

# ‘Biological’, ‘phylogenetic’ and ‘monophyletic’ species – same or different?

PER ALSTRÖM & KRISTER MILD

**H**umans have presumably always given names to different organisms. Historically, almost any recognisable form was called a species. Virtually all plants have been classified based on such a ‘morphological’ or ‘phenetic’ species concept (Gornall 1997). The same is probably true for most other organisms. The discovery of evolution in the 19th Century brought a completely new perspective on the nature of species. In 1942, Ernst Mayr formulated the ‘biological’ species concept (hereafter BSC), which soon became widely accepted among zoologists, especially ornithologists. However, the BSC has also been criticised, and several alternative species concepts have been proposed, for example, ‘evolutionary’ (Simpson 1961), ‘ecological’ (Van Valen 1976), ‘recognition’ (Paterson 1985) and ‘cohesion’ (Templeton 1989) concepts. None of these has ever been widely applied to birds. In particular, the BSC has recently been challenged by proponents of two kinds of ‘phylogenetic’ species concepts, the ‘phylogenetic’ species concept (hereafter PSC) and the ‘monophyletic’ species concept (hereafter MSC) (e.g. Rosen 1978, Nelson & Platnick 1981, Mishler & Donoghue 1982, Cracraft 1983, Lidén & Oxelman 1989, Nixon & Wheeler 1990, Davis & Nixon 1992, Zink & McKittrick 1995). Lists of ‘phylogenetic’ species of birds have been published for at least two areas, the Azores (Hazevoet 1995) and the Netherlands (Sangster et al. 1999), as well as for at least one major group of birds, the birds-of-paradise (Paradisaeidae) (Cracraft 1992).

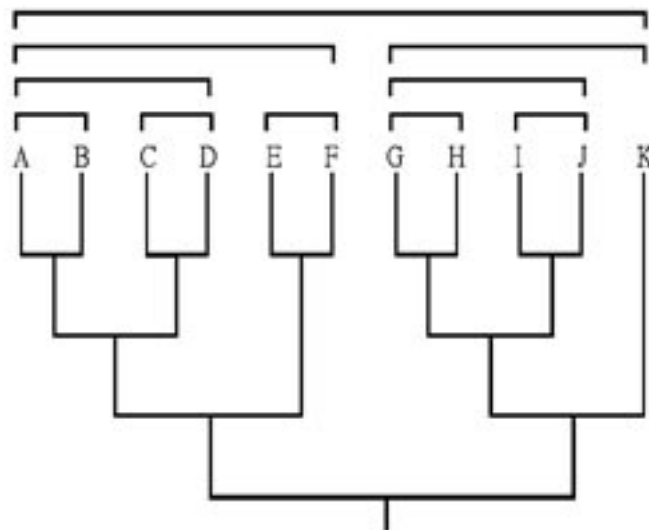
According to de Queiroz (1998) “all modern species definitions are variations on the same general species concept,” and they should be viewed as complementary rather than incompatible. He concludes that the main discrepancies between the different species concepts result from their focus on different stages in the divergence of lineages: diagnostic differences (the hallmark of the PSC) evolve before reproductive isolation (the crux of the BSC). We agree with that, and argue below that, also in their practical application, the differences between the BSC, MSC and PSC, especially the two former, are not so great as is generally believed.

The British Ornithologists’ Union has recently proposed guidelines to assist in

the assignment of species rank (Helbig *et al.* 2002).

## The ‘Biological’ Species Concept

The BSC rests on the notion that species are ‘harmonious gene pools’ that are protected from each other by reproductive isolating barriers (Mayr 1996). Species are defined as “groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups” (Mayr 1942). The cornerstones of this concept are the capacity to interbreed with individuals of the same species and the reproductive isolation from individuals of other species. Reproductive isolation refers to



**Fig. 1. Tree showing relationships between 11 taxa (A–K). All of the monophyletic groups have been marked. All other combinations of taxa are non-monophyletic.**



DNA data suggest that eastern and western Yellow Wagtails are distantly related to each other, and accordingly that they should be treated as at least two species. Under the PSC and the MSC the Yellow Wagtail could be split into up to eight species.

