

# Comparative Ethology and Molecular Genetics as Tools for Phylogenetic Reconstructions: The Example of the Genus *Oenanthe*

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**Abstract**—A phylogeny of the genus *Oenanthe*, constructed using an integrated approach (with regard to characters of external morphology, behavioral ecology, and signal behavior), is compared with three phylogenetic hypotheses based on molecular data. Consideration is given to the problems arising in studies on molecular phylogeny where mtDNA is used as the only marker. Special emphasis is made on the negative consequences for zoological nomenclature that may result from its untimely modification based on the results that need further verification by more adequate research procedures.

**Keywords:** phylogenetic hypothesis, integrated approach to phylogenetic reconstructions, comparative ethology, adaptively neutral characters as a phylogenetic signal, molecular phylogenetics. birds, Wheatears of the genus *Oenanthe*.

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## INTRODUCTION

In a recent paper by Olsson et al. (2010), attention is focused on incongruity between the results of phylogenetic analysis by molecular methods and those based on the data of traditional zoological research. In particular, the authors emphasize significant topological divergence between the phylogenetic trees derived from data on the structure of mitochondrial DNA (mtDNA) and the systems based on organismal phylogeny (in the authors' terminology), or on noncladistic interpretation of morphological and ecological differences in characteristics of taxa.

It is important to note that behavioral characteristics are not mentioned at all in this paper. The reason is apparent: comparative ethological analysis has become increasingly rare in studies dealing with phylogenetic reconstructions. Meanwhile, it is the idea of the evolutionary conservatism of ethological traits as an important phylogenetic signal that provided a powerful stimulus for the development of classical ethology in the 1930s and 1940s (Lorenz, 1939, 1941; Beridge, 1990; Panov, 2005a).

Here, these important problems will be considered using the example of Wheatears (genus *Oenanthe*), because three phylogenetic hypotheses have been proposed for this group. One of them (the earliest) is based on comprehensive analysis of external morphological characters, behavioral ecology, and extensive data on the structure of signal behavior in individual species (Panov, 1999, 2005b). The other two hypothe-

ses are based mostly (Aliabadian et al., 2007) or completely (Outlaw, Voelker, and Bowie, 2009) on comparative genetic analysis with the use of mtDNA markers.

## STUDY OBJECT

Wheatears are passerine birds varying in size from the goldfinch to a small thrush. The phylogenetic roots of the genus *Oenanthe* lie in Africa, from where it has colonized open expanses of Eurasia. Only one species, the Northern Wheatear *O. oenanthe*, has populated subpolar regions of the New World, where it arrived via two different routes. According to different estimates, the genus includes from 15 to 21 species (45–47 subspecies). This incongruity is explained by an as yet unclear taxonomic status of some forms (subspecies or true species) and indistinct boundaries between the genus *Oenanthe* and several genera of small African passerines from the subfamily Turdinae, the family Muscicapidae. I refer primarily to the genus *Cercomela* and also the genera *Myrmecocichla* and *Saxicola* (stonechats) (Panov, 2005b, pp. 21, 370).<sup>1</sup>

<sup>1</sup> The monophyly of the genus *Oenanthe* and five *Cercomela* species has been recently confirmed at the molecular genetic level, while another four species from the genus *Cercomela* (in its previous interpretation) have proved to be unrelated to this monophyletic group (Outlaw, Voelker, and Bowie, 2009) (see Fig. 2). The conclusion concerning the paraphyly of the genera *Oenanthe* and *Cercomela* is confirmed in the study by Sangster et al. (2010).

One more difficulty in the systematics of the genus *Oenanthe* at the species level arises because of its extensive polymorphism in plumage color (Fig. 1). In some cases, this polymorphism has been shown to result from active hybridization between species-rank taxa (so-called hybrid polymorphism) (Haffer 1977; Grabovskii, Panov, and Rubtsov, 1992; Panov, Grabovskii, and Lyubushchenko, 1993).

## RESULTS

### *Comparison of the Author's Results with Those of Two Research Teams Relying on Molecular Marker Technology*

In the paper by Aliabadian et al. (2007), the authors analyze the material on only 11 out of the 21 species that, in my opinion, comprise the genus *Oenanthe* (among them, *chrysopygia* and *lugubris* are so-called problematic species).

Therefore the comparison of their results with the data presented in my publications (Panov, 1999, 2005b) cannot be sufficiently productive (cf., Figs. 2a and 2b). Nevertheless, the above authors have made such a comparison to conclude that their comparative genetic analysis confirms only a few of my conclusions. One of them is that the Variable Wheatear *O. picata* is not a close relative of the Mourning Wheatear *O. lugens*, contrary to previous views based on comparisons of morphological characters between these species (Hall and Moreau, 1970; Mayr and Stresmann, 1950; Tye, 1989). A relevant fact is that the grounds for this conclusion lie in the results of comparative ethological analysis.

In addition, the Mourning and Finsch's Wheatears (*O. lugens* and *O. finschii*) in my scheme are deprived of the status of subspecies previously assigned to them, e.g., by Gladkov (1954). This conclusion, derived from comparative ethological data, also agrees with the results of molecular analysis performed by Aliabadian et al. (2007). However, Outlaw, Voelker, and Bowie (2009) reject it.

One more coincidence (though incomplete) between our conclusions is that the Red-rumped Wheatear (*O. moesta*) in my scheme is at the base of the cluster comprising *O. finschii* and sibling species *O. lugens* and *O. lugubris*. The same is true of the scheme by Aliabadian et al., except that this cluster (with *O. moesta* in the basal position) is supplemented by four more species: *O. picata*, *O. alboniger*, *O. chrysopygia*, and *O. leucopyga*. It is relevant to note that the relative arrangement of six out of eight species included in this cluster by Aliabadian et al. looks markedly different in

the scheme by Outlaw, Voelker, and Bowie (2009) (see below).

Thus, assuming that studies with the use of molecular markers such as mtDNA yield the ultimate truth (which is rather quite questionable; see Discussion), the above comparisons confirm the validity of certain conclusions derived from the results of comparative ethological analysis. As for discrepancies between the results of these two approaches, they will be discussed in detail below.

