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Abstract The incidence of hybridisation in birds differs greatly between orders and is expected to be low in orders comprising few species. The divers or loons (Gaviiformes) are a species-poor group in which apparent hybridisation has been reported infrequently. Here we report on a hybrid diver stored in the collections of the Zoological Museum Amsterdam. The bird shows a heterogeneous set of characters, some shared with the putative parent species White-billed Diver *Gavia adamsii* and Great Northern Diver *G. immer*, others being intermediate between the two. A Canonical Discriminant Function analysis positions the bird between these two putative parent species, making a hybrid status quite likely. We evaluate the evidence for hybridisation in the order Gaviiformes and conclude that hybridisation has been suspected in four of the five species, though documentation is limited. If this high incidence could be confirmed, it would rank among the highest of any avian order, contradicting the assumption that incidence of hybridisation in small orders is relatively low.

Keywords *Gavia adamsii* · *Gavia immer* · Hybridisation · Speciation

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Introduction

The identification of hybrids between closely related taxa bears relevance for studies of gene flow and the evolution of mechanisms of genetic isolation and, hence, of speciation (Barton 2001). Furthermore, hybridisation, or the interbreeding of species, is of pivotal importance in framing ideas about the nature of taxonomic judgements to be made about particular populations. Hybridisation is commonly recorded in birds (Gray 1958) and about one in ten species of birds is known to have bred in nature with another species and produced hybrid offspring (Grant and Grant 1992; Randler 2002). The incidence of hybridisation varies geographically and ecologically; it appears to be more common in temperate regions compared to the tropics and is more frequent in terrestrial birds than in sea birds (Grant and Grant 1992). Variation among orders of birds is marked, with the incidence of occurrence (i.e. the number of species within an order that have hybridised divided by the total number of species in that order) as high as >70% among the 162 species of Anseriformes (Gray 1958), whereas in taxa like Bucerotiformes hybridisation has hitherto not been recorded. The incidence of recorded hybridisation within orders is expected to be relatively low in those orders that comprise few species (Grant and Grant 1992), and indeed there is a strong positive relation between the number of species in an order and the incidence of hybridisation (Kendall's $\tau = 0.47$, $n = 23$, $P = 0.002$: data from Table. 1, 2 Grant and Grant 1992).

One of the orders for which only scant data on naturally occurring hybrids are available are the divers or loons (Gaviiformes). The Gaviiformes contain a single family, Gaviidae, comprising one genus of five species which breed in lakes and slow-flowing rivers in northern tundra and taiga and winter in the shallow coastal zone of seas and large lakes of the temperate region. The five species are made up of two largely allopatric species pairs and of the sister-taxon of these four, Red-throated Diver *Gavia stellata* (Boertmann 1990; Wink et al.

Table 1 Measurements in mm [average, (SD, *n*), range] of White-billed Diver *Gavia adamsii* and Great Northern Diver *G. immer*, and their purported hybrid (ZMA 54666)

Character	White-billed Diver *G. adamsii*	ZMA 54666	Great Northern Diver *G. immer*
1. Wing length, 1st year males	366.8 (15.8; 4) 355–390	369	359.0 (– ; 2) 353–365
2. Bill length, 1st year males	87.2 (4.60; 4) 83–92	89.8	81.4 (1.65; 8) 79–84
3. Bill depth, 1st year males	25.2 (1.50; 4) 23.8–27.3	25.5	23.5 (0.52; 8) 23.0–24.3
4. Maxilla depth, males	5.9 (0.52; 12) 5.5–7.4	5.3	4.8 (0.33; 27) 4.2–5.4
5. Loral feathering, all ages both sexes	7.26 (1.22; 20) 4.8–9.2	4.0	3.74 (1.16; 62) 1.5–6.6
6. Chin feathering, all ages both sexes	18.8 (2.02; 20) 16–24	20.0	10.2 (2.20; 62) 4–16