1. *Motacilla flava flavissima*. © Ray Tipper, England, 4.8.1990
2. *Motacilla flava flavissima*. © Ray Tipper, England, 31.5.1992
3. *Motacilla flava taivana*. © Ray Tipper, Hong Kong, 25.10.1987
4. *Motacilla flava tscutschensis*. © Ray Tipper, Hong Kong, 9.5.1987

intrinsic isolation by means of reproductive isolating barriers (as opposed to extrinsic, geographical, isolation). In other words, species are defined based on the actual or, when it comes to disjunct populations, potential interactions between populations. Different taxa are treated as conspecific if they interbreed to the extent that they can be assumed to eventually fuse. Taxa that are not presently in contact are classified as the same species if they can be expected to fuse if their ranges would meet.

### 'Phylogenetic' Species Concepts

There are two main 'phylogenetic' species concepts: (1) the 'phylogenetic' species concept (PSC; formulated or supported

by Nelson & Platnick 1981, Cracraft 1983, 1989, Nixon & Wheeler 1990, Davis & Nixon 1992, Zink & McKittrick 1995) and (2) the 'monophyletic' species concept (MSC; supported by Mishler & Donoghue 1982, Donoghue 1985, Mishler 1985, Lidén & Oxelman 1989, Lidén 1990, and ourselves). (Lidén & Oxelman 1989 referred to the MSC as *the* phylogenetic species concept, while they classified the PSC as the 'operational' species concept. However, since the first one is widely known as the PSC that terminology is followed here to avoid confusion.)

Unlike the BSC, both the PSC and MSC give primacy to evolutionary history. The PSC attempts to delineate the (basal) products of a process of differentiation. The presence of one or more (fixed) unique character(s) in a popula-

tion is considered to be evidence that it has had a unique evolutionary history. Cracraft's (1989) definition, which has received most attention among ornithologists, reads: "A phylogenetic species is an irreducible (basal) cluster of organisms, diagnosably different from other such clusters, and within which there is a parental pattern of ancestry and descent." That it is "irreducible" means that it cannot be further subdivided. "Diagnosably different" means that the individuals in the group should display unique characters. The unique characters can be, for example, morphological, biochemical, and/or ethological, and must be unique for the cluster. The demand for "parental pattern of ancestry and descent" in effect disqualifies single individuals, different morphs, different

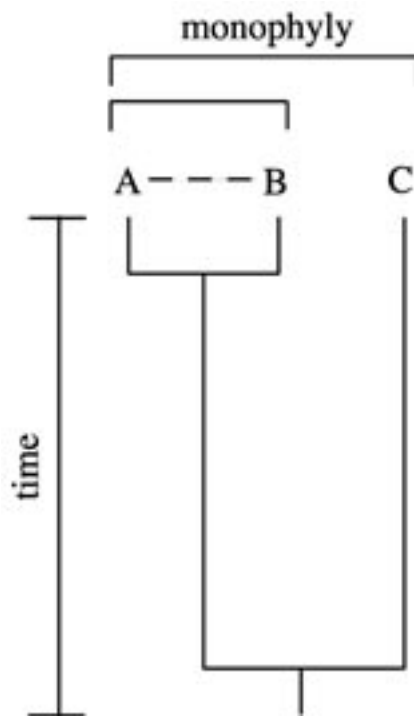


Fig. 2. The three taxa A, B and C are diagnosably different (e.g., A shows a white supercilium, B a yellow supercilium and C lacks a supercilium). From this it can be deduced that they have had separate evolutionary histories for some time (i.e., there has been little or no gene flow between them in that period). A and B have recently come into contact as the result of range expansion, and they interbreed to the extent that they are expected to fuse some time in the future (unless reproductive isolating barriers evolve before that). Both A and B are reproductively isolated from C. Under the BSC, A and B are treated as subspecies of the same species (because of the rampant interbreeding between them), while C is treated as a separate species (due to lack of interbreeding with A and B). Under the MSC, three classifications are possible: (1) A, B and C are considered to be three separate species (since all are distinct), (2) A, B and C are treated as the same species (since they form a monophyletic group), or (3) A and B are classified as the same species (since they form a monophyletic group, whose members are believed to have diverged recently) while C is a separate species. We favour the third alternative. Under the PSC, A, B and C are treated as three separate species (since they are diagnosably different). If A and B eventually fuse as a result of hybridisation, they will no longer be recognised as separate taxa by any species concept.

sexes, different stages in an individual's development and groups of individuals sharing some unique character(s) of mitochondrial DNA (since mitochondrial

