Bonn. zool. Beitr.	Bd. 40	H. 3/4	S. 165—182	Bonn, Dezember 1989

Superspecies in the genus *Oenanthe* (Aves, Turdidae)

Alan Tye

Abstract. Relationships within the genus *Oenanthe* (wheatears) are debatable, there having been no thorough review of the genus as a whole. In the present paper, all species (Palaearctic and Afrotropical) are considered, and a suggested phylogeny and scheme of superspecies and species-groups generated, taking into account ecological, geographical and morphological factors. The position of the genus is considered in relation to its near relatives *Cercomela*, *Myrmecocichla*, *Thamnolea* and *Saxicola*. Wheatears can be grouped into five superspecies or species-groups (comprising 13 species), with five independent species of less certain relationships. Wheatears of the Saharo-Sindian (N. Africa to central Asia) arid belt show evidence of much recent fragmentation of populations, suggesting that the arid zone has itself been subject to fragmentation in recent geological time. Current distributions suggest that there have been several waves of speciation and subsequent spread through, and sometimes beyond, this arid zone.

Key words. Aves, Turdidae, *Oenanthe*, genus limits, superspecies, relationships, ranges, Saharo-Sindian, arid-zone birds.

Introduction

The wheatears *Oenanthe* spp. are a predominantly Palaearctic and Afrotropical genus, with one species extending to the Nearctic in Greenland, northeast Canada and Alaska. There has been no thorough study of wheatear relationships at the level of superspecies since the formulations of Hall & Moreau (1970) for Afrotropical species and Voous (1977) for Palaearctic species: the genus has never been considered as a whole. However, there have been several recent investigations of particular groups of species (e. g. Haffer 1977; Loskot 1986; Panow 1986 for *O. hispanica* and *O. pleschanka*; Panow 1980 for *O. picata*) which clarify certain relationships, and some earlier studies (e. g. Stresemann 1925; Vaurie 1949; Mayr & Stresemann 1950) retain much of their validity. Unfortunately, in some instances relationships between particular species have been suggested without publication of detailed reasons (e. g. Ripley 1962). In view of this background, it seems worthwhile to undertake a re-examination of the genus as a whole.

Intrageneric relationships are obscured by an unusually high lability of plumage characters (Mayr & Stresemann 1950). Species and subspecies are differentiated by variations on two themes of black-and-white or sandy plumage, but many species are polymorphic in one or more of crown, throat or belly colour. Also, the degree of polymorphism or of sexual or age dimorphism may vary between races of a single species. Characters involved in polymorphism or sexual dimorphism in some species are responsible for subspecific differentiation in others and for distinction between yet other full species (see Mayr & Stresemann 1950). Although the many polymorphisms cloud a study of intrageneric relationships, in some instances they may help in indicating the origin of different subspecies and species from polymorphic forms of an ancestral species (Mayr & Stresemann 1950).

In wheatears, plumage pattern has possibly been subject to more rapid evolutionary change than general plumage colour (cf. Short 1976). The patterns involved are rather simple ones, involving blocks of colour such as crown, back, throat, breast etc. which probably represent simple genetic controls (Mayr & Stresemann 1950). Apart from black and white, the plumage pigment complexes of wheatears may be controlled by genetic complexes more elaborate than those controlling elements of plumage pattern. The evidence from polymorphisms and geographic subspecies suggests that pattern in wheatears is more labile than colour, so that colour may be more significant in indicating relationships between species.

As in any group of birds, a definitive statement about intrageneric relationships (if such can ever be made) must await a detailed molecular genetic study, accompanied by refinement of the techniques for interpreting the results of such work. Here, I draw together ideas about both Palaearctic and Afrotropical species and attempt to generate a scheme of superspecies and species-groups for the genus as a whole, based primarily on ecological, geographical and morphological data. Recent studies and earlier work are critically evaluated and incorporated with information from my own field studies in the U. K., West Africa and Kuwait and from examinations of material appertaining to all species, primarily at the British Museum (Natural History).

In the present paper I define a superspecies as a group of allopatric or almost completely allopatric taxa that were once races of a single species but which have now achieved species status (as defined by Amadon 1966, Snow 1978). A species-group is a group of partly-sympatric species that are very closely related, having invaded each other's ranges following allopatric speciation (cf. Hall & Moreau 1970, Snow 1978).

The place of the genus in the Turdidae

Oenanthe is a poorly-defined genus within which I recognize 18 species, having removed the Buff-streaked Chat *bifasciata* to *Saxicola* (Tye 1989). It intergrades with *Cercomela* through the southern African *C. sinuata* species-group (see Hall & Moreau 1970). These share with *Oenanthe* a white or rufous rump and base of tail, with a black terminal portion of the tail. *Cercomela* and *Oenanthe* also share many elements of ecology and behaviour, and have similar egg colour, egg pattern and nest structure (see Lynes 1924—26).