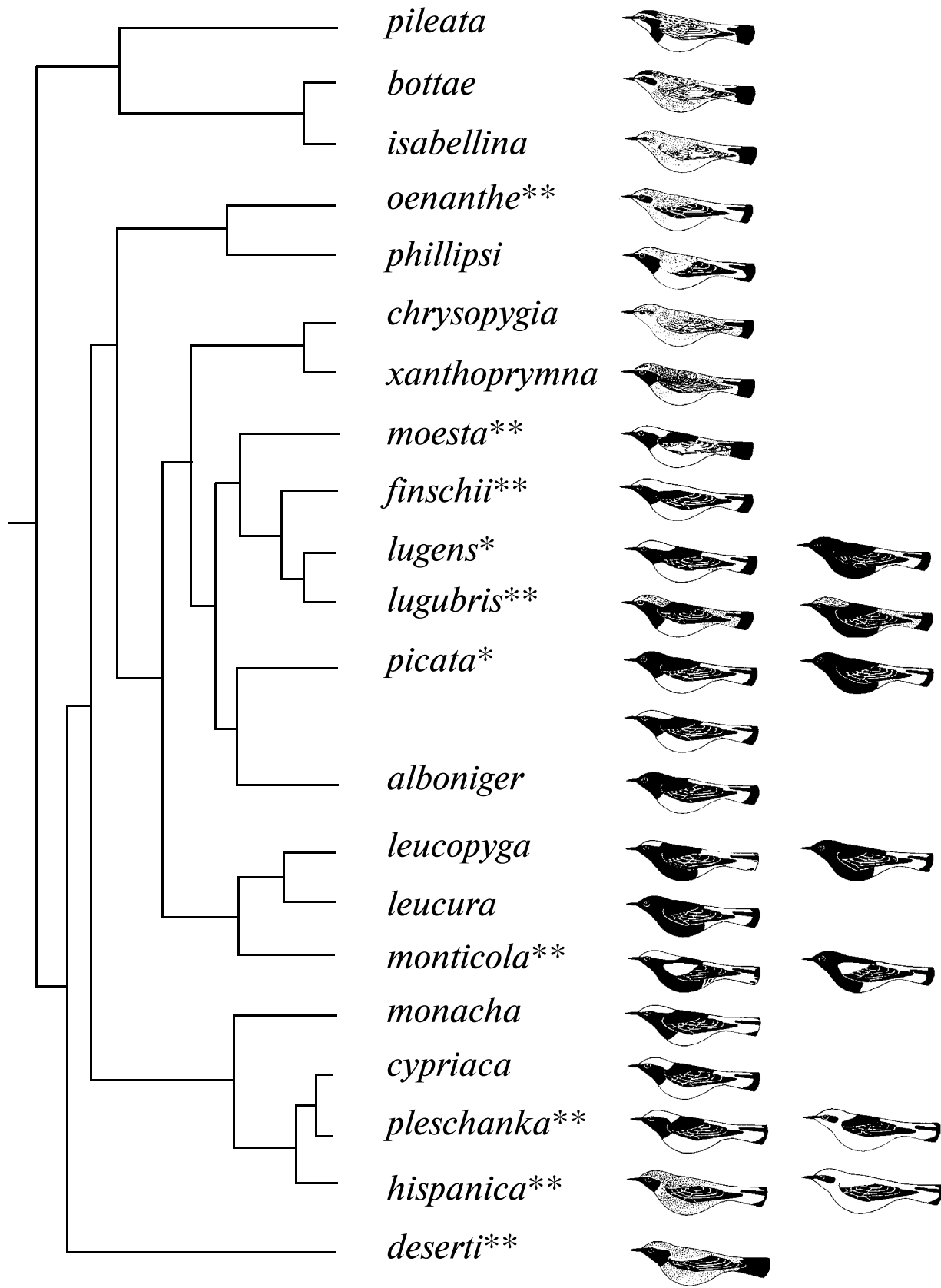
Let us now compare my scheme with that by Outlaw, Voelker, and Bowie (2009), which has an advantage over the previous scheme by Aliabadian et al. in that it includes 17 instead of 11 *Oenanthe* species. It is noteworthy how significantly the phylogenetic tree changes after being supplemented with new species. This comparison provides evidence for additional coincidences between the results obtained by different methods (cf., Figs. 2a and 2b). Thus, the clusters consisting of *O. isabellina*, *O. bottae*, and *O. pileata* (in the basal position) coincide completely. In both schemes, the White-crowned (*O. leucopyga*) and Black (*O. leucura*) Wheatears are sibling species, so that the former species does not fall into the large cluster I, as in the scheme by Aliabadian et al. Contrary to these authors, we do not regard the Isabelline (*O. isabellina*) and Northern (*O. oenanthe*) Wheatears as sibling species, and the same also applies to the desert (*O. deserti*) and Peid (*O. pleschanka*) Wheatears. Furthermore the hooded Wheatear (*O. monacha*) in both schemes is placed in the basal position relative to the pair of sibling species *O. hispanica* and *O. pleschanka* (the Black-eared and Peid Wheatears). I have arrived at such a conclusion on the basis of comparative ethological analysis and data on the behavioral ecology of Wheatears.<sup>2</sup>

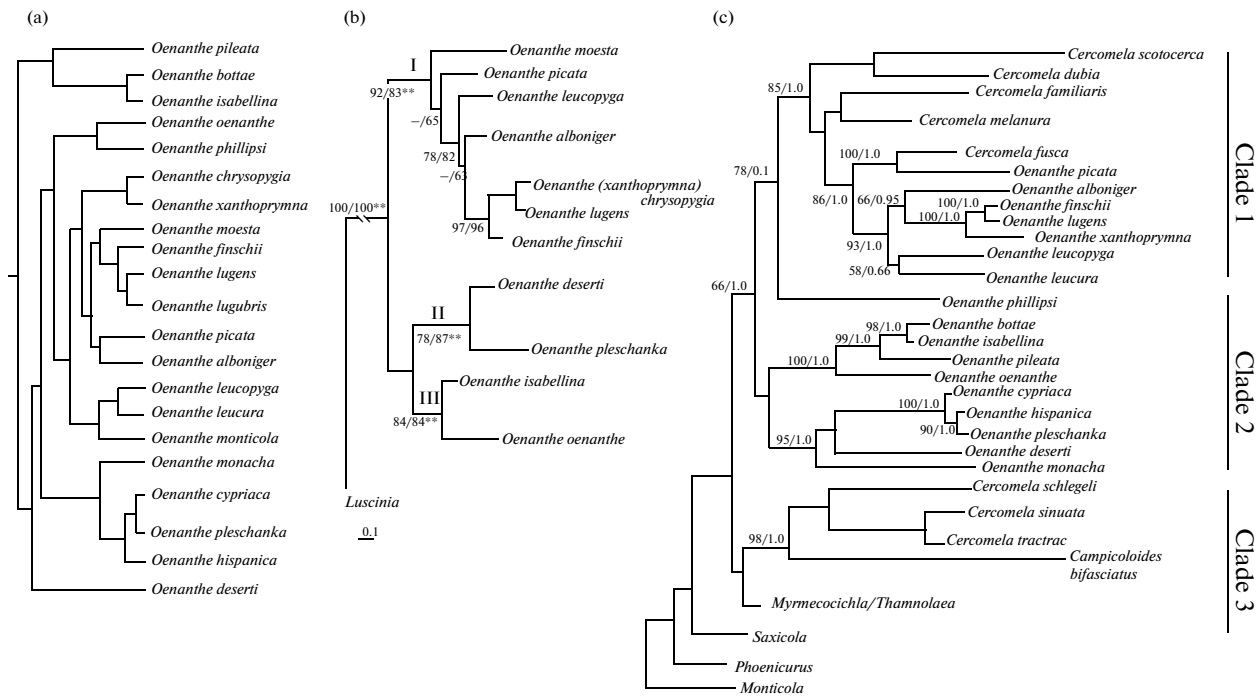
### *The Most Significant Discrepancies between the Schemes Based on Comparative Ethological and Molecular Data*