#### BSC/MSC

*M. aguimp* with subspecies *aguimp* and *vidua*  
*M. maderaspatensis*  
*M. samveasnae*  
*M. grandis*  
*M. cinerea* with subspecies *cinerea*, *patriciae* and *schmitzi*  
*M. citreola* with subspecies *citreola* and *calcarata*<sup>1</sup>  
*M. flava* with subspecies *flavissima*, *flava*, *beema*, *thunbergi*, *iberiae*, *cinereocapilla*, *pygmaea*, *feldegg*, *lutea* and *leucocephala*<sup>2</sup>

*M. tschutschensis* with subspecies *tschutschensis*, *taivana* and *macronyx*<sup>2</sup>  
*M. alba* with subspecies *yarrellii*, *alba*, *subpersonata*, *baicalensis*, *ocularis*, *lugens*, *leucopsis*, *alboides* and *personata*<sup>3</sup>

#### PSC(/MSC)

*M. aguimp*<sup>4</sup>  
*M. maderaspatensis*  
*M. samveasnae*  
*M. grandis*  
*M. cinerea*<sup>5</sup>  
*M. citreola*  
*M. calcarata*  
*M. lutea*<sup>6</sup>  
*M. flava*<sup>7</sup>  
*M. thunbergi*<sup>8</sup>  
*M. iberiae*<sup>9</sup>  
*M. feldegg*  
*M. tschutschensis*  
*M. taivana*  
*M. macronyx*<sup>8</sup>  
*M. yarrellii*  
*M. alba*  
*M. subpersonata*  
*M. baicalensis*  
*M. ocularis*  
*M. lugens*  
*M. leucopsis*  
*M. alboides*  
*M. personata*

Table 1. Possible classification of the Palearctic wagtails under different species concepts. The classification in the right column is acceptable under the MSC, but we favour the MSC alternative in the left column to stress the presumed recent divergence of the taxa that are treated as subspecies.

1. We believe that *citreola* and *calcarata* are recently diverged sister taxa (contra results from mitochondrial DNA [Ödeen & Alström 2001, Alström & Ödeen 2002, Voelker 2002] but in agreement with nuclear DNA data [Ödeen & Alström 2001, Alström & Ödeen 2002]).
2. According to DNA data (Ödeen & Alström 2001, Alström & Ödeen 2002, Voelker 2002), the Yellow Wagtail is non-monophyletic. If that is true, the Yellow Wagtail must be treated as at least two separate species under the MSC. The classification under the BSC depends on whether the different taxa can be expected to eventually fuse as a result of interbreeding. Although *tschutschensis* interbreeds with *beema* and *thunbergi*, the genetic divergence between *tschutschensis* and *beema/thunbergi* is so large that they seem unlikely to ever merge with each other. Accordingly, the Yellow Wagtail complex is probably most appropriately classified as two species under the BSC.
3. Since the White Wagtail complex is divided into two monophyletic groups (clades) according to mitochondrial DNA data (Ödeen & Alström 2001, Alström & Ödeen 2002), it could be treated as at least two species under the MSC. The relatively small genetic divergence between these two clades and the frequent interbreeding between *personata* from one clade and *alba* and *baicalensis* from the other clade suggests that the White Wagtail is best treated as a single species under the BSC.
4. The taxon *vidua* is not considered diagnosably different from *aguimp* with which it is, therefore, by priority, synonymised.
5. The taxa *patriciae* and *schmitzi* are not considered diagnosably different from *cinerea* with which they are, therefore, by priority, synonymised.
6. The taxon *flavissima* is not considered diagnosably different from *lutea* with which it is, therefore, by priority, synonymised.
7. The taxon *beema* is not considered diagnosably different from *flava* with which it is, therefore, by priority, synonymised.
8. The taxa *thunbergi* and *macronyx* are diagnosably different by molecular markers only.
9. The taxa *cinereocapilla* and *pygmaea* are not considered diagnosably different from each other or from *iberiae* with which they are, therefore, by priority, synonymised.

DNA is inherited maternally) (Cracraft 1983). Nixon & Wheeler (1990) and Davis & Nixon (1992), who formulated a similar phylogenetic species concept,

stressed that diagnostic characters should be fixed in the population(s), that is, they should be found in all comparable individuals.

Unlike other species concepts, the MSC has not been explicitly formulated. Its proponents (Mishler & Donoghue 1982, Donoghue 1985, Mishler 1985, Lidén & Oxelman 1989, Lidén 1990) stress that species should be monophyletic (cf. Fig. 1), in other words, that different populations of the same species should be more closely related to each other than to populations of other species. This approach, therefore, requires that a hypothesis of relationship be formulated before species are defined. However, although desirable, such a hypothesis need not be based on an analysis using modern methods of phylogenetic inference. For example, the different subspecies of White Wagtail were considered to be each other's closest relatives long before their relationships were analysed by modern methods.

