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HYBRIDIZATION IN THE ANATIDAE AND ITS TAXONOMIC IMPLICATIONS

By PAUL A. JOHNSGARD

Without doubt, waterfowl of the family Anatidae have provided the greatest number and variety of bird hybrids originating from both natural and captive conditions. The recent compilation by Gray (1958) has listed approximately 400 interspecies hybrid combinations in this group, which are far more than have occurred in any other single bird family. Such a remarkable propensity for hybridization in this group provides a great many possibilities for studying the genetics of speciation and the genetics of plumage and behavior, and it also provides a valuable tool for judging species relationships. It may generally be said that the more closely two species are related the more readily these species will hybridize and the more likely they are to produce fertile offspring. In waterfowl, chromosomal incompatibility and sterility factors are thought to be infrequent, a circumstance which would favor the large number of hybrids encountered in this group. In addition to this, however, it can probably be safely concluded that the Anatidae are extremely close-knit in an evolutionary sense, for their behavior, anatomy, and other characteristics all indicate a monophyletic origin. It was for these reasons that Delacour and Mayr (1945), in their revision of the group, sensibly broadened the species, generic, and subfamilial categories, and in so doing greatly clarified natural relationships.

Gray's compilation, although it provides an incomparable source of hybrid records, does not attempt to synthesize these data into any kind of biologically meaningful pattern. For the past several years I have independently been collecting records and information on waterfowl hybrids for the purpose of obtaining additional evidence for species relationships and in order better to understand problems of isolating mechanisms under natural conditions. With the publication of Gray's bibliography, little purpose would be served by presenting my compilation *in toto*, since the two lists are practically identical. However, I believe that condensed graphic summaries, arranged by natural subgroups (tribes) rather than alphabetically as done by Gray, have sufficient value and interest to be presented here.

SUMMARY OF INTRATRIBAL HYBRIDS

Inasmuch as the great majority of anatid hybrids involve species of the same tribe, and because practically all natural hybrids known are of this kind, they will be dealt with first. Closely related sympatric species which will occasionally hybridize in the wild are most important from the standpoint of isolating mechanisms. The frequency of such hybridization and the fertility of the resulting progeny are of particular importance in this connection. For each tribe in which intratribal hybrids have been recorded a graph (figs. 1-6) has been prepared which indicates the known combinations and also provides an indication of the relative frequency of such hybridization and the degree of hybrid fertility when it is known. Except for the Ringed Teal ("*Anas*" *leucophrys* of Delacour and Mayr, 1945), which is considered here to be congeneric with *Amazonetta brasiliensis* of the Cairinini (see Dersheid, 1938), the species constitution of each tribe is that proposed by Delacour and Mayr. However, the exact sequence of species often differs somewhat to conform with what I believe more closely approximates relationships when expressed in a linear fashion. References concerning nearly all the indicated hybrid combinations can be found in Gray (1958).

