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COMMENTARY

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THE PROBLEM OF MOLT AND PLUMAGE HOMOLOGIES AND THE FIRST PLUMAGE CYCLE

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Abstract. The recent paper by Howell et al. (2003) recognizes that birds have evolved special plumages before entering the adult plumage cycle that should, therefore, be named differently in the terminology introduced by Humphrey and Parkes (1959) for plumages and molts (the H-P system). We agree with the principle of this suggestion, but we nevertheless suggest that birds take different lengths of time and different numbers of molts to enter the adult molt cycle and to acquire the adult plumage. We suggest that this variation should not be concealed by the assumption of an artificial first cycle of the same length as subsequent cycles, but should be reflected in the terminology of plumages and molts. We also suggest a distinction between entering the adult molt cycle and entering the adult plumage cycle. A main problem of the H-P system and Howell et al.'s modification is the claim that it is based on the concept of homology. In our opinion, there are no firm and convincing criteria on which to base a plausible phylogeny of plumages and molts. We would prefer to call Howell et al.'s modified H-P system a ''terminology'' for molts and plumages without the claim to determine homologies. We suggest that plumages or molts having the same Howell et al. term should be called ''comparable,'' rather than homologous. Moreover, it is debatable whether the phylogeny of molt is always the same as the phylogeny of plumages, as the H-P system claims by linking one molt to one plumage. We believe that the H-P system and Howell et al.'s modification of it remains too rigid to adequately reflect the evolution of molts and plumages.

Key words: homology, interrupted molt, molt, phylogeny, plumage, serial molt, terminology.

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El Problema de las Homologías de la Muda y el Plumaje y el Primer Ciclo del Plumaje

Resumen. El artículo reciente de Howell et al. (2003) reconoce que las aves han desarrollado a través de la evolución plumajes especiales que ocurren antes del ciclo del plumaje adulto y que deberían, por lo tanto, tener un nombre diferente en la terminología introducida por Humphrey y Parkes (1959) para los plumajes y las mudas (el sistema H-P). Nosotros estamos de acuerdo con el principio de esta sugerencia, pero sin embargo sugerimos que las aves toman diferentes períodos de tiempo y diferentes números de mudas para entrar al ciclo de muda adulto y para adquirir el plumaje adulto. Sugerimos que esta variación no debería ser enmascarada por la suposición de un primer ciclo artificial de la misma longitud de los ciclos subsecuentes, sino que debería reflejarse en la terminología de plumajes y mudas. También sugerimos una distinción entre entrar al ciclo de muda adulto y entrar al ciclo de plumaje adulto. Un problema principal del sistema H-P y de la modificación de Howell et al. es la idea de que están basados en el concepto de homología. Nuestra opinión es que no existen criterios firmes y convincentes sobre los cuales basar una filogenia plausible de los plumajes y las mudas. Preferiríamos tratar al sistema H-P modificado por Howell et al. como una ''terminología'' para mudas y plumajes, sin pretender determinar homologías. Sugerimos que los plumajes o las mudas que tienen el mismo término en el sistema de Howell et al. deberían llamarse ''comparables'' en lugar de homólogos. Más aún, es debatible si la filogenia de la muda es siempre igual a la filogenia de los plumajes, como el sistema H-P asevera al conectar una muda con un plumaje. Creemos que el sistema H-P y la modificación de Howell et al. son todavía demasiado rígidos para reflejar adecuadamente la evolución de la muda y los plumajes.

The recent paper by Howell et al. (2003) is a welcome impulse to reanimate the discussion on the comparative study of plumages and molts. It suggests a solution to a problem, already discussed by Stresemann (1963) and Amadon (1966), in the terminology introduced by Humphrey and Parkes (1959) for molts and plumages (the H-P system).

Here we do not want to revisit all the points mentioned earlier on the H-P system (e.g., Stresemann 1963, Humphrey and Parkes 1963, Amadon 1966, Willoughby 1992, Rohwer et al. 1992, Jenni and Winkler 1994). We would like to draw attention to two points that (re-) emerge from the Howell et al. (2003) paper: (1) problems with the first plumage cycle and (2) the claim that the H-P system is based on the concept of homology.