### Delimitation of least-inclusive taxa

Much of the disagreement between proponents of different species concepts has focused on the principles by which least-inclusive taxa are delimited. Delimitation of least-inclusive taxa refers to the identification of the smallest name-bearing units. All taxonomists, irrespective of which species concept they favour, delimit least-inclusive taxa using morphological and other characteristics. The PSC is unique among the three species concepts discussed here in explicitly stating how least-inclusive taxa should be delimited: 'smallest diagnosable clusters'. The stringent principles used to delimit least-inclusive taxa under the PSC could

equally well be adopted by proponents of the BSC and MSC – in which case the same least-inclusive taxa would, theoretically, be recognised by all taxonomists, irrespective of which species concept they favoured. However, in reality the delimitation of allopatric least-inclusive taxa is often highly subjective, irrespective of the method and species concept applied. This is evidenced by the fact that different taxonomists often have differing opinions regarding the validity of certain taxa. For example, Mayr & Greenway (1960) recognised 41 least-inclusive wagtail taxa in the Palearctic, whereas Alström *et al.* (2003) only accept 30 of these. (Although the classification of Mayr & Greenway is based on the BSC, whereas Alström *et al.* is based on the MSC, that is not the source of the conflict.)

### Ranking of least-inclusive taxa

Under the BSC, least-inclusive taxa are ranked as either monotypic species or as subspecies of polytypic species. Determining the rank of a certain taxon under this concept is often highly subjective, and depends on the degree of observed or inferred reproductive isolation between this and other taxa (Fig. 2). If two or more taxa meet and form a hybrid zone, the degree of hybridisation, the fertility of the parental birds and the hybrids, the viability of the hybrids and the geographical and temporal stability of the hybrid zone need to be studied. Hybridising taxa are generally considered separate species under the BSC when: (a) hybridisation is very limited; (b) hybrid pairs have much

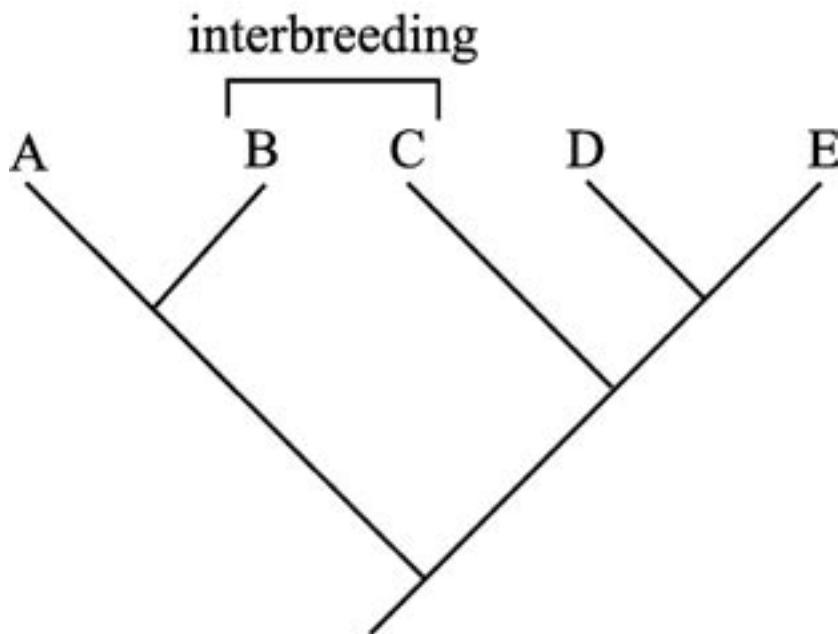
reduced fertility compared to pure pairs; (c) hybrids are sterile or have significantly reduced fertility; (d) hybrids are considerably less viable than their parents; (e) the hybrid zone is narrow and temporally stable (suggesting the existence of incomplete reproductive isolating barriers); or (f) if the geographical overlap increases as a result of a range extension, and hybridisation mainly occurs in the 'front wave', while it gradually ceases in areas where the taxa have been in contact longer (suggesting the evolution of reproductive isolating barriers). If these requirements are not met, the taxa are generally considered to be subspecies of the same 'biological' species – no matter how distinct they are in morphological, vocal and other aspects.