Aliabadian et al. (2007) emphasize a high degree of coincidence between phylogenetic trees derived from data on the external morphology of species (22 characters), on the one hand, and the results of molecular genetic analysis, on the other hand (Fig. 3). A quite different picture is observed when we compare the lat-

<sup>2</sup> This conclusion contradicts the opinion of Tye (1989), who considers *O. monacha* to be closely related to species belonging to a different cluster, which in the study by Aliabadian et al. (2007) is designated by letter A (here, cluster I in Fig. 2b).

**Fig. 1.** Tentative scheme of phylogeny of the genus *Oenanthe*. For species characterized by genetic polymorphism, both variants of male plumage coloration (or at least two variants, as in the case of *O. monticola*) are shown. For *O. leucopyga* with the same variant of polymorphism as in *O. leucura*, age-related variation is illustrated (young birds have a black head). Asterisks indicate species in which sexual dichromatism is characteristic of all populations (\*\*\*) or does not always manifest itself in all subspecies (\*). In other species (no asterisk), males and females have the same or similar plumage coloration.





**Fig. 2.** Comparison of phylogenetic hypotheses based on (a) comprehensive comparative studies of Palearctic Wheatears (Panov, 1999, 2005b) and data on molecular systematics of the genus *Oenanthe* by (b) Aliabadian et al. (2007) and (c) Outlaw, Voelker, and Bowie (2009).

ter with the scheme based on the behavioral characteristics of species.

The most obvious differences between my scheme and the two other schemes considered above concern the positions of two species, namely, the Isabelline and Desert Wheatears. In my scheme, they both occupy a basal position relative to all other species, which is explained by the fact that general ethological features of these birds differentiate them from all other representatives of the genus. It is for this reason, rather than specific features of plumage coloration, that the Isabelline and Desert Wheatears were positioned in such a way.<sup>3</sup>

It may be that the source of contradictions is in my concept that the above species have been formed at the early stages of divergence within the genus *Oenanthe*. As noted by Aliabadian et al. (2007, p. 671), branches with less support in phylogenetic trees of birds usually occur at the basal branch nodes. An apparent explanation is that the resolving power of methods used in phylogenetic research is insufficient for definite conclusions concerning the early stages of divergence,

<sup>3</sup> Aliabadian et al. (2007, p. 606, the caption to Fig. 1) erroneously interpret my approach, considering that it is based on the comparison of coloration characters. In fact, I am an active opponent of such a procedure (see Panov, 1999, 2005b).

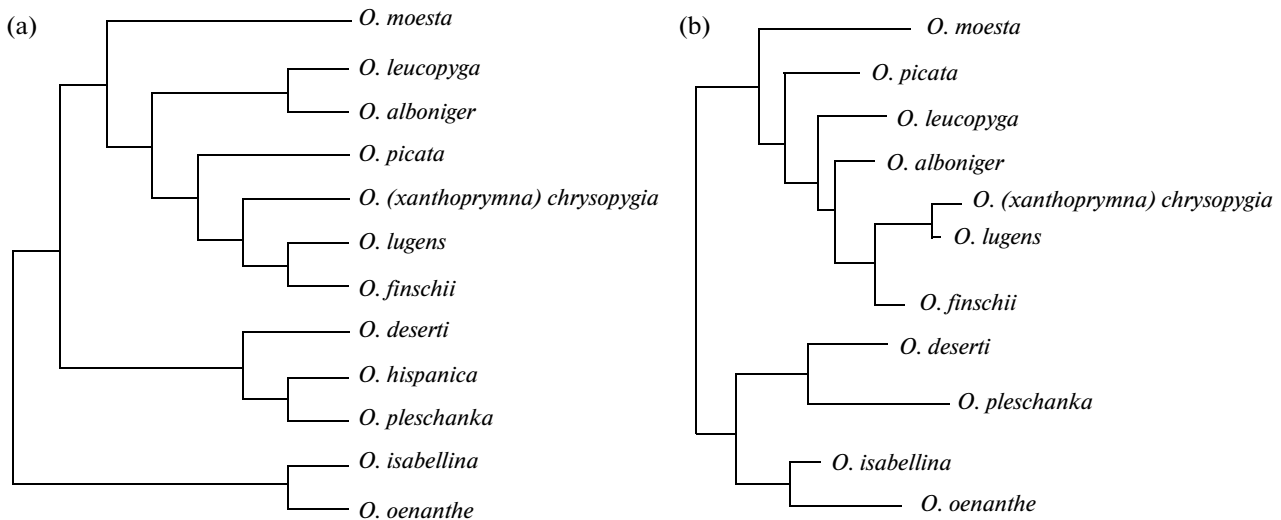
since “noise” such as homoplasies masks the phylogenetic signal.<sup>4</sup>

Comparatively analyzing motor habits, specific features of nest building, and some other aspects of behavior, I have pointed out similarity in this respect between the Isabelline Wheatear and the African Black Chat *Myrmecocichla melaena* (the sole representative of the genus for which published data on signal behavior are available) and between the Desert Wheatear and species of the genus *Cercomela*. It can be seen from Fig. 2b that, according to molecular genetic analysis, the genus *Cercomela* indeed occupies a basal position relative to the genus *Oenanthe*, while *Myrmecocichla* has common roots with both these genera.