2002). One pair is formed by the smaller-sized Arctic Loon or Black-throated Diver *G. arctica* and Pacific Loon or Pacific Diver *G. pacifica* which show some divergence in morphology (Walsh 1988; Roberson 1989; McCaskie et al. 1990; Dunn and Rose 1992), but hardly in anatomy or DNA (Boertmann 1990; Wink et al. 2002). The other pair consists of the larger Common Loon or Great Northern Diver *G. immer* and Yellow-billed Loon or White-billed Diver *G. adamsii* which are more divergent in morphological and anatomical characters and in DNA (Boertmann 1990; North 1994; Wink et al. 2002). *Gavia arctica* and *G. pacifica* overlap in breeding range in NE Siberia (Il'ichev and Flint 1982; Kishchinskii and Flint 1983; Solov'ev et al. 1993) and NW Alaska (AOU 1998; Douglas and Sowl 1993), *G. immer and G. adamsii* overlap in Alaska and NW Canada (Godfrey 1986; AOU 1998). We here report on an apparent hybrid diver and discuss the evidence of hybrids in the Gaviidae. More specifically, we aimed at (1) providing an accurate evaluation of a putative hybrid *G. adamsii* × *G. immer* deposited in the collections of the Zoological Museum Amsterdam (ZMA 54666), and (2) offering a comprehensive overview of (presumed) hybrids that have been reported in the Gaviidae.

Methods

Morphological measurements

The specimen (ZMA 54666) is a mounted first winter male, collected 4th December 1890 at Schellingwoude (NE Amsterdam, The Netherlands) which defies immediate identification as either of the two large species, *G. adamsii* or *G. immer* (Fig. 1). To establish whether the specimen is indeed a hybrid the differentiating characters between the two purported parental species had to be established. We selected 15 characters from a series of identification papers (Binford and Remsen 1974; Burn and Mather 1974; Schwarz 1978; van IJzendoorn 1985; Appleby et al. 1986; Busching 1987; Barthel and Mullarney 1988; Jonsson and Tysse 1990; Phillips 1990; North 1994, and Camphuysen 1995):

1. Wing length (fully stretched and flattened)
2. Bill length from feathering at forehead to tip
3. Bill depth of both mandibles, at level of middle of nostril (taken only when bill was properly closed in skin)
4. Maxilla depth, i.e. the minimum distance from nostril to cutting edge
5. Loral feathering, i.e. extent of feathering at lateral base of upper mandible beyond basal corner of nostril
6. Chin feathering, i.e. the distance between distal tip of feathering on chin and that on the lateral base of the under mandible
7. Colouration of distal halve of culmen ridge (1 = light yellow-horn, 2 = light brown, 3 = medium brown, 4 = dark brown, 5 = black)
8. Colouration of primary shafts (1 = pale horn, 2 = medium horn - distal quarter dark horn, 3 = medium horn - distal quarter black, 4 = dark horn - distal quarter black, 5 = all black)
9. Shape of culmen (1 = straight, 5 = decurved)
10. Shape of cross section of upper mandible below nostril (1 = flattened, 5 = bulging)
11. Gonys knob, i.e. presence of knob on lower mandible at gonydeal angle (1 = none, 5 = distinct)
12. Gonys fushion, i.e. the extent of fusion between the rami of the under mandible (1 = long furrow, 5 = surface almost entirely smooth)
13. Extent of white at side of head (1 = white to well above the eye, 5 = mainly black)
14. Presence of a contrasting dark ear patch (1 = distinct, 5 = none)
15. Presence of a narrow dark mid-line on hindneck (1 = distinct, 5 = none)

For definition of bill measurements see Fig. 2. For the non-mensural characters 9–15, three standard birds were selected for each character, two showing the extremes of variation and one showing an intermediate stage; other birds were compared to these three, thus obtaining five categories: birds more or less matching one of the extremes or the intermediate, and birds roughly halfway between one of the extremes and the intermediate. The values of these five categories were chosen in such a way that category one shows the character of a typical *G. adamsii* and category five the one of typical *G. immer*.

These 15 characters were measured by CSR on 70 skins of *G. immer* and 21 skins of *G. adamsii* deposited in

Table 2 Plumage characters of White-billed Diver *Gavia adamsii* and Great Northern Diver *G. immer*, and their purported hybrid (ZMA 54666). See text for further details