Taxa with non-overlapping distributions are classified as separate species under the BSC if it seems unlikely that they would interbreed freely in case of sympatry. The probability of interbreeding is inferred from the degree of similarity in morphology, vocalisations and other variables. Alternatively, experiments can be carried out to test whether sexual signals, such as song, are sufficiently different between taxa to prevent interbreeding between them in case of contact (however, interpreting the results from such experiments is not straightforward; cf. Alström & Olsson 1992 and Alström *et al.* 1997).

Most proponents of the PSC (Crafft 1983, 1989, McKittrick & Zink 1988, Hazevoet 1995, Zink 1997, Sangster *et al.* 1999) accept only one rank, species. In other words, all least-inclusive taxa are



Carrion and Hooded Crows qualify as at least two separate species under the PSC and MSC, although their status under the BSC is more difficult to decide. © Jari Peltomäki (left) and © Antero Topp, Helsinki (right).



**Fig. 3.** Under the BSC, the non-sister taxa B and C are treated as conspecific if they interbreed to the extent that they can be expected to eventually fuse. Under the PSC and MSC, non-monophyletic taxa are not acceptable. Accordingly, B and C are treated as separate species under the PSC and MSC, despite the rampant interbreeding between them.

treated as species under the PSC (on the condition that they are diagnosable) (Fig. 2). In contrast, Nixon & Wheeler (1990) and Davis & Nixon (1992) accept infraspecific taxa, but remark that these do not exhibit fixed differences from other taxa. The focus of the PSC on unique characters (or unique combinations of characters) renders it in practice similar to a morphological/phenetic species concept (Gornall 1997).

Any monophyletic group may be classified as a species under the MSC. However, in reality only least-inclusive taxa that are believed to have diverged relatively recently are classified as conspecific under the MSC (Fig. 2). Evidence of recent divergence comes from slight differentiation in morphological, vocal, behavioural or genetic traits in comparison with taxa that are treated as separate species. Ranking is thus often subjective. However, it is stressed that ranking has to be arbitrary, since evolution is a gradual process and an historical (phylogenetic) ‘continuum can only be arbitrarily divided’ (Lidén 1990). This rationale is different from that of the BSC, under which taxa are treated as conspecific if it is expected that present (or possible future) interbreeding may lead to fusion of these taxa. Importantly, unlike the BSC, subspecies of the same ‘monophyletic’ species are required to form a monophyletic group (cf. Figs. 2 and 3).

## Discussion

Sympatric, reproductively isolated taxa are treated as separate species under all species concepts. However, the taxonomic rank of least-inclusive taxa with disjunct or marginally overlapping ranges often differs under different species concepts (Fig. 2 and Table 1). Many such taxa can be expected to have diverged comparatively recently. Initially, recently diverged populations will exhibit no, or only slight and overlapping differences from each other. With time, genotypic, phenotypic and culturally inherited differences, such as song in oscine passerines, will accumulate in the separate populations. The rate of change can be expected to vary tremendously, both among lineages and among traits. During the initial stages in the differentiation process, the recently diverged taxa are necessarily difficult to define, no matter by which principles they are delimited. Several taxa in the western Yellow Wagtail *Motacilla flava* complex are presently at this stage (cf. Table 1). For example, adult males of *iberiae*, *cinereocapilla* and *pygmaea* differ on average from each other by morphological characters, but the overlap is too extensive to allow separation of all individuals. In other aspects they are not separable. Under the BSC, such poorly defined taxa are usually treated as subspe-

cies, since they are considered likely to eventually fuse if their ranges meet (Fig. 2). Such taxa can be treated as subspecies also under the MSC (provided they are considered sufficiently distinct to be recognised) (Fig. 2). In contrast, populations that do not meet the diagnosability criterion lack formal recognition under the PSC (Fig. 2).

Differences will eventually become fixed in diverging taxa. The number of fixed differences will increase with time. For example, *alba* and *yarrellii* in the recently diverged White Wagtail *Motacilla alba* complex exhibit fixed differences in plumage, but not in other variables. The older African Pied *M. aguimp*, Mekong *M. samveasnae*, White-browed *M. maderaspatensis* and Japanese *M. grandis* Wagtails are diagnosably different by morphology, songs, calls and mitochondrial DNA. Taxa that are at this evolutionary stage, displaying fixed inter-taxon differences, are invariably treated as species under the PSC, and may be treated that way also under the MSC (Fig. 2). Under the BSC, they are often classified as subspecies, since they are unlikely to be completely reproductively isolated from each other (cf. Fig. 2 and Table 1).