#### *Specific Behavioral Features of the Isabelline Wheatear Compared to Other Species of the Genus Oenanthe*

To make this comparison more illustrative, it is expedient to take the Northern Wheatear as the second species, since it is regarded as a very close relative of the Isabelline Wheatear in both molecular phylogenetic schemes (according to Aliabadian et al. (2007), these are sibling species). It is relevant to note that, among ornithologists directly involved in comparative

<sup>4</sup> Homoplasies are character traits that reflect similar variations in the genomes resulting from parallelism in DNA base substitution.



**Fig. 3.** Comparison of phylogenetic hypotheses based on (a) analysis of 21 external morphological characters and (b) molecular data (according to Aliabadian et al., 2007).

research on the biology of Wheatears, not only I but also Haffer (1977) and Tye (1989) have denied their close relationship.

The reason is apparent: differences in the behavioral ecology of these two species are not limited to peculiarities, they are systemic. The Isabelline Wheatear was originally connected to tropical and subtropical plain habitats such as savannah, steppes, or, to a lesser extent, deserts; subsequently, it has also occupies physiognomically similar habitats in mountain regions (e.g., alpine meadows). The Northern Wheatear, judging from characteristics of its range, is a species originally connected to dissected mountain regions, and its expansion to the plains (up to the tundra zone in the north) is a secondary phenomenon.

It appears that adaptations of the two species to their initial preferred habitats manifest themselves in minor differences in their external morphology. These birds are similar in body size, but the Isabelline Wheatear has a longer tarsus and a larger bill. The former character obviously reflects adaptation to over-ground locomotion (running), and the increase in bill size may be specific features of nest building (see below) and foraging by probing the soil.

In agreement with the aforesaid, these species also differ in nesting strategy, preferring different types of nesting shelters. In this respect, the Isabelline Wheatear is a specialist species, whereas the Northern Wheatear is a typical generalist highly opportunistic in the choice of nest site. The Isabelline Wheatear is closely connected with burrowing rodents: even the range of this species in a given region remains within the boundaries of their ranges and expands only when the rodents spread out. The nesting of Isabelline Wheatears has been described in the burrows of at least 18 rodent species. The nests are built deep in the ground (down to 150–210 cm), with both members of

the nesting pair supposedly digging the nest chamber with their bills. The necessity to perform nesting activities in deep burrows, in absolute darkness, accounts for certain features of orientation behavior characteristic only of this species (Dorzhev and Khertuev, 1992).

As for the Northern Wheatear, its autochthonous range lies in the mountains, and the birds in their original habitats build nests in shallow crevices and niches in the rocks and hollows in talus slopes. Since nesting shelters of this kind lack any distinct specificity, the need for them can be satisfied in any landscape. This has allowed the species to expand northward up to the Arctic Ocean coast and to become a typical synanthropic species. In anthropogenically transformed landscapes, the Northern Wheatears nest in garbage dumps, firewood piles, chimneys, and even birdhouses hung in an open pine stand.

An objection may be raised that all these differences in behavioral ecology between the species are unrelated to the topic at issue, since the aforementioned behavioral traits are adaptations and cannot therefore be regarded as a reliable phylogenetic signal. This is indeed true, but it is also difficult to imagine that the taxa so basically different in nesting strategy would diverge no farther than to the level of sibling species. Anyway, to cast more doubt on such a possibility, I will now consider the behavioral traits that can hardly be regarded as adaptations to the environments typical for the species.

In particular, such traits include stereotyped motor reactions that either pertain to everyday activities of a given bird species or perform a specific signal function. In the Isabelline Wheatear, rhythmic tail wagging (like that commonly observed in wagtails) is a distinctive stereotyped reaction that is absent in the Northern Wheatear. Therefore, it can be used as a highly reliable

criterion for discriminating in the field between females of these species, which are highly similar in plumage coloration. Moreover, among ten *Oenanthe* species whose behavior I have studied in detail, this reaction is characteristic of only one species (in addition to *O. isabellina*), namely, the Desert Wheatear, in which it is manifested somewhat differently (see below).

In the category of behavior to which specialists usually assign signal functions, typical for Wheatears are so-called aerial displays. In most species, these are sporadic flights several seconds long, with the bird taking off from a song perch site dominating over the landscape. Although these flights have certain species specificity in terms of motor pattern, in most species they barely differ (only in particulars) from the routine aerial locomotion pertaining to everyday activities (Fig. 4). In comparison to other *Oenanthe* species, differences between the routine and display flights appear to be minimum in the Northern Wheatear and maximum in the Isabelline Wheatear.

The male display flight of the Isabelline Wheatear accounts for its Russian name “plyasun’ya,” which is translated as “dancer.” Its scheme is shown in Fig. 5. The bird fans the tail and, rhythmically flapping the wings at a small amplitude, slowly (as with effort) ascends in the air along an oblique trajectory, hovers at a certain point for several seconds (with the wings flapping rapidly), and then glides downward or dives.

No less apparent are that differences between the Isabelline Wheatear and the Northern Wheatear (and all other *Oenanthe* species described in this respect) in specific motor habits pertaining to courtship behavior. A characteristic feature of such displays in male Isabelline Wheatears is that the bird keeps the tail upright and demonstrates the female his oral cavity, which is coal black in color. Figure 6 illustrates the principal differences between the courtship displays of the Isabelline and Northern Wheatears.

Another, more specific difference between these species concerns vocalization: the Isabelline Wheatear is one of the most skillful imitators among birds (hence its local nickname “desert nightingale”), whereas the Northern Wheatear is not characterized by the ability to imitate the voices of other birds or animals.

It should be noted here that all stereotyped motor reactions, both routine and signal, are almost completely isomorphic (differing only in minor particulars) not only in true sibling species (e.g., the Black-eared and Peid Wheatears) but also in species fairly remote phylogenetically but included in the same “large” clusters, such as the Finsch’s, Variable, and white-crowned Wheatears (see Fig. 2B), (Panov, 2009, pp. 232–244). The result of ethological comparisons

between the Isabelline and northern Wheatears is absolutely different, which casts heavy doubt on the conclusion that these species are closely related, which follows from the results of molecular data. Comparative ethological analysis provides conclusive evidence for an isolated position of the Isabelline Wheatear in the phylogenetic structure of the genus *Oenanthe*. Some of its stereotyped habits are similar to those described for representatives of the genus *Myrmecocichla* (Fig. 7), which suggests the proximity of the Isabelline Wheatear to the phylogenetic roots of this genus.