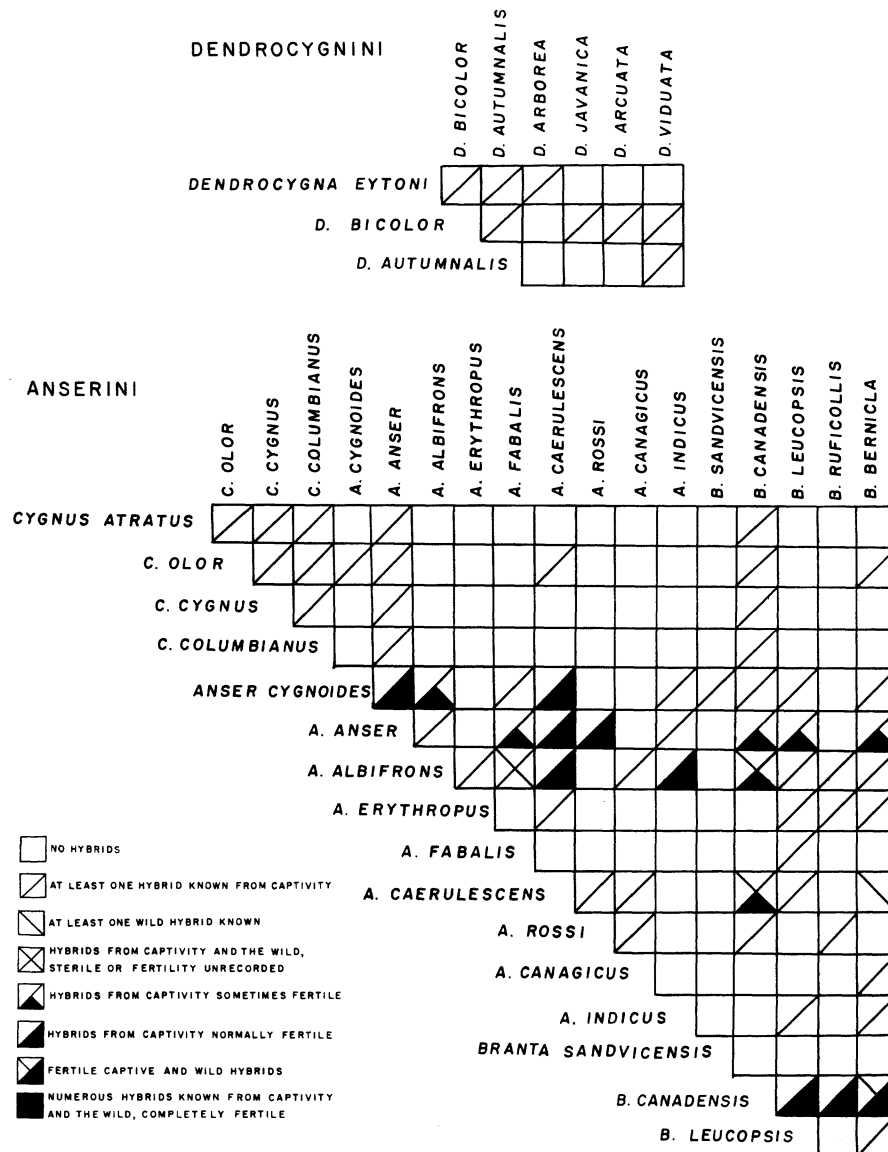


Fig. 1. Above, intratribal hybrid combinations recorded in the Dendrocygnini.
 Below, intratribal hybrid combinations recorded in the Anserini.

Subfamily Anseranatinae

No hybrids involving the monotypic species of this subfamily, the Magpie Goose (*Anseranas semipalmata*), have been recorded. The species' anatomy deviates markedly from the rest of the group (Miller, 1919), and it is probable that hybridization with other species is genetically impossible.

Subfamily Anserinae

Dendrocygnini.—Evidence from hybrids within the whistling duck group sheds little light on relationships (fig. 1). It is significant however that no intertribal hybrids in-

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TADORNINI	C. POLIOCEPHALA	C. RUBIDICEPS	C. PICTA	C. CYANOPTERA	N. JUBATUS	A. AEGYPTIACUS	T. TADORNOIDES	T. VARIEGATA	T. CANA	T. FERRUGINEA	T. RADJAH	T. TADORNA
CHLOEPHAGA MELANOPTERA												
C. POLIOCEPHALA												
C. RUBIDICEPS												
C. PICTA												
CYANOCHEN CYANOPTERA												
NEOCHEN JUBATUS												
ALOPOCHEN AEGYPTIACUS												
TADORNA TADORNOIDES												
T. VARIEGATA												
T. CANA												
T. FERRUGINEA												
T. RADJAH												
T. TADORNA												

Fig. 2. Intratribal hybrid combinations recorded in the Tadornini. See figure 1 for meaning of symbols.

CAIRININI	C. MOSCHATA	C. JUBATA	A. LEUCOPHRYS	A. BRASILIENSIS	A. GALERICULATA	A. SPONSA
PLECTROPTERUS GAMBENSIS						
CAIRINA MOSCHATA						
CHENONETTA JUBATA						
AMAZONETTA LEUCOPHRYS						
A. BRASILIENSIS						
AIX GALERICULATA						

Fig. 3. Intratribal hybrid combinations recorded in the Cairinini.

volving this group are known except for a highly dubious record mentioned by Delacour (1927) for *Dendrocygna viduata* x *Netta peposaca*. This suggests that the tribe is more isolated from the other anatids than are the geese and swans.