Character	White-billed Diver *G. adamsii*	ZMA 54666	Great Northern Diver *G. immer*
7. Culmen ridge, all ages both sexes			
Category 1, light-yellow horn	21 (100%)		0 (0%)
Category 2	0 (0%)		0 (0%)
Category 3	0 (0%)	x	0 (0%)
Category 4	0 (0%)		1 (1%)
Category 5, black	0 (0%)		69 (99%)
8. Primary shaft, all ages both sexes			
Category 1, pale horn	11 (61%)		0 (0%)
Category 2	5 (28%)		1 (3%)
Category 3	1 (6%)		2 (6%)
Category 4	1 (6%)	x	3 (9%)
Category 5, all black	0 (0%)		29 (83%)
9. Culmen shape, all ages both sexes			
Category 1, straight	10 (50%)		5 (7%)
Category 2	6 (30%)	x	6 (9%)
Category 3	2 (10%)		5 (7%)
Category 4	0 (0%)		10 (15%)
Category 5, decurved	2 (10%)		42 (63%)
10. Mandible shape, all ages both sexes			
Category 1, flattened	16 (76%)		0 (0%)
Category 2	4 (19%)		1 (1%)
Category 3	1 (5%)		3 (4%)
Category 4	0 (0%)	x	19 (27%)
Category 5, bulging	0 (0%)		47 (67%)
11. Gonys knob, all ages both sexes			
Category 1, none	5 (14%)	x	60 (86%)
Category 2	7 (33%)		7 (10%)
Category 3	2 (10%)		2 (3%)
Category 4	4 (19%)		0 (0%)
Category 5, distinct	3 (14%)		1 (1%)
12. Gonys fushion, all ages both sexes			
Category 1, long furrow	19 (90%)		5 (7%)
Category 2	2 (10%)		13 (19%)
Category 3	0 (0%)	x	19 (27%)
Category 4	0 (0%)		18 (26%)
Category 5, smooth	0 (0%)		15 (21%)
13. Lateral head colouration, both sexes, excl. nuptial plumage			
Category 1, white to well above eye	9 (69%)	x	6 (13%)
Category 2	4 (31%)		8 (17%)
Category 3	0 (0%)		17 (36%)
Category 4	0 (0%)		8 (17%)
Category 5, mainly black	0 (0%)		8 (17%)
14. Dark ear patch, both sexes, excl. nuptial plumage			
Category 1, distinct	7 (64%)		0 (0%)
Category 2	0 (0%)		0 (0%)
Category 3	0 (0%)	x	3 (7%)
Category 4	2 (18%)		0 (0%)
Category 5, none	2 (18%)		40 (93%)
15. Narrow dark mid-line neck, both sexes, excl. nuptial plumage			
Category 1, distinct	10 (91%)		3 (7%)
Category 2	0 (0%)		0 (0%)
Category 3	1 (9%)		4 (10%)
Category 4	0 (0%)		0 (0%)
Category 5, none	0 (0%)	x	34 (83%)

the ZMA, Naturalis (RMNH, Leiden, the Netherlands), and The National Natural History Museum (BMNH, Tring, UK), and on the purported hybrid. These specimens included birds of >6 months in various plumages . They were sorted according to age (first—winter or adult; second winter and third-year birds were classified as adult), plumage (nuptial or winter), and sex. Specimens of *G. adamsii* originated from the Netherlands (9), Scandinavia (3), Japan (3), and N America (6) and of *G. immer* from the Netherlands (21), W France (39), Scandinavia (3), and Iceland/SE Greenland (6).

Analysis

Analysis on how the characters measured in ZMA 54666 differed from the purported parent species were conducted for each character separately and, with a

Fig. 1 Hybrid diver ZMA 54666 (*Gavia adamsii* × *G. immer*), obtained near Amsterdam (Netherlands). Photo: L.A. van der Laan

Canonical Discriminant Function (CDF) analysis, for a set of continuous characters. In the first analysis, the 15 characters were each checked for significant sexual or age-related differences. If these were apparent, comparisons with ZMA 54666 (a first-year male in non-breeding plumage) were restricted to the relevant classes (e.g. first-year males only, all birds excluding breeding adults, etc.). In adult males, adult females or first-year females, the distribution of measurements of characters 1–4 appeared not to differ significantly from a normal distribution, and, hence, despite small sample sizes, we assumed the measurements of these characters to follow a normal distribution in first-year males as well. When the observed value of ZMA 54666 for characters 1–6 was not within mean ± 1.96 SD or mean ± 2.56 SD for those found in *G. adamsii* and / or *G. immer* we considered the