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THE FIRST PLUMAGE CYCLE

The main change to the H-P system proposed by Howell et al. (2003) is based on the recognition that birds have evolved special plumages before entering the adult plumage cycle. Therefore, not only the juvenile plumage, but also postjuvenile (newly termed formative) plumages may not be comparable, or even homologous, to plumages of the adult cycle. This is a big step forward and a major achievement.

Howell et al. (2003) apparently assume that the first cycle is of the same duration as subsequent cycles, keeping in line with the rigid H-P system. In consequence, the plumage produced by the complete postjuvenile molt of, for example, the House Sparrow (*Passer domesticus*, which then also develops sexual dichromatism) is named formative (following Table 1 in Howell et al. 2003), although this plumage looks exactly the same as in the adult bird and also has the same function. Thus, two similar plumages are named differently. In Palearctic passerine species with their first complete molt on the African wintering grounds (e.g., at the age of about 4–6 months), it remains unclear whether this molt should be named prebasic or formative. The molt resembles a prebasic molt but occurs substantially earlier, and therefore may not meet Howell et al.'s criterion of correspondence with prebasic molts in the Simple Basic Strategy.

Birds take different lengths of time and different numbers of molts to enter the adult molt cycle and to acquire the adult plumage. We suggest that this variation should not be concealed by the assumption of an artificial first cycle of the same length as subsequent cycles, but should be reflected in the terminology of molts and plumages. We also suggest a distinction between entering the adult molt cycle and entering the adult plumage cycle. The young bird enters the adult molt cycle when it first performs the same molt as the adult. It enters the adult plumage cycle when it acquires for the first time the same plumage as the adult. In many species, the adult plumage cycle is achieved at the same time as the adult molt cycle. A House Sparrow, as an example, enters the adult molt and plumage cycle at the age of about 3–4 months by a complete postjuvenile molt. The Garden Warbler (*Sylvia borin*) enters the adult molt and plumage cycle at the age of about 6 months by a complete molt on the African wintering grounds. Passerines with a single annual molt enter the adult molt and plumage cycle at the age of about 14 months when undergoing their first complete postbreeding molt. However, in some species, the adult plumage cycle is entered later than the adult molt cycle. Passerines with a prebreeding (prealternate) molt enter the adult molt cycle with the prebreeding molt and the adult plumage cycle with the first complete postbreeding molt when the last juvenile feathers are replaced. Large gulls enter the adult molt cycle at the age of about 9 months, but it takes them 3–4 years to attain the adult plumage. We therefore advocate a system with a first period (i.e., the period juvenile—postjuvenile—immature, before the bird enters the adult cycle) that may not have the same length as the adult cycle, but may be shorter with fewer molts or plumages, or longer with more molts or plumages, than the adult cycle. We also opt for a system that dissociates molt and plumage cycles where necessary.

Howell et al. (2003:636) adopted a definition of molt, ''the normal and regular growth of feathers by which plumages are attained,'' which is different from the usual one: ''the normal *shedding* of feathers and the replacement of most or all of these by a new generation of feathers'' (Humphrey and Parkes 1959:6, italics ours; see also Campbell and Lack 1985:361). This leads to the statement that the juvenile plumage is ''always attained by a complete molt'' (Howell et al. 2003:642), even in the numerous species without a downy plumage (all Piciformes, many Psittaciformes, most Coraciiformes and some Corvidae); thus without shedding feathers before acquiring the juvenile plumage. We advocate keeping the conventional definition of molt.

THE HOMOLOGY CLAIM

The H-P system claims to be based on the concept of homology, the phylogenetic relationship of plumages and molts (Humphrey and Parkes 1959), and this claim is maintained until today (Rohwer et al. 1992, Howell et al. 2003). As an extensive amount of literature demonstrates, the determination of homologies is a difficult task and a great aim, even in features which have been studied in much detail and for which fossil records are available (see for instance the recent discussions on such an apparently simple thing as the numbering of forelimb digits in the context of the origin of birds; Prum 2003). Also Howell et al. (2003:637) apparently feel uneasy when they write that ''a crux of the H-P system is how one identifies homologies.'' According to Rohwer et al. (1992:298), molt homologies should be determined by comparing ''the timing, extent, and color change in each molt with that of closely related species that have already been described.''

