil evidence for the waterfowl evolution (Aves: Anseriformes)]. Diss., Czechoslovak Academy of Sciences Praha, 320 pp.
- Mlíkovský, J., L. Bělka, K. Zemek, 1985: Morphogenesis and the problem of morphospecies. In: J. Mlíkovský, V. J. A. Novák, eds., *Evolution and morphogenesis*: 201—211. Praha: Academia.
- Mourer-Chauviré, C., 1978: Le bassin lacustre miocène de Bes-Konak (Anatolie-Turquie): géologie et introduction à la paléontologie des vertébrates II/5. Oiseaux. *Geobios*, 11: 52—54.
- Nelson, C. H., 1976: A key to downy cygnets with analysis of plumage characters. *Wilson Bull.*, 88: 4—15.
- Ogilvie, M. A., 1972: Distribution, numbers and migration. In: P. Scott, ed., *The swans*: 29—55. London: Joseph.
- Olson, S. L., 1977a: The identity of the fossil ducks described from Australia by C. W. DeVis. *Emu*, 77: 127—131.
- Olson, S. L., 1977b: Notes on subfossil Anatidae from New Zealand, including a new species of pink-headed duck (*Malacorhynchus*). *Emu*, 77: 132—135.
- Olson, S. L., 1981: The generic allocation of *Ibis pagana* Milne-Edwards, with a review of fossil ibises (Aves: Threskiornithidae). *J. Vert. Paleontol.*, 1: 165—170.
- Olson, S. L., A. Feduccia, 1980: Presbyornis and the origin of the Anseriformes (Aves: Charadriomorphae). *Smithson. Contrib. Zool.*, 323: 1—24.
- Ono, K., 1980: Comparative osteology of three species of Japanese cormorants of the genus *Phalacrocorax* (Aves: Pelecaniformes). *Bull. natl. Sci. Mus. (C)*, 6: 129—151.
- Paris, P., 1912: Oiseaux fossiles de France. *Rev. Franc. Ornithol.*, 4: 283—298.
- Peters, J. L., 1931: *Check-list of birds of the world*. Vol. I. Cambridge: Harvard University Press, 345 pp.
- Petzold, H.-G., 1964: Vergleichend-ethologische Beobachtungen an Schwänen. *Beitr. Vogelk.*, 10: 1—126.
- Piechocki, R., 1968: Beiträge zur Avifauna der Mongolei. Teil I. Non-Passeriformes. *Mitt. zool. Mus. Berlin*, 44: 149—292.
- Piechocki, R., M. Stubbe, K. Uhlenhaut, D. Sumjaa, 1981: Beiträge zur Avifauna der Mongolei. Teil III. Non-Passeriformes. *Ann. Ornithol.*, 5: 71—128.
- Raikow, R. J., 1971: The osteology and taxonomic position of the white-backed duck, *Thalassornis leuconotus*. *Wilson Bull.*, 83: 270—277.
- Reichenbach, H. G. L., 1852: *Das natürliche System der Vögel*. Dresden: Expe-

- dition der vollständigen Naturgeschichte; und Berlin: Hofmeister, VIII + xxxi + 36 pp.
- Rich, P. V., C. A. Walker, 1983: A new genus of Miocene flamingo from East Africa. *Ostrich*, 54: 95—104.
- Scopoli, J. A., 1769: *Annus I. historico-naturalis*. Leipzig: C. G. Hilscher, 168 pp.
- Serebrovskij, P. V., 1940: Novye nachodki ptic iz binagadinskich otloženij (New finds of birds from Binagada deposits). *Dokl. AN SSSR*, 27: 766—768.
- Serebrovskij, P. V., 1941: Ostatki plejstocenovych ptic iz binagadinskich otloženij (Remains of Pleistocene birds from Binagada deposits). *Dokl. AN SSSR*, 33: 473—475.
- Short, L. L., 1970: A new anseriform genus and species from the Nebraska Pliocene. *Auk*, 87: 537—543.
- Shufeldt, R. W., 1915: Fossil birds in the Marsh collection of Yale University. *Trans. Connecticut Acad. Arts Sci.*, 19: 1—110.