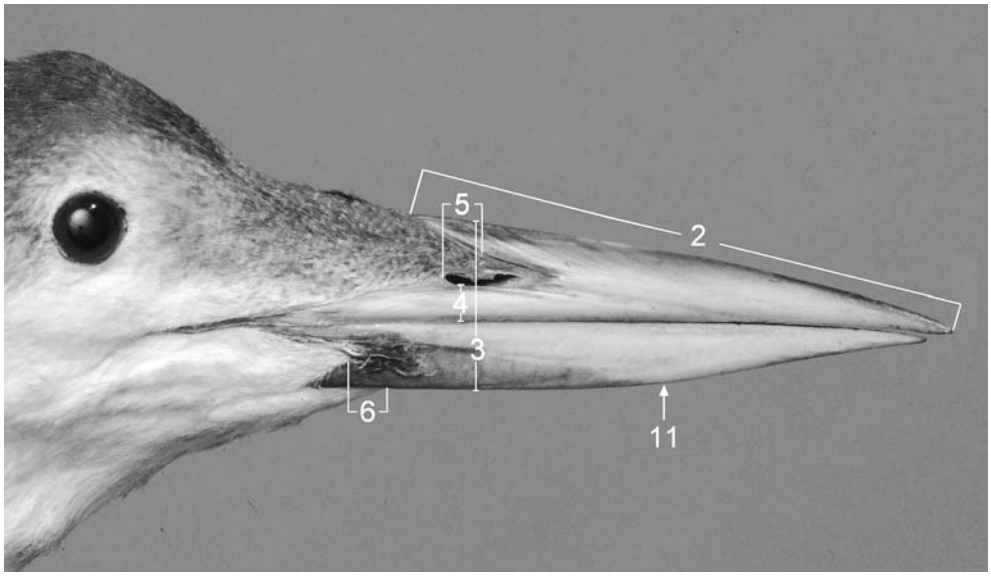

Fig. 2 Lateral view of the head of ZMA 54666, a hybrid between White-billed Diver *Gavia adamsii* and Great Northern Diver *G. immer*, with measuring methods

difference significant at $P = 0.05$ or $P = 0.01$ level, respectively (Quinn and Keough 2002). For testing whether characters 7–15 in ZMA 54666 departed significantly from *G. adamsii* and / or *G. immer* we used Fisher's Exact Probability tests (Siegel 1956) with the observed value for ZMA 54666 tested against the less extreme values observed in the putative parent species. The CDF analysis was undertaken on characters 1–6 for males only. Significance was assumed if $P < 0.05$ in a two-tailed test.

Additionally, we compiled records of (apparent) hybrids in Gaviidae in the literature, and evaluated their status on the basis of the description provided and the differentiating characters as identified above.

Results

Evaluation of a hybrid *G adamsii* × *G immer*

For the wing and bill measurements (characters 1–4) in at least one of the two species females were significantly smaller than males (Student's *t* test, *G. immer*, characters 1–4, all $t > 2.96$, $df = 24$–41, all $P < 0.02$; *G. adamsii*, character 1, $t = 3.07$, $df = 6$, $P = 0.02$) and first-year males were significantly smaller than adult males (Student's *t* test, *G. immer*, character 3, $t = 2.04$, $df = 25$, $P = 0.05$; *G. adamsii*, character 1–2, $t > 2.43$ $df = 8$–11, $P < 0.03$). Characters 5–12 did not show significant age- or sex-related differences (Mann-Whitney U, all $P > 0.05$), and hence for comparison specimens were included irrespective of age or sex. Character 13–15 were strongly age-dependent (Mann-Whitney U, all $P < 0.05$) and we excluded adult breeding birds in the comparisons, since the head and neck of these birds are all black.

For males of the two putative parent species, the overall assignment of individuals to their original sample by the CDF analysis was 100%, thus showing a clear-cut separation between the two species. This was valid when we included characters 1–6 (not shown) and, when, because of small sample sizes, character 1 was omitted from the analysis (Fig. 3). When the males were grouped according to age (first year and adult) and species (*G. immer* and *G. adamsii*), thus creating four groups, the overall assignment of individuals to their original sample by the CDF analysis was 74.3%.

ZMA 54666 is a large bird which at first sight has bill shape and head markings as in *G. adamsii*, but which has nevertheless always been registered in ZMA as a *G. immer*. Detailed analysis of the 15 characters listed in Methods revealed the following: ZMA 54666 is significantly larger than *G. immer* in characters 2, 3 and 6 (all $P < 0.01$), whereas character 5 is significantly smaller than that observed in *G. adamsii* ($P < 0.01$). ZMA 54666 differs significantly from *G. adamsii* in characters 7, 10 and 12 (Fisher's Exact probability Test, all $P = 0.045$) and from *G. immer* in character 7 (Fisher's Exact probability Test, $P = 0.014$). In the CDF analysis ZMA 54666 is precisely positioned between the two putative parent species, whether characters 1–6 are included in the analysis (not shown) or only characters 2–6 (Fig. 3).