The main problem here is that, in our opinion, there are no firm and convincing criteria on which to base a plausible phylogeny of plumages and molts. Both have various characteristics, for instance timing, extent and sequence of molt, and color of plumage, which are regulated by different factors and control mechanisms (color: Kimball and Ligon 1999; timing and extent: Gwinner et al. 1971, Noskov and Rymkevich 1985), or their control is hardly known (sequence of molt). It is quite unclear how these characteristics should be weighted when establishing a homology of plumages and molts.

Color, the appearance or display function, of plumage was used earlier as the main criterion to name plumages (Stresemann 1963, Amadon 1966) and is also evident in the ''color change'' criterion by Rohwer et al. (1992). However, it still remains unclear, and probably differs among taxa, whether the bright or the dull plumage is the ancestral one (Amadon 1966, Kimball and Ligon 1999).

The number of plumages and the extent of molts during the (mostly) annual cycle seems to be the main criterion for assigning terms to plumages and molts in the H-P system. However, as Humphrey and Parkes (1959) and Howell et al. (2003) mention, it is likely that nonbasic plumages are not homologous among species (except for closely related taxa; but see the *Sylvia* example below), and that they may have evolved independently in different groups of birds. Be-

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cause nonbasic plumages may not be homologous, the H-P system can only suggest that the juvenile and the basic plumages are homologous across all birds. If one allows for the same plumage to be produced by a complete or an incomplete molt, there are no sound arguments to state that even the basic plumage of the H-P system is homologous across all birds. It is conceivable that an originally additional plumage (produced by an incomplete molt, hence alternate) may now be produced by a complete molt. If the complete prebasic molt remains, there are two complete annual molts (for examples see Prys-Jones 1991). If, however, the formerly complete prebasic molt is reduced to an incomplete molt, uncritical application of the H-P system would name the formerly incomplete, now complete molt the prebasic one and the reduced molt the alternate. Hence, homology among molts and plumages would be lost. As has been shown in many species, the extent of a molt may vary widely even within a species. An illustrative case are the *Sylvia* species.

The western Whitethroat (*Sylvia c. communis*) undergoes a complete postbreeding (prebasic) molt after the breeding season and before autumn migration, and a partial prebreeding (prealternate) molt on the African wintering grounds before spring migration. The closely related Garden Warbler, however, undergoes its complete molt on the African wintering grounds (hence it should be named a prebasic molt) and has an additional partial (postbreeding) molt after the breeding season. Howell et al. (2003:647) state that ''An alternate plumage, attained by a prealternate molt, is any plumage inserted into the basic cycle,'' so this additional molt should be named prealternate, but we doubt that it can be regarded as homologous to the prealternate molt of the Whitethroat. The extent of the postbreeding molt of the Garden Warbler is quite variable and a few molt completely (Jenni and Winkler 1994). On the African wintering grounds, the entire plumage always seems to be renewed completely (there are no spring birds found with two feather generations). It thus seems that, relative to the Whitethroat, the Garden Warbler has reduced the extent of the formerly complete postbreeding molt to a partial molt and expanded the extent of the formerly partial prebreeding molt to a complete molt (but the direction of this hypothesized evolution is unknown and may be the opposite). Intermediate stages are found in many Sylviidae; for example, the Barred Warbler (*S. nisoria*) and the eastern Whitethroat (*S. communis icterops*) which have two incomplete, but largely complementary molts: an extensive part of the plumage, including remiges, is molted postbreeding in the breeding area, and an extensive part, including remiges, prebreeding in Africa (Hasselqvist et al. 1988, Jenni and Winkler 1994). Since many feathers are molted twice per year, this cannot be regarded as a single molt interrupted during autumn migration. Hence, uncritical application of the H-P system would name the homologous molts of the Garden Warbler and the western Whitethroat differently, and it remains unclear how to name the two incomplete molts of the Barred Warbler.

Other problems are that a molt may be interrupted in time and that two molts may overlap, as mentioned by Humphrey and Parkes (1959). Two examples may illustrate these problems, the case of interrupted molts in passerines and other species, and the case of serial molt (*Staffelmauser*) occurring in raptors, storks and other large birds.

In some species, the molt of remiges can be interrupted during migration or reproduction and subsequently resumed from the point of interruption (e.g., Black Kite [*Milvus migrans*], Forsman 1999; some passerines, Jenni and Winkler 1994). Humphrey and Parkes (1959) specifically mention temporally discontinuous molts. Therefore, if one allows for one plumage to be produced by two parts of an interrupted molt, one accepts that one plumage is produced by two physiological molt events. The criterion of the pattern and sequence of feather renewal is given preference to the criterion of the temporal occurrence of molt.