#### *Specific Behavioral Features of the Desert Wheatear Compared to Other Species of the Genus Oenanthe*

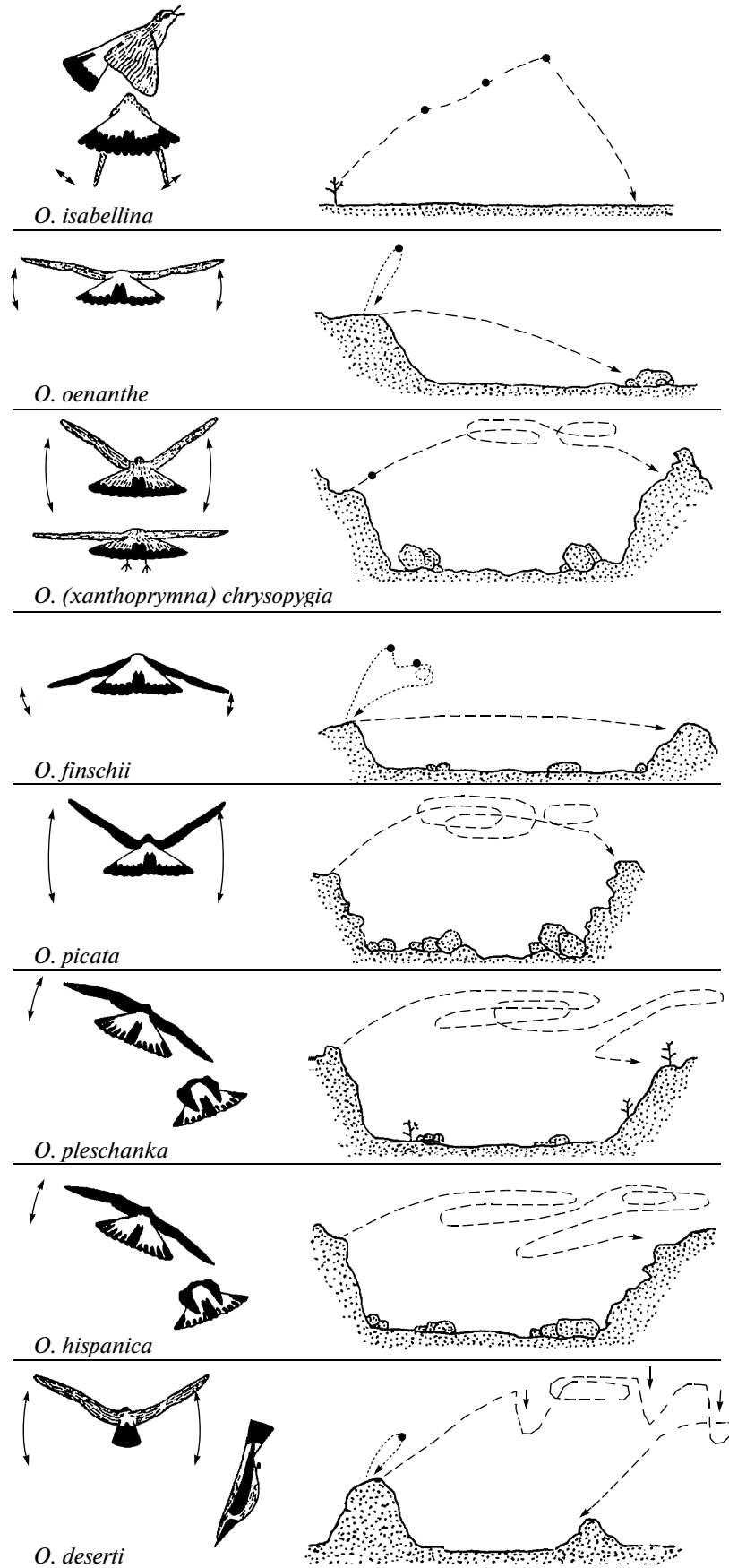
In the molecular phylogenetic schemes, the Desert Wheatear is either classified as a sibling species of the Peid Wheatear (Aliabadian et al., 2007) or is placed at the base of the cluster formed by three very close species: the Peid, Cyprus (*O. cyprica*, and Black-eared Wheatears (Outlaw, Voelker, and Bowie, 2009). Both conclusions basically disagree with my data as well as with the results of previous attempts to determine the position of this species in the taxonomic structure of the genus *Oenanthe*. Their (Vaurie, 1949; Roselaar, 1988; Tye, 1989) unanimously included the Desert Wheatear in the group of so-called black-and-white petrophilous species, together with the Variable, Finsch’s, and Mourning Wheatears (Fig. 2b, cluster I).

The position of the desert Wheatear in my scheme is basal relative to all other species except the Isabelline Wheatear and two other species closely related to it (Fig. 2a). Below, this conclusion will be substantiated by data on the behavioral ecology of the species, including its motor habits and vocalization pattern.

With regard to the type of preferred habitats, the Desert Wheatear generally belongs to the plain faunal complex, rather than to the group of petrophilous species (the Variable, Finsch’s, and Mourning Wheatears) to which it was attributed previously. The Desert Wheatear is somewhat similar in this aspect to the Isabelline Wheatear, but its biotopic preferences are markedly different. It typically populates high-mountain plains classified as gravel and stone deserts (e.g., in northern Libya or on the Pamir Plateau) or flat or undulating sand deserts or clay deserts. The major distinctive feature of the Desert Wheatear is its ability to settle in barren landscapes practically devoid of vegetation, where the bird fauna is very poor.<sup>5</sup>

<sup>5</sup> On the Pamir Plateau, for example, the Northern Horned Lark *Eremophila alpestris* is the only bird species occurring in such barren areas in appreciable numbers, in addition to the desert Wheatear.

Fig. 4. Amplitudes of wing movements and trajectories of male display flights in eight *Oenanthe* species (according to Panov, 1999, 2005b).