Anserini.—The great abundance of swan x goose hybrids known (fig. 1) certainly vindicates the submerging of the previously upheld subfamilies Cygnae and Anserinae,

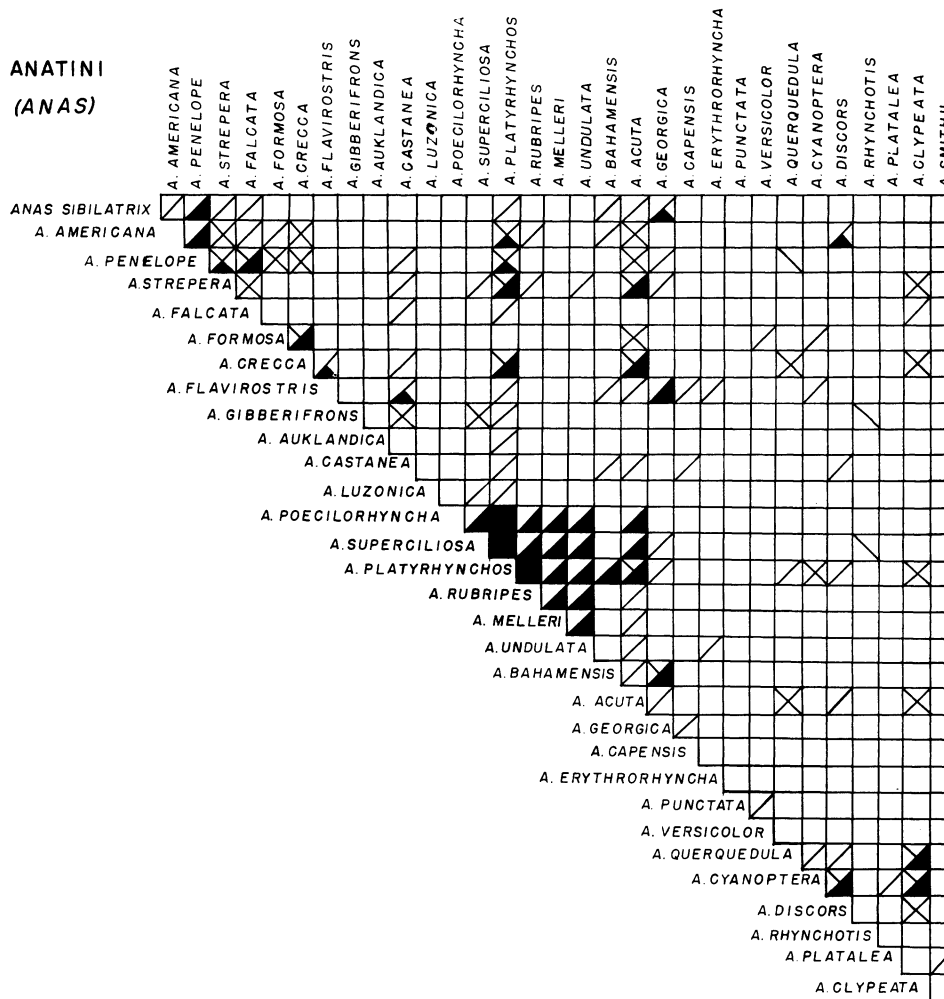


Fig. 4. Intratribal hybrid combinations recorded in the Anatini (genus *Anas* only, see text).

and the numerous goose hybrids also provide justification for discarding several monotypic genera such as *Eulabeia* and *Cygnopsis*. Even with the broad generic concept of Delacour and Mayr (1945), the several fertile intergeneric crosses between *Anser* and *Branta* indicate the very close relationship existing between these two morphologically fairly distinct groups.

Subfamily Anatinae

Tadornini.—Hybridization in captivity involving species of this tribe is relatively prevalent (fig. 2), probably largely as a result of the active part the female takes in

selecting the strongest possible mate, often regardless of its species. Since several of the species are only rarely kept in captivity, the potential list of hybrids has undoubtedly not yet been filled. The fertile intergeneric crosses among *Alopochen*, *Tadorna*, *Cyanochen*, and *Neochen* indicate that the number of genera currently accepted is overly large, and possibly some of these monotypic genera are unrealistic.