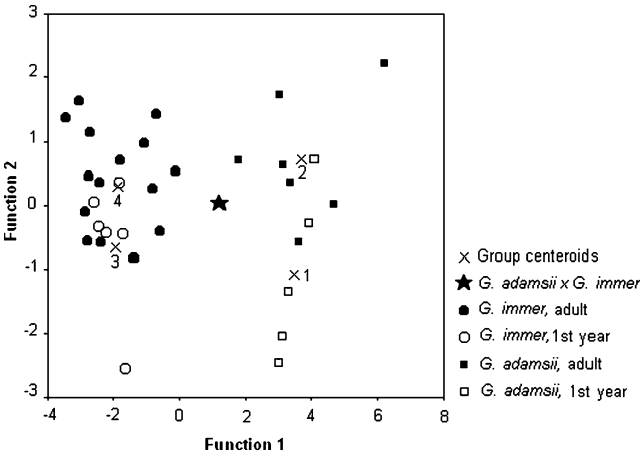

Fig. 3 Canonical Discriminant Function analysis of male White-billed Diver *Gavia adamsii* ($n = 12$) and male Great Northern Diver *G. immer* ($n = 23$) and ZMA 54666 a hybrid between these two species. Function one and two account for 93.7% and 5.4% of the variance, respectively

Other hybrid divers

We found descriptions of putative hybridisation for three species combinations, involving four of the five species of divers, plus one case of presumed back-crossing. A pair consisting of *G. adamsii* and *G. immer* accompanied by two chicks has been observed in the foothills of the Brooks Range (Alaska, USA) (McIntyre and Barr 1997). Whether these young were indeed offspring of both of the adults seen or whether they fledged successfully is unknown. A supposed hybrid between *G. adamsii* and *G. immer* is stored in the Royal Ontario Museum (no. 76360), collected 7th December 1956 at Port Credit (Ontario, Canada) (Palmer 1962; Godfrey 1986; Phillips 1990). Its supposed hybrid status is based on only a few characters (bill shape, colour of upper parts, colour of primary shafts), features known to be not infallible for identification, and a more thorough examination of the skin should be undertaken to confirm that the bird really is a hybrid.

Among many skins of *G. pacifica* and *G. arctica* examined by Storer (1978), six appeared to show hybrid characters between these species. Hybridisation has also been suggested to explain the variation among these divers on the Commander Islands, NE Siberia (Johansen 1961), but Russell (2002) considers the occurrence of *G. pacifica* × *G. arctica* hybrids to be undocumented. Nevertheless, occasional pairs consisting of *G. pacifica* and *G. arctica* have been observed in the overlap area in NE Siberia, though without proof that hybrid offspring have been produced (Solov'ev et al. 1993).

A pair consisting of *G. immer* and *G. pacifica* was observed on a small lake in the Inuvik region (NW Canada). It was accompanied by two chicks, of which at least one fledged (Robertson and Fraker 1974). These chicks could have been hybrids.

A mixed pair of female *G. arctica* and male *G. immer* have been observed on Bear Island (Svalbard), both taking their share in the incubation of the single egg laid; the egg was predated by foxes before it hatched and no hybrids resulted (Løvenskiold 1964). In Scotland, an aberrant large diver which from plumage characters may have been a hybrid *G. arctica* × *G. immer* was paired with a *G. arctica* (Hunter and Dennis 1972). The aberrant bird, supposed to be a male on behaviour, was accompanied by a chick, but the purported hybrid nature of both father and chick remains unproven. Other supposed hybrids between *G. arctica* and *G. immer* (e.g. Van Havre 1931) have been shown to involve unusually large individuals of *G. arctica* (Voous 1961). Thus, hybridisation may take place within sister species pairs as well as between members of different species pairs, but the occurrence of hybrid offspring remains largely unproven. We consider the bird in ZMA the best documented case of hybridisation in Gaviidae to date.