The White Wagtail complex is chosen here as a further example of differences and similarities in classification between different species concepts (Table 1). Under the BSC, it is usually considered to be a single species with several subspecies, because the different least-inclusive taxa (subspecies) interbreed where their ranges meet. The MSC may classify these taxa in exactly the same way, but not because they interbreed but because they are believed to be more closely related to each other than to other wagtails (i.e. they form a monophyletic group); ranking as subspecies rather than as species in this case is based on the belief that the entire group has diverged recently in comparison with taxa that are ranked as species. Alternatively, since inclusiveness is arbitrary under the MSC, the White Wagtail complex can be divided into two to nine species. The only requirements are that any polytypic species includes only subspecies that form monophyletic groups, and that non-monophyletic taxa are not created by the elevation of certain taxa to species rank (as is the case if e.g. *lugens* is treated as a species separate from the others; cf. Ödeen & Alström 2001, Alström & Ödeen 2002, Voelker 2002).



The White Wagtail can be split into up to nine species under the PSC and MSC, although it is probably best treated as a single species under the BSC. Although the plumages are distinctive, the different taxa differ only very marginally, if at all, in mitochondrial DNA.

*Motacilla alba alba* © Ray Tipper, Portugal, 19.1.2004.

*Motacilla alba ocularis* © Ray Tipper, Hong Kong, 27.11.1994.

*Motacilla alba leucopsis* © Ray Tipper, Hong Kong, 19.10.1987.

*Motacilla alba lugens* © Ray Tipper, Hong Kong, 10.1.1988.

Under the PSC, all of the White Wagtail taxa are separate species (although some of the taxa traditionally recognised are not considered to be diagnosable, and are hence not recognised at all by PSC proponents).

Intrinsic reproductive isolation is crucial in maintaining differences between species in sympatry. However, species definitions based on interbreeding and reproductive isolation, such as the BSC, inevitably misrepresent evolutionary history when non-monophyletic taxa are classified as the same species (Fig. 3). Under the BSC, the future outcome of interactions between different taxa is considered more important than the past history of these taxa. Whether that is a problem or an advantage is a matter of

taste. In our opinion, it is irrelevant for the present classification whether two distinct taxa with separate evolutionary histories might fuse sometime in the future as a result of interbreeding.

It has been argued by PSC advocates that it is imperative that all taxa have the same rank. This dogma rests on the belief that all least-inclusive taxa are equal and comparable. However, it is a necessary consequence of the process of evolution that all least-inclusive taxa are *not* equal (e.g. Lidén & Oxelman 1989, Lidén 1990, O'Hara 1993). As an example, consider the six least-inclusive wagtail taxa *alba* (White Wagtail), *cinerea* (Grey Wagtail), *thunbergi* ('Grey-headed Yellow Wagtail'), *flava* ('Blue-headed Yellow Wagtail'), *iberiae* ('Spanish Yellow Wagtail') and *cinereocapilla* ('Ashy-headed

Yellow Wagtail'). The four latter (belonging to the western Yellow Wagtail complex) are similar in most morphological, vocal, behavioural and ecological aspects, have parapatric breeding distributions and interbreed where their ranges meet. They are usually treated as conspecific under the BSC and MSC, although at least the two former merit recognition as species under the PSC. Moreover, according to DNA (Ödeen & Alström 2001, Alström & Ödeen 2002) they form a monophyletic, presumably recently diverged, group. In contrast, *alba* and *cinerea* are strikingly different from each other and from the Yellow Wagtail complex in a number of morphological, vocal, behavioural and ecological variables, and are sympatric with each other and with the Yellow Wagtail complex without inter-

## Glossary

**Allopatry (adj. allopatric):** Two taxa are allopatric when they occur in separate geographical areas, at least during the breeding season. Disjunct allopatry is the classic allopatry (opposite to sympatric), and means that taxa are completely separated geographically. Parapatry (adj. parapatric) describes the situation in which two ranges are contiguous without or with only a marginal overlap (in case of overlap, parapatric taxa are marginally sympatric, q.v.).

**Clade:** Synonymous with monophyletic group in a phylogenetic tree.

**Lineage:** "A single line of ancestry and descent"; "a population extended through time" (de Queiroz 1998).

**Mitochondrial DNA:** DNA coding for mitochondrial genes. Found in the cytoplasm of the cell (unlike nuclear DNA; q.v.).