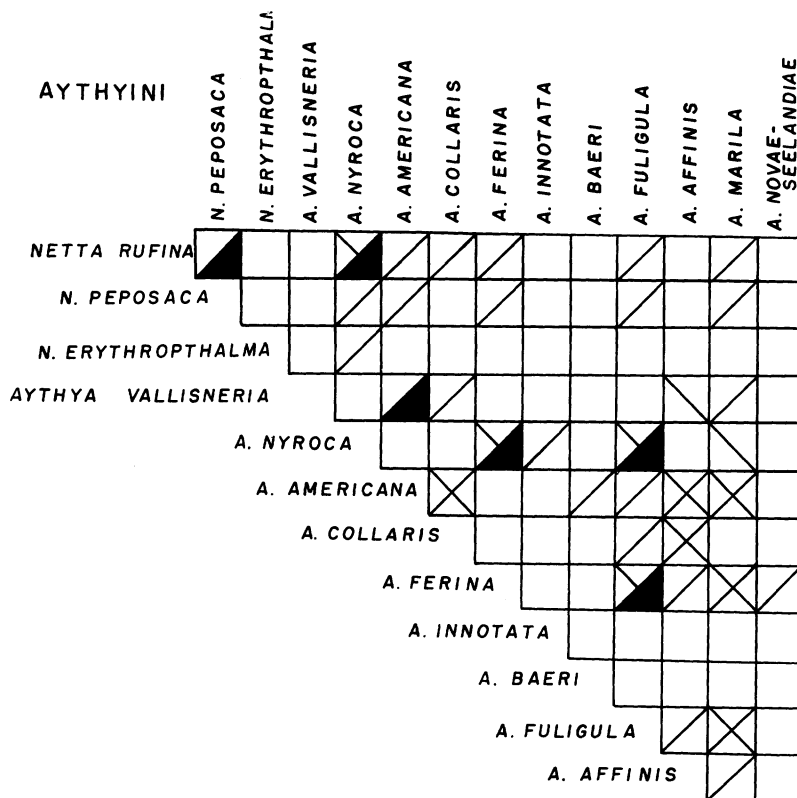


Fig. 5. Intratribal hybrid combinations recorded in the Aythyini.

Cairinini.—The surprising paucity of hybrids within the perching duck group (fig. 3) seems explainable by the possibility that the included species represent a collection of relatively isolated forms which share several rather primitive characteristics and seem to represent the generalized anatine condition from which the other groups have adaptively radiated. None of the intratribal hybrids are known to be fertile, but apparently hybrids between the Muscovy (*Cairina moschata*) and the Mallard (*Anas platyrhynchos*) are rarely fertile. The apparent absence of hybrids of the Wood Duck (*Aix sponsa*) with the Mandarin Duck (*Aix galericulata*) might be explained on the basis of gross chromosomal differences (Yamashina, 1952), but several alleged examples of this cross have been recorded. The Wood Duck has hybridized with a great many species of *Anas*, with some of which the Mandarin has also hybridized, but behavioral (Lorenz, 1951–1953) and serological (Cotter, 1957) evidence indicates that they belong in the present tribe.

Anatini.—A single questionable record (see Gray, 1958) of a hybrid between the New Zealand Blue Duck (*Hymenolaimus malacorhynchus*) and the Gray Duck (*Anas*

superciliosa) is the only one which does not involve only those species considered by Delacour and Mayr (1945) to belong to the genus *Anas*. So many hybrid combinations among species of this genus are known (fig. 4), and such a remarkably high incidence of fertility is present, that one must conclude that the species of dabbling ducks are much more closely related to one another than is often indicated by their external appearance.

MERGINI	M. PERSPICILLATA	S. MOLLISSIMA	S. SPECTABILIS	B. ISLANDICA	B. CLANGULA	M. ABBELLUS	M. CUCULLATUS	M. SERRATOR	M. MERGANSER
MELANITTA FUSCA									
M. PERSPICILLATA									
SOMATERIA MOLLISSIMA									
M. SPECTABILIS									
BUCEPHALA ISLANDICA									
B. CLANGULA									
MERGUS ABBELLUS									
M. CUCULLATUS									

Fig. 6. Intratribal hybrid combinations recorded in the Mergini.

Delacour and Mayr's recommendations of a single, inclusive genus rather than the more than twenty which have been proposed is fully justified on this basis. Fertile hybrids of *Anas* and species of the tribes Tadornini and Aythyini have been occasionally reported, which circumstance illustrates the astonishing capacity for interspecies fertility found in this group.