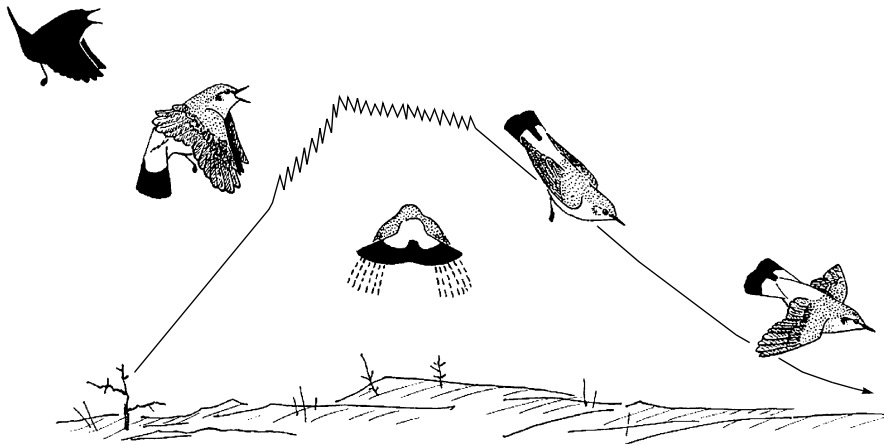


Fig. 5. Display flight of male Isabelline Wheatear (according to Panov, 2005b).

These ecological features make the desert Wheatear similar to species of the genus *Cercomela*, which prefer arid stone deserts (the Blackstart *C. melanura*) and sand deserts of southern and northern Africa.

In accordance with the general pattern of such habitats, the Desert Wheatear is an opportunist in its

choice of nesting shelters. In the absence of dissected stony substrate with numerous hollows, these birds can successfully nest on the ground surface, usually at the bases of shrubs. In sand deserts of southern Kazakhstan, they expand to black saxaul (*Arthrophytum ammodendron*) stands, finding nesting shelters in tree hollows or under piles of coarse woody debris (Shnitnikov, 1949). An interesting fact is that female Desert Wheatears nesting in hollows (rodent burrows or natural cavities in stony or clay cliff edges) do not dig deep into the ground but build the nest near the entrance, so that it is clearly visible from outside (Fig. 8). Such a behavior may be evidence that close ancestors of the Desert Wheatear were largely similar in this respect to many representatives of the genus *Cercomela* characterized by half-open nesting.

A characteristic stereotyped motor habit of the Desert Wheatear is rhythmical tail wagging, similar to that observed in wagtails, which allows reliable differentiation between females of this species and similarly colored female Northern or Isabelline Wheatears. Unlike the last species, the Desert Wheatear wags the

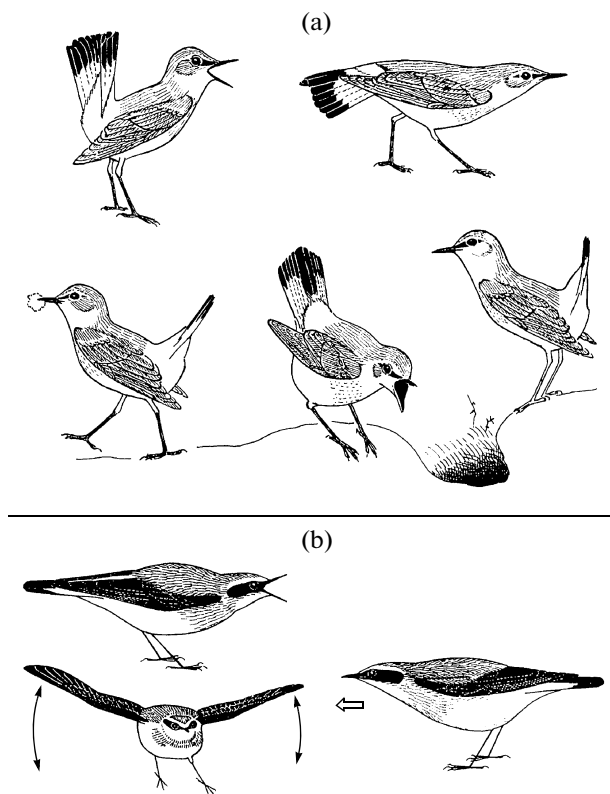


Fig. 6. Differences in signal behavior between (a) Isabelline and (b) Northern Wheatears at stages of pair formation and nest building (according to Panov, 1999, 2005b).

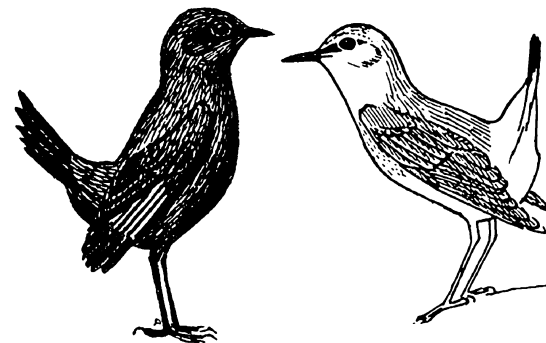


Fig. 7. Similarity between the postures of the Black Chat *Myrmecocichla melaena* (on the left) and Isabelline Wheatear (on the right). The left picture is from the book by Perlo van Ber (1992).



tail more rapidly and in a variable rhythm, slightly spreading the most lateral feathers during each movement. According to T. Farcas (personal communication), approximately the same tail movements are also characteristic of the South African Tractrac Chat (*Cercomela tractrac*). My observations on the Blackstart (*Cercomela melanura*) show that, although this bird does not wag the tail, it also rhythmically spreads and folds tail feathers as does the desert Wheatear during tail movements.

Since the available literature contains no data on the ethology of the *Cercomela* species to which I approximate the Desert Wheatear, it is impossible to provide detailed arguments either in favor or against its close relationship to representatives of this genus. In any case, however, it is obvious for me that the general behavioral pattern of the Desert Wheatear is different from that observed in other congeneric species, including the sibling species *O. hispanica* and *O. pleschanka* to which the desert Wheatear is approximated on the basis of molecular data (Fig. 2c). Therefore, candidates for the role of probable close ancestors of the Desert Wheatear are more likely to be found in other related genera. In my opinion, the search for them should focus on the genus *Cercomela*.

Other noteworthy features of the Desert Wheatear are as follows:

(1) The specific coloration of the tail, which is black with the white base (as in some species of the genus *Cercomela*) rather than white with black central feathers and a black band at the tip, as in other *Oenanthe* species.

(2) Striking credulity toward the observer (which is also characteristic of certain species of the genus *Cercomela*).