Discussion

Of the 15 characters checked, ZMA 54666 differs significantly from *G. adamsii* in four characters (5, 7, 10, 12), whereas it differs significantly from *G. immer* in four characters (2, 3, 6, 7). As such, the hybrid is similar to *G. adamsii* in three characters (2, 3, 6), similar to *G. immer* in four characters (5, 10, 12, 15), seven characters fit both species (1, 4, 8, 9, 11, 13, 14), while in one character the bird shows an intermediate state (7). CDF analysis revealed a clear-cut separation between *G. adamsii* and *G. immer* on characters 1–6, and ZMA 54666 was positioned intermediately between these two species. On the basis of this heterogeneous set of characters, we conclude that ZMA 54666 is a hybrid between the two species, and as such the specimen is the first example of a hybrid between these two species.

From wing measurements (character 1), the sample of *G. immer* from the Netherlands and France agrees well with a sample of breeding birds from Baffin Island, Greenland and Iceland given by Heubeck et al. (1993) and Weir et al. (1996). The birds from mainland W Europe do not appear to include small-sized wintering birds from breeding grounds further south in N America, unlike the birds wintering in Scotland in which 7% of 69 birds examined shared measurements with birds from NW, C, and SE Canada (Heubeck et al. 1993; Weir et al. 1996). If *G. immer* from NW Canada does not reach mainland W Europe, the origin of hybrid ZMA 54666 is unclear, as NW, Canada is part of the area were *G. adamsii* and *G. immer* overlap in breeding range and were hybrids are most likely produced. However, both species winter off the Norwegian coast (Haftorn 1971) and both migrate through Norway and Sweden (Risberg 1990; Folvik and Mjøs 1995; Hirschfeld 2000). A *G. immer* joining a migrant *G. adamsii* towards its breeding grounds in N Russia or a *G. adamsii* joining a migrant *G. immer* to its breeding grounds on Iceland or Greenland may easily lead to mixed pairings and occasional hybrids.

Given that there are only five species of divers and that all occur sympatrically with one or more species in at least parts of their range, there are ten possible combinations of hybrids. Above we evaluated the evidence for the occurrence of hybrids in divers and established that indeed hybridisation may have occurred between four species in four combinations. As such, the incidence of hybridisation (sensu Grant and Grant 1992) in divers is 80% (four of the five known species were involved), ranking the order among those with the greatest propensity to hybridise. If the recorded hybridisation in Gaviiformes could be proven in all cases, the group would contradict the assumption that incidence of hybridisation in small orders is relatively low. Hybridisation in some of the larger orders (e.g. Galliformes and Anseriformes) has been acknowledged for more than a 100 years (Randler 2004) and this together with the often markedly aberrant plumage characters of the hybrids possibly lead to greater attention of recording hybrids in these orders.

Zusammenfassung

Hybridisation bei Seetauchern (Gaviiformes)

Die Häufigkeit von Hybridisation unterscheidet sich erheblich zwischen Vogelordnungen und der Anteil hybridsierender Arten ist im allgemeinen in artenarmen Ordnungen geringer. Auch in der nur fünf Arten umfassenden Ordnung der Seetaucher wurde selten über mutmaßliche Hybridisation berichtet. Wir beschreiben hier einen Vogel (ZMA 54666) mit heterogener Merkmalskombination aus der Sammlung des Zoologischen Museums Amsterdam. Einige Merkmale stimmten mit Gelbschnabeltaucher Gavia adamsii, andere mit Eistaucher G. immer überein, wieder andere waren intermediär ausgeprägt. Eine Kanonische Diskriminanzanalyse aller Merkmalsausprägungen positionierte den Vogel zwischen den beiden mutmaßlichen Elternarten, wodurch sein Hybridstatus sehr wahrscheinlich wird. Eine Literaturübersicht zeigt, dass Hybridisation zwischen Seetauchern zwar selten, aber immerhin zwischen vier der fünf Arten sowie in einem Fall als F1-Rückkreuzung vermutet wurde, obwohl die Belege in allen Fällen dürftig sind. Sollte sich dieser hohe Anteil an in Hybridisation verwickelten Arten bestätigen, stünden Seetaucher in dieser Hinsicht unter allen Vogelordnungen mit an der Spitze. Dies wider-

spräche der Annahme, in artenarmen Ordnungen sei ein geringerer Anteil der Arten an Hybridisation beteiligt als in großen Ordnungen.

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