- Swainson, W., 1837: On the natural history and classification of birds. Vol. II. London.
- Tintant, H., 1980: Problématique de l'espèce en paléozoologie. In: C. Bocquet, J. Générumont, M. Lamotte, eds., Les problèmes de l'espèce dans le règne animal. Vol. III: 321—372. Paris: Société Zoologique de France.
- Tugarinov, A. Ja., 1940a: Novye nachodki pliocenovoj ornitofauny Odessy (New finds of the Pliocene ornithofauna of Odessa). *Dokl. AN SSSR*, 26: 311—313.
- Tugarinov, A. Ja., 1940b: Novye dannye dlja tretičnoj ornitofauny SSSR (New data on the Tertiary ornithofauna of the USSR). *Dokl. AN SSSR*, 26: 314—316.
- Tugarinov, A. Ja., 1941: Plastičnatokljuyve (The waterfowl). In: Fauna SSSR. Pticy (Fauna of the USSR. Birds). Vol. I (4): 1—383. Moskva: AN SSSR.
- Van Beneden, P. J., 1883: Sur quelques formes nouvelles des terrains tertiaires du pays. *Bull. Acad. roy. Sci. nat. Belgique*, (3) 6: 132—134.
- Van Impe, J., 1980: Ecologie et ethologie des Oies des Moissons, *Anser fabalis fabalis* et *Anser fabalis rossicus*. *Gerfaut*, 70: 499—558.
- Van Impe, J., 1981: Sur la cladogenese et l'évolution d'*Anser fabalis fabalis* et d'*Anser fabalis rossicus*. *Gerfaut*, 71: 163—174.
- Van Tets, G. F., 1976: Australasia and the origin of shags and cormorants, Phalacrocoracidae. In: H. J. Frith, J. H. Calaby, eds., Proceedings of the 16th international ornithological congress: 121—124. Canberra: Australian Academy of Sciences.
- Van Tets, G. F., P. V. Rich, 1980: A review of the DeVis fossil pigeons of Australia. *Mem. Queensland Mus.*, 20: 89—94 (includes a revision of *Nyroca effodiata* DeVis 1906).
- Vaurie, C., 1964: A survey of the birds of Mongolia. *Bull. amer. Mus. nat. Hist.*, 127: 103—143.
- Vaurie, C., 1965: The birds of the Palearctic fauna. Non-Passeriformes. London: Witherby, 763 pp.
- Vieillot, L. J. P., 1816: Nouveau dictionnaire d'histoire naturelle. Vol. V. Paris: Déterville.
- Vigors, N. A., 1825: Observation on the natural affinities that connect the orders and families of birds. *Trans. Linn. Soc. London*, 14: 395—517.
- Wagler, J. G., 1832: Neue Vögel. *Isis*, 1832: 1221 ff.
- Wetmore, A., 1935: On the genera *Oligocorax* and *Miocorax*. *Auk*, 52: 75—76.
- Woelfle, E., 1967: Vergleichend morphologische Untersuchungen an Einzelknochen des postkranialen Skelettes in Mitteleuropa vorkommender Enten, Halbgänse und Säger. Diss., Ludwig-Maximilian-Universität München, 203 pp.
- Wolters, H. E., 1975—1982: Die Vogelarten der Erde. Berlin: Paul Parey, 748 pp.
- Woolfenden, G. E., 1961: Postcranial osteology of the waterfowl. *Bull. Florida State Mus., Biol. Sci.*, 6: 1—129.
- Yarrell, W., 1830: On a new species of wild swan, taken in England and hitherto confounded with the hooper. *Trans. Linn. Soc. London*, 16: 445—454.
- Yeh, H., 1980: Fossil birds from Linqu, Shandong. *Vert. palasiat*, 18: 116—125 (in Chinese, with English summary).

*Authors' addresses:* Jiří Mlíkovský, Department of Evolutionary Biology, Czechoslovak Academy of Sciences, Na Folimance 5, CS 120 00 Praha 2, Czechoslovakia.  
Petr Švec, Institute of Entomology, Czechoslovak Academy of Sciences, Branišovská 31, CS 370 05 České Budějovice, Czechoslovakia.