**Monophyly (adj. monophyletic):** Having a single evolutionary ancestry; "a group whose parts [members] share a more recent common ancestry with each other than with parts [members] of other such groups" (Härlin 1998). See Fig. 1.

**Monotypic species:** A species without any subspecies. Cf. Polytypic species.

**Nuclear DNA:** The main DNA contained in the cell nucleus (unlike mitochondrial DNA [q.v.] which is in the cytoplasm).

**Phylogeny (adj. phylogenetic):** The evolutionary history of a taxon.

**Polytypic species:** A species divided into subspecies. Cf. Monotypic species.

**Reproductive isolating barriers:** (1) External factors such as differences in voice, plumage or courtship behaviour that prevent mating, or (2) internal factors that prevent the formation of fertilised eggs or reduce fertility or viability in hybrids.

**Sympatry (adj. sympatric):** Two taxa are sympatric when they occur in the same geographic area (mainly used for breeding distributions). Opposite to allopatric (q.v.).

**Taxon (plural taxa):** Any formally established scientific name, at any level in the taxonomic hierarchy, for example, a species, subspecies or genus. A least-inclusive taxon is the 'smallest' named unit, that is, one which has not been further divided, hence either a monotypic species or a subspecies of a polytypic species. (According to ICZN 1999, a taxon need not have a formal name; it uses 'nominal taxon' for taxa with names.)

breeding. Both *alba* and *cinerea* are always treated as distinct species, and according to DNA (Ödeen & Alström 2001, Alström & Ödeen 2002, Voelker 2002) they are not very closely related to each other or to the western Yellow Wagtail complex. Much of the emotional resistance against the PSC among ornithologists and bird-watchers surely stems from the fact that most of them cannot accept the idea that all least-inclusive taxa are equal, and therefore dislike the idea of assigning the same rank to all least-inclusive taxa.

We favour concepts that give primacy to evolutionary history. We prefer the MSC over the PSC since the former accepts arbitrary inclusiveness of taxa. However, in most cases we do not find it an important issue whether a certain least-inclusive taxon is treated as a species or a subspecies.

In our opinion, the main advantage of classifying all least-inclusive taxa as species is that they receive more attention (which can be crucial for endangered taxa) and, importantly, that the risk of accepting non-monophyletic species is reduced. In many evolutionary studies, it is crucial to deal with least-inclusive taxa rather than polytypic species, and we strongly advocate evolutionary biologists and bird-watchers to make it a standard practice to report which least-inclusive taxon/taxa they have studied.

## References

- Alström, P., Mild, K. & Zetterström, B. 2003. *Pipits and Wagtails of Europe, Asia and North America: identification and systematics*. A & C Black, London and Princeton University Press, Princeton.
- Alström, P. & Ödeen, A. 2002. Incongruence between mitochondrial DNA, nuclear DNA and non-molecular data in the avian genus *Motacilla*: implications for estimates of species phylogenies. In P. Alström. *Species limits and systematics in some passerine birds*. Uppsala University, Uppsala.
- Alström, P. & Olsson, U. 1992. Taxonomic status of *Phylloscopus affinis* and *P. subaffinis*. *Bull. Brit. Orn. Club* 112: 111–126.
- Alström, P., Olsson, U. & Colston, P. 1997. Re-evaluation of the taxonomic status of *Phylloscopus proregulus kansuensis* Meise. *Bull. Brit. Orn. Club* 117: 177–193.
- Cracraft, J. 1983. Species concepts and speciation analysis. Pp. 159–187 in R. F. Johnston (ed.) *Current Ornithology*. Plenum Press, New York.
- Cracraft, J. 1989. Speciation and its ontology: the empirical consequences of alternative species concepts for understanding patterns and processes of differentiation. Pp. 28–59 in D. Otte & J. A. Endler (eds.) *Speciation and its consequences*. Sinauer, Sunderland, Mass.
- Cracraft, J. 1992. The species of the birds-of-paradise (Paradisaeidae): applying the phylogenetic species concept to a complex pattern of diversification. *Cladistics* 8: 1–43.
- Davis, J. I. & Nixon, K. C. 1992. Populations, genetic variation, and the delimitation of phylogenetic species. *Syst. Biol.* 41: 421–435.
- Donoghue, M. J. 1985. A critique of the biological species concept and recommendations for a phylogenetic alternative. *Bryologist* 88: 172–181.
- Gornall, R. J. 1997. Practical aspects of the species concepts in plants. Pp. 171–190 in Claridge, M. F., Dawah, H. A. & Wilson, M. R. (eds.) *Species: The units of biodiversity*. Chapman & Hall, London
- Härlin, M. 1998. Taxonomic names and phylogenetic trees. *Zoologica Scripta* 27: 381–390.
- Hazevoet, C. J. 1995. *The Birds of the Cape Verde Islands*. British Ornithologists' Union (Check-list No. 13), Tring.
- Helbig, A. J., Knox, A. G., Parkin, D. T., Sangster, G. & Collinson, M.