In adult large storks and raptors, every year during the annual molt a new molt wave starts which is finished only several years later after having been interrupted for some months each year (Sutter 1980, Edelstam 1984). Hence, in an adult bird several molt waves run simultaneously through the remiges and are turned on and off within the annual cycle of the bird (serial molt or *Staffelmauser*). Is the annual rhythm of the occurrence of molt (one molt period per year) or the pattern of feather renewal the criterion by which to homologize molt? Howell et al. (2003) merely accept the occurrence of a single molt period per year as a criterion (the physiological turning on and off). They do not take into account the main characteristic of this molt (that it is serial), although it might be a phylogenetically more important criterion (is it plausible to suggest a homology between the annual molt of a House Sparrow and a large raptor by naming it prebasic?). In contrast to the case of simple interrupted molts mentioned above, in the case of overlapping interrupted molts (serial molts) Howell et al. (2003) give preference to the criterion of the temporal occurrence of molt and not the molt pattern.

A side question is what a feather generation in the H-P system actually is. Humphrey and Parkes (1959) confined the term plumage to a single feather generation. However, they did not really define what a feather generation is, but agreed with Stresemann (1948:190) that ''the resumption of feather growth after a period of interrupted moult does not mean at all that a new plumage is assumed.'' If one accepts that a single molt can be interrupted and resumed, and produces a single feather generation (or plumage, as defined by Humphrey and Parkes 1959), several molts produce several plumages simultaneously in large raptors and storks, a situation not accounted for by Howell et al. (2003).

From this, the question follows whether the homology or phylogeny of molt is always the same as the homology or phylogeny of plumages, as the H-P system claims by linking one molt to one plumage. To elucidate the phylogenies, we rather think of two different, but interrelated processes, controlled by different mechanisms and with different phylogenies: the sequence of plumages (e.g., downy—juvenile—postjuvenile—annual postbreeding) and the pattern (i.e., complete, partial, interrupted, serial, etc.) and temporal occurrence of molt.

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CONCLUDING REMARKS

We clearly welcome the endeavor for a comparative study of plumages and molts on the basis of phylogeny. We are also aware that we criticize, but hardly offer solutions in this comment. However, it appears to us that the uncertainties of identifying the homologies of plumages and molts are overwhelming. We believe that the terminology of the H-P system as modified by Howell et al. (2003) is still too rigid. It unnecessarily restricts our ability to find homologies and phylogenies and cannot adequately reflect the evolution of molts and plumages. An open, unrestricted view, however, is necessary to elucidate the evolution of plumages and molts. Accepting that plumage cycles and molts are more diverse than reflected in the H-P system, the four main molt patterns suggested by Howell et al. (2003:651) cannot be ''a powerful tool for comparative studies, not least for the evolution of molt strategies across taxa.'' The inherent claim for finding homology in plumages and molts with the H-P system is misleading and does not give justice to the interesting and complex process of their evolution. We therefore advocate calling Howell et al.'s modified H-P system a ''terminology'' for molts and plumages without the claim of determining homologies. We suggest calling plumages or molts having the same Howell et al. term ''comparable'' (within the H-P system), rather than homologous.

A terminology should facilitate communication. What do the terms of the H-P system actually tell a reader unfamiliar with molt and plumage of a species? For a bird with a simple pattern such as a single annual complete molt, there are obviously no problems and any sensible terminology could do. For birds with more complex plumage and molt cycles, the H-P system tells us which molt is the complete (the prebasic). The terms prealternate and presupplementary molts indicate a partial molt, but need to be explained, because these terms do not tell the reader when this molt occurs in the annual cycle or relative to other molts, nor what kind of plumage is produced. The modifications by Howell et al. (2003) do not clarify the situation, because now the new term ''formative'' needs to be explained and the numbering of the basic plumages has changed. The terms used by others (e.g., Amadon 1966, Roselaar in Cramp 1977–1994, Jenni and Winkler 1994), despite some disadvantages, are descriptive and much more self-explanatory and, thus, facilitate communication. Moreover, these terms do not claim to reflect homologies.

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