Aythyini.—The high percentage of the potential hybrids among species of diving ducks that are actually realized (fig. 5) forces one to conclude that the Aythyini represent a very closely related group of species, with two being the maximum number of genera that can be reasonably allowed. Indeed, perhaps the best reason for retaining *Netta* is because it provides such an excellent transitional link between the Anatini and the Aythyini, having provided fertile hybrids with both *Anas* and *Aythya*. The great number of hybrids of *Anas* x *Aythya* (five combinations of which have been found to be fertile) and electrophoretic evidence from egg-white proteins (McCabe and Deutsch, 1952) both argue for a very close relationship between the groups.

Mergini.—The relatively few hybrid records for the sea duck group (fig. 6) very likely reflects their relative infrequency in captive collections, the difficulties of breeding them, and their secondary importance as sporting birds, which reduces the number of

wild-taken hybrids. Except for the remarkable intertribal hybrid between *Anas castanea* and *Clangula hyemalis*, which Delacour (1956) bred at Cleres, and an equally curious hybrid between *Aix galericulata* and *Clangula hyemalis* from Tring (specimen in the American Museum of Natural History), most of the hybrids represent wild-taken specimens. The recent evidence (Humphrey, 1958) that eiders should be placed in a separate tribe near the dabbling ducks might be supported by two alleged crosses of *Anas* x *Somateria*, but behavioral evidence (D. F. McKinney, unpublished MS) argues strongly against this.

Table 1

Intratribal and intertribal hybrid combinations recorded in the Anatidae. Numbers indicate total interspecific hybrid combinations recorded within and among tribes. Reciprocal crosses (such as Mallard x Pintail and Pintail x Mallard) are considered as single combinations.

	Anseranatini	Dendrocygnini	Anserini	Tadornini	Cairinini	Anatini	Aythini	Mergini	Oxyurini
Anseranatini
Dendrocygnini	8
Anserini	65	15	5	3
Tadornini	15	21	8	5	1	1
Cairinini	5	8	5	28	8	2
Anatini	3	5	28	115	45	7
Aythini	1	8	45	35	6
Mergini	1	2	7	6	9
Oxyurini	1

Oxyurini.—Except for a highly questionable record of a hybrid between a Ruddy Duck (*Oxyura jamaicensis*) and a Greater Scaup (*Aythya marila*) mentioned by Sibley (1938), there are no positive records of interspecific hybridization involving any species of the stiff-tailed ducks. Bond (1950) has indicated that intermediate forms between *Oxyura jamaicensis andina* and *O. ferruginea* occur in Colombia, but these probably should be considered subspecific intergrades rather than hybrids (Johnsgard, unpublished MS). One possible hybrid between *ferruginea* and *Oxyura vittata* has also been mentioned (Hellmayr, 1932), but the evidence for this cross is still inadequate.

SUMMARY OF INTERGENERIC AND INTERTRIBAL HYBRIDS

A compilation of records of intergeneric and intertribal hybrids provides a means of estimating the degree of genetic isolation existing among these higher categories. As such it helps to establish a sequence of categories that most closely reflects actual relationships. Thus by totalling the number of known intergeneric hybrid combinations (not total hybrids), a rough index is obtained to the degree of genetic difference among various genera (fig. 7). Such a compilation clearly indicates the great latitude of hybrid potentiality present in the group (very questionable records are not included), particularly in the subfamily Anatinae. Thus, for example, the Mallard (*Anas platyrhynchos*) has been hybridized with both the Gray-lag Goose (*Anser anser*) and the Common Merganser (*Merganser merganser*), two species which practically encompass the greatest range of morphological variation encountered in the entire family Anatidae.

If a compilation of hybrid records is made at the tribal level (intertribal and intra-

tribal combinations), as has been done in table 1, a further fact becomes clear. This is that the tribe Cairinini belongs between the Tadornini and the Anatini, rather than between the Aythyini and the Mergini, as originally suggested by Delacour and Mayr (1945). In addition, the table illustrates the fact that the whistling ducks (Dendrocygnini) are a distinctly isolated group, whereas the geese and swans (Anserini) are not