**Motacilla flava beema.** © Ray Tipper, Oman, 10.12.2002

2002. Guidelines for assigning species rank. *Ibis* 144: 518–525.

ICZN = International Commission on Zoological Nomenclature. 1999. *International Code of Zoological Nomenclature*. 4th edn. International Trust for Zoological Nomenclature, London.

Lidén, M. 1991. Replicators, hierarchy, and the species problem. *Cladistics* 6: 183–186.

Lidén, M. & Oxelman, B. 1989. Species — pattern or process? *Taxon* 38: 228–232.

Mayr, E. 1942. *Systematics and the origin of species*. Columbia University Press, New York.

Mayr, E. 1996. What is a species, and what is not? *Philosophy of Science Association* 63: 262–277.

Mayr, E. & Greenway, J. C., Jr. (eds.) 1960. *Check-list of birds of the world*. Vol. IX. Cambridge, Mass.

Mishler, B. D. 1985. The morphological, developmental, and phylogenetic basis of species concepts in bryophytes. *Bryologist* 88: 207–214.

Mishler, B. D. & Donoghue, M. J. 1982. Species concepts: a case of pluralism. *Syst. Zool.* 31: 491–503.

Nelson, G. & Platnick, N. I. 1981. *Systematics and Biogeography: Cladistics and Vicariance*. Columbia University Press, New York.

Nixon, K. C. & Wheeler, Q. D. 1990. An amplification of the phylogenetic species concept. *Cladistics* 6: 211–223.

Ödeen, A. & Alström, P. 2001. Evolution of secondary sexual traits in wagtails (genus *Motacilla*). In A. Ödeen. *Effects of post-glacial range expansions and*

*population bottlenecks on species richness*. Uppsala University, Uppsala.

O'Hara, R. J. 1993. Systematic generalization, historical fate, and the species problem. *Syst. Biol.* 42: 231–246.

Paterson, H. 1985. The recognition concept of species. Pp. 21–29 in Vrba, E. (ed.) *Species and Speciation*. Transvaal Mus. Monogr. No. 4, Pretoria.

de Queiroz, K. 1998. The general lineage concept of species, species criteria, and the process of speciation. A conceptual unification and terminological recommendations. Pp. 57–75 in Howard, D. J. & Berlocher, S. H. (eds.) *Endless forms: species and speciation*. Oxford University Press, Oxford.

Rosen, D. E. 1978. Vicariant patterns and historical explanation in biogeography. *Syst. Zool.* 27: 159–188.

Sangster, G., Hazevoet, C. J., van den Berg, A. B., Roselaar, C. S. & Sluys, R. 1999. Dutch avifaunal list: species concepts, taxonomic instability, and taxonomic changes in 1977–1998. *Ardea* 87: 139–165.

Simpson, G. G. 1961. *Principles of Animal Taxonomy*. Columbia University Press, New York.

Templeton, A. 1989. The Meaning of Species and Speciation: A Genetic Perspective. In Otte, D. & Endler, J. A. (ed.) *Speciation and Its Consequences*. Sinauer, Sunderland, Mass.

Van Valen, L. 1976. Ecological species, multispecies and oaks. *Taxon* 25: 233–239.

Voelker, G. 2002. Systematics and historical biogeography of wagtails: dispersal versus vicariance revisited. *Condor* 104: 725–739.

Zink, R. M. 1997. Species concepts. *Bull. Brit. Orn. Club* 117: 97–109.

Zink, R. M. & McKittrick, M. C. 1995. The debate over species concepts and its implications for ornithology. *Auk* 112: 701–719.

**Per Alström**, Department of Systematic Zoology, Evolutionary Biology Centre, Uppsala University, Norbyvägen 18 D, SE-75236 Uppsala, Sweden. E-mail per.alstrom@ebc.uu.se

**Krister Mild**, Koppurvägen 23, SE-17672 Järfälla, Sweden. E-mail krister.mild@hem.utfors.se



**Motacilla flava iberiae.** © Ray Tipper, Espanja, 20.3.2003.