(3) Aversion to bathing (which is a comforting behavior in other *Oenanthe* species). All other Wheatears that I have observed in captivity, including the Isabelline Wheatear, like to bathe in hot weather, while desert Wheatears limit themselves to wetting the forehead in the drinking bowl and feel obviously uncomfortable under a shower from a syringe, which is largely explained by the fact that it takes a long time for their plumage to dry.<sup>6</sup> This feature is traceable to specific living conditions essential to the ancestors of the Desert Wheatear, which lived in the extreme environment of arid deserts (see above).

(4) Features of hunting behavior related to specialization on small (mosquito-size) prey. After catching a large insect, the bird pecks at it and eats bit by bit.

(5) A very simple structure of the song, which consists of only three whistling notes and shows no signs of imitation (unlike the songs of the Black-eared and Peid Wheatears, which are skilled imitators). Its clos-

<sup>6</sup> According to my observations, many species of Wheatears willingly bathe in the rain, while Blackstarts *Cercomela melanura* hide in shelters immediately after the rain starts.

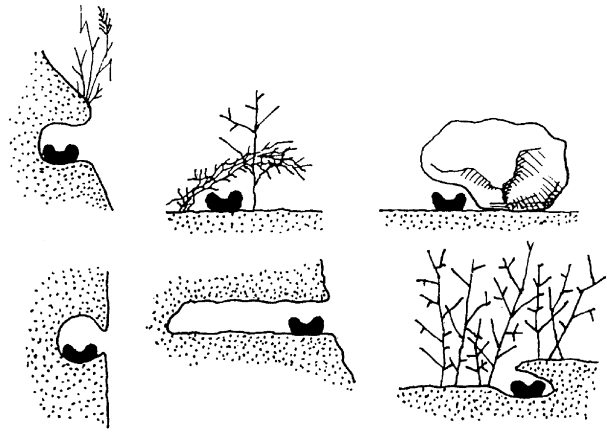


Fig. 8. Variants of nest placement by the desert Wheatear.

est structural analog among all small Turdine species known to me is the song of the Blackstart.

(6) An original pattern of male display flight (Fig. 4, bottom panel): the bird rhythmically flaps the wings, banking from side to side in the horizontal plane, then makes a sharp climb and, after hovering for a moment, dives with tail feathers slightly spread. Male Desert Wheatears are fairly consistent in performing such aerial evolutions, and their behavior in this respect is similar to the behavior of Black-eared Wheatears, although the flight pattern itself is absolutely different.

## DISCUSSION

Comparative ethological analysis, as any other approach to phylogenetic reconstructions, has its advantages and drawbacks. It is rarely used today mainly because of high labor expenditures for collecting the adequate initial material and the extreme scarcity of relevant published data, which is an obstacle to large-scale comparisons. Specialists in molecular phylogeny are in a more favorable situation, since ample resources of genetic databases are at their disposal.

The second obstacle to implementation of this approach is accounted for by the objective nature of the phenomena that are the subject matter of comparative ethological analysis. As recently shown for another group of birds, the divergence of stereotyped behavioral acts appears to be a process of recombination of the original archetypal traits that have already existed in the initially compact group of species ancestral to a given phylogenetic lineage (Panov, 2011). In this respect, reconstructions based on comparative ethological analysis hardly differ in essence from phylogenetic schemes constructed using other categories of characters, either morphological or pertaining to the genome structure.

It is the combinatory behavioral pattern of species such as the Desert Wheatear (see above) that makes it extremely difficult to determine their actual place in

the system. We are dealing with a mosaic made up of characters supposedly typical for a certain ancestral group of species (in this case, of the genus *Cercomela*) and, on the other hand, of characters acquired in the course of subsequent species evolution and pertaining to the integrated image of a “typical” Wheatear. Many features of signal behavior characteristic of the Desert Wheatear prove to be also common to representatives of both clades shown in Fig. 2b, namely, the cluster of petrophilous species (such as the Variable and Mourning Wheatears) and the cluster that includes the sibling species *O. hispanica* and *O. pleschanka*.

Since behavioral “characters” are mostly continuous rather than discrete, attempts to construct formalized trees based on the methods of quantitative taxonomy are hardly productive. They may create an impression of analytical accuracy but, in fact, distort the real picture of relationships between taxa. Phylogenetic trees constructed using molecular markers are often considered to have no such drawbacks, because these markers are essentially discrete. However, this widespread opinion is largely due to the fact that zoologists are not fully aware of potential stumbling blocks in the application of these methods.

A detailed analysis of causes underlying poor correspondence of molecular phylogenetic reconstructions to the actual situation is given in the study by Bannikova (2004), where the author lists a great variety of factors affecting the congruence of phylogenetic trees and the bootstrap support and resolution of branching order. These factors are especially numerous in the case of mtDNA. Among them, special attention should be paid to a high rate of nucleotide substitution, which accounts for the fact that differences in the mtDNA sequence between the species that diverged from the common ancestor 80 million years ago are barely greater than between the species that diverged no more than 20 million years ago.

As noted by Bannikova (2004), it is now absolutely clear that “... different regions of the genome contribute information of unequal value to phylogenetic hypotheses and can provide different phylogenetic signals or quench the signal by noise from homoplasies. Success in modern molecular biological research largely depends on the correct choice of a gene or a combination of genes in a sequence. Therefore, research planning in molecular phylogenetics is directly connected with the accumulation of information on the mode of evolution of genome regions used in phylogenetics.” The last item falls into the domain of genomics, where the task is to substantiate the choice of genes that can reflect the evolution of organisms with the highest degree of reliability.