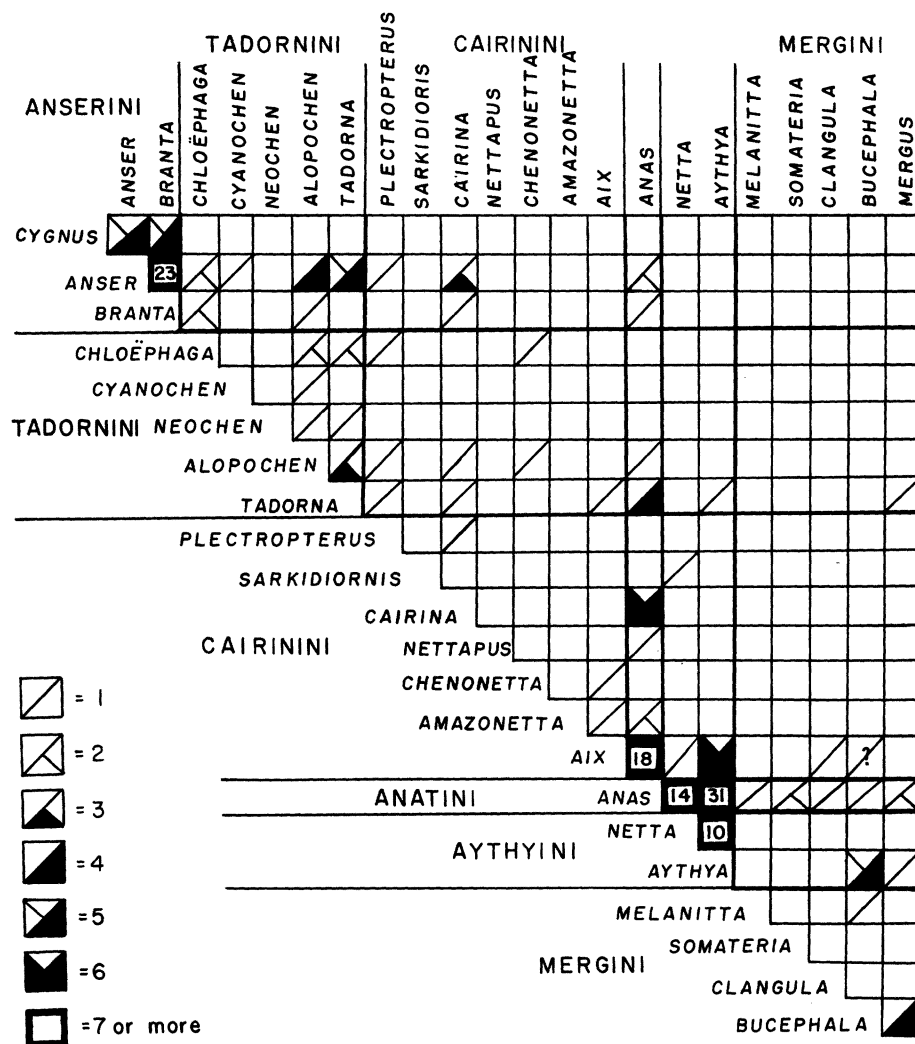


Fig. 7. Intratribal and intertribal hybrid combinations recorded among the genera of the Anatidae. Numbers indicated in key refer to total intergeneric combinations recorded.

markedly set off from the Anatinae. Likewise the stiff-tail group (Oxyurini) appears to be rather isolated from the other tribes. However, the rather obvious overall conclusion to be drawn from all these facts is that broad nomenclatural categories are greatly preferable to narrow ones in the Anatidae and that they help to emphasize actual biological relationships far better than does the highly "split" taxonomic hierarchy which is still in general usage as in the fifth edition of the American Ornithologists' Union Check-list.

CONCLUSIONS

A compilation of published and unpublished records of hybridization in the family Anatidae indicates that the genera and tribes proposed by Delacour and Mayr (1945) are well grounded. With but a single exception, that of the Cairinini, fertile hybrids resulting from intrageneric crosses and intratribal hybrids are more frequent than are intertribal combinations. The exceptional situation found in the Cairinini is largely the result of the Wood Duck (*Aix sponsa*), which has hybridized with 16 species of *Anas* but with only two species of its own tribe. This and other evidence clearly indicates that the correct position of the Cairinini is between the Tadornini and the Anatini, rather than between the Aythyini and the Mergini. Furthermore, most of the lumping of genera, especially in the Anserini, Anatini and Aythyini, as proposed by Delacour and Mayr, is well justified by the hybrid records.

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