Bannikova considers that the main factor of further success (or disappointment) in molecular phylogenetics is the accumulation of knowledge about trends in the evolution of the genome, rather than advancement in research technology. Meanwhile, it appears that recent developments in this field are mainly oriented

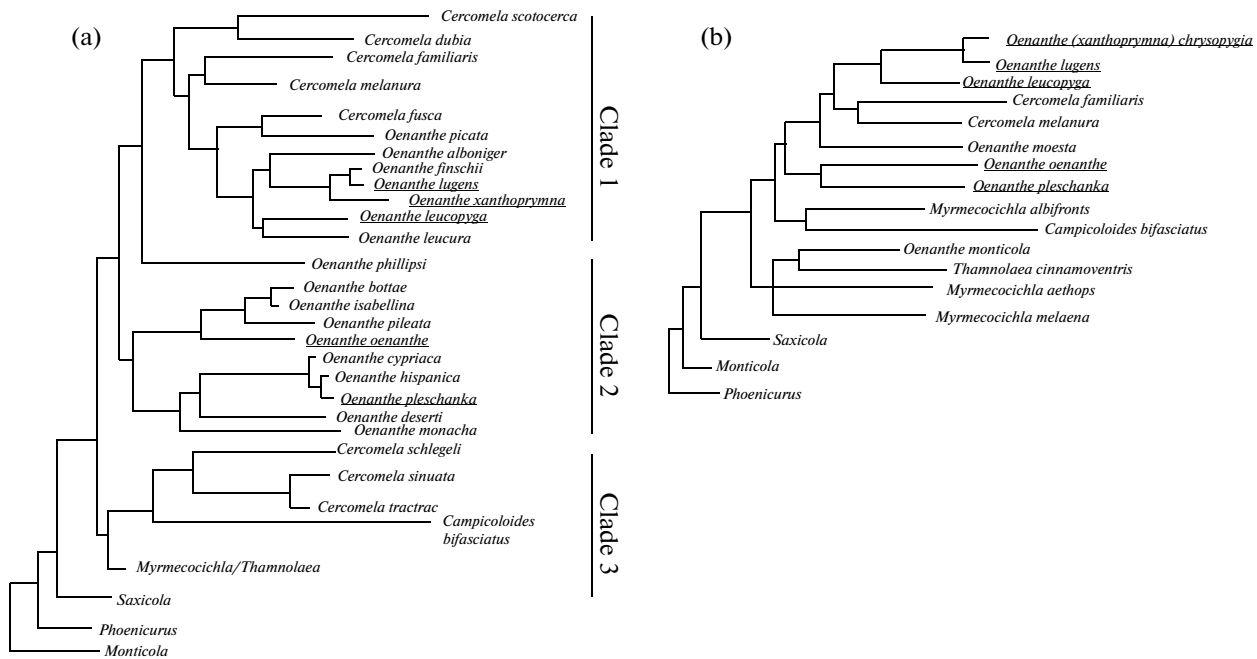
toward further automation of experimental procedures and complication of the mathematical apparatus for phylogenetic algorithms. In my opinion, all the aforesaid shows that this field of knowledge itself is still in its early childhood if not infancy.

The application of molecular biological methods to problems of evolution and systematics is complicated by a number of circumstances. A review of relevant publications cited in this paper creates the impression that any continuity in such studies is absent, since the method itself allows the researcher to approach any object from scratch, having no preliminary knowledge about it. Any research in zoology has a wide overlap with previous studies and a relatively low degree of novelty, whereas the analysis of a certain DNA region yields an absolutely new product, not connected with those obtained previously. In other words, any preliminary hypothesis is absent, and there is no need for it; the gene studied is taken out of the black box. Strictly speaking, the schemes constructed on this basis reflect not so much the kinship of species as the relationships between the genes studied. At the current level of molecular systematics, such schemes can hardly provide sufficiently reliable information about the real phylogenetic relationships between the carriers of these genes.

The results of phylogenetic studies on lower-rank taxa (genera and species) are often contradictory, and problems in them often cannot be resolved using mtDNA markers (Bannikova, 2004). The high rate of mtDNA divergence (five to ten times that of nuclear DNA) imposes limits on the time scale within which these markers can provide useful information at the supraspecific level. Therefore, studies dealing with problems of evolution on a large time scale should better be performed using more conserved sequences of the nuclear DNA. Although such markers have obvious advantages, they are used in phylogenetic studies much less frequently than mtDNA markers because of difficulties in their isolation from the large and complex genomes of eukaryotes. Moreover, the genes whose sequences are known usually differ between the species of interest, which strongly complicates or precludes interspecific comparisons.

Sangster et al. (2010) included six Wheatear species in their study on the phylogeny of the family Muscipidae, in which not only mtDNA but also three nuclear genes were used. Figure 9 shows the positions of these species on the resulting tree in comparison with the previous scheme by Outlaw, Voelker, and Bowie (2009). It can be seen how the results depend on the number of species from a given lineage included in analysis. Thus, the Northern and Peid Wheatears in the scheme by Sangster et al. are sibling species (Fig. 9b), whereas their positions in the other scheme are relatively far apart (Fig. 9a).

Of special concern are hasty conclusions drawn by Sangster et al. from the results of their study: they propose to pool together no less than four passerine gen-



**Fig. 9.** Comparison of species locations on branches of the phylogenetic trees constructed by (a) Outlaw, Voelker, and Bowie (2009) and (b) Sangster et al. (2010).

era, reducing the names *Cercomela*, *Myrmecocichla*, and *Thamnolaea* to synonyms of *Oenanthe* and including all their constituent species into the last genus. Moreover, they propose to supplement it with one more species, the Buff-streaked Wheatear, previously classified with stonechats under the name *Saxicola bifasciata* (Urquart, 2002), and then separated into the monotypic genus *Campicoloides* (Outlaw, Voelker, and Bowie, 2009).

The authors of studies on molecular systematics compete with each other in attempts to modify in a certain way the taxonomic schemes established in zoology, which is quite understandable: research in this field is well supported by various grants, and the results may create the impression that ultimate truth is already at hand. It would be appropriate to see that this research follows a certain unified, methodologically valid strategy, but the real situation is different. Thus, Outlaw, Voelker, and Bowie (2009) divided the genus *Cercomela* into three lineages and proposed to include one of them (five species) in the genus *Oenanthe* and to separate three species into the new genus *Emarginata* and one species into the monotypic genus *Pinarochroa*. Only one year later, Sangster et al. (2010) refuted these conclusions and, along with pooling all these genera, supplemented them with three more genera combined under the same name.

On the basis of molecular data, Urban Olsson (head of research team at the Department of Zoology, University of Gothenburg), has divided shrike species *Lanius excubitor* and *L. meridionalis* into four and five species, respectively; on the other hand, Olson in

coauthorship with Dutch ornithologist George Sangster has proposed to pool four genera of the family Turdidae into a single genus. It is difficult to reveal any logic in these conclusions. The main trouble, however, is that ornithologists credibly and readily respond to such findings and make premature amendments in faunistic lists and identification keys. This is how the increasing chaos in the taxonomic nomenclature has come to be, creating the burden that future generations of zoologists will inevitably have to deal with (see Panov, 2009; Panov and Bannikova, 2010).

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