On the other hand, *Oenanthe* seems close to *Thamnolea* and *Myrmecocichla*, several species of which have a predominantly black-and-white plumage pattern like that of many wheatears. *Thamnolea* and *Myrmecocichla* spp. have all-black tails, unlike most *Oenanthe*, but shared with one subspecies of the Mountain Wheatear *O. monticola nigricauda*. Indeed, the Mountain Wheatear looks remarkably like some *Myrmecocichla* spp., with a similar pattern of white wing-coverts. *Thamnolea* appears to represent a lineage more adapted to bare, rocky habitats, while *Oenanthe* is more associated with open deserts and steppes. In this respect, the black-and-white *Oenanthe* spp., which tend to occur in rockier habitats (see below) probably represent the "primitive" state in the genus, while the browner, less-contrasting species which are more associated with plains habitats possess the derived state (cf. Mayr &

Stresemann 1950). *Myrmecocichla* spp. also live in open habitats but in general are more gregarious, less territorial birds than *Oenanthe.*

Oenanthe also shows behavioural and morphological links with *Saxicola. Saxicola* spp. prefer bushier habitats, foraging mainly by sallying to ground or aerial sallying from elevated perches (Greig-Smith 1982; Moreno 1984; Leisler & Winkler 1985; Cramp 1988; Tye 1988). *Oenanthe* represents a more terrestrial lineage: many species run on the ground to capture terrestrial prey although ground- and aerial sallying are also used by most wheatears (see e. g. Cornwallis 1975; Tye in press).

The genera *Oenanthe*, *Cercomela*, *Myrmecocichla*, *Thamnolea* and *Saxicola* (perhaps with others) appear to represent lineages generated by an early chat radiation. Their precise relationships one with another, and the points at which they separated are somewhat obscure. *Oenanthe* spans a variety of forms, from highly contrasting black-and-white to near-uniform sandy. A similar range of variation is found in each of the two genera which are perhaps most closely-related to *Oenanthe*, namely *Cercomela* and *Myrmecocichla.* It seems possible that some *Oenanthe* spp. (e. g. *O. monticola*) may be more closely related to some similarly-patterned *Myrmecocichla* spp. than to some other *Oenanthe* spp. Similarly, the sandier-coloured *Oenanthe* may be closer to the sandy-coloured *Cercomela* spp. than to the black-and-white *Oenanthe* spp.: in this sense the genus may not be monophyletic.

O. alboniger superspecies

I include here Hume's Wheatear *O. alboniger*, the White-crowned Black Wheatear *O. leucopyga* and the Black Wheatear *O. leucura. Oenanthe leucopyga* and *leucura* were linked in a superspecies by Hall & Moreau (1970) who also tentatively suggested that *O. monacha* should be included with them. However, I discuss below reasons for omitting *O. monacha* from this group. Panow (1974) suggested that *alboniger*, *leucopyga* and *leucura* formed a monophyletic group.

The members of this superspecies are among the largest wheatears, and are the purest black-and-white species of the genus. The black tends to a glossy blue tint and is without brown tinge except in *leucura.* Both sexes have this plumage colour in *alboniger* and *leucopyga* but the female of *leucura* is dark brown. *O. leucopyga* has the whitest tail-pattern of the genus (a character shared with *O. monacha*), with black restricted to the central pairs of rectrices and the others marked solely and inconsistently by smudges near the tips. *O. alboniger* and *leucura* have a broader terminal black band. Apart from the difference in tail pattern, male *leucura* are almost identical in plumage to immature *leucopyga.*

The members of the *alboniger* superspecies are found in rocky habitats in the deserts of north Africa and the Middle East, and in southwest Europe. *O. alboniger* may represent what was originally a southwest Asian isolate of the group and *O. leucura* a west Mediterranean isolate, to which ranges they remain restricted (Fig. 1). *O. leucopyga* appears to represent a middle-eastern isolate, which may later have spread westwards across north Africa (Fig. 1). The ranges of *leucopyga* and *leucura* meet in northwest Africa, where *leucura* generally occurs north of *leucopyga.* Where their ranges meet, the two species are almost completely separated by altitude: *leucura* is found higher in the Atlas Mountains but breeds at lower altitudes in areas

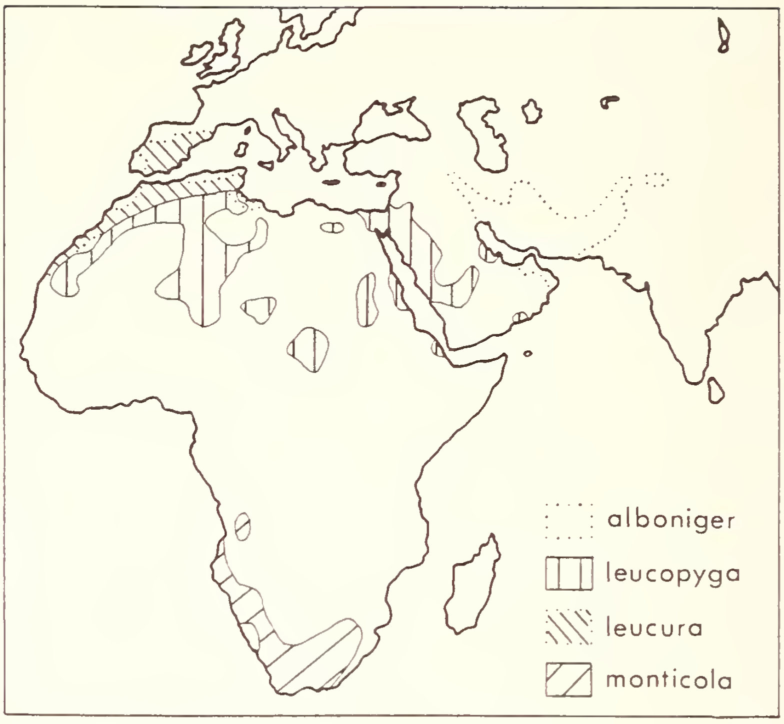

Fig. 1: Breeding ranges of the *O. alboniger* superspecies and of *O. monticola*. Data for the maps forming Figs. 1—8 obtained mainly from Cornwallis (1975), Cramp (1988), Glutz von Blotzheim & Bauer (1988) and Tye (in press), with supplementary detail from other sources.

where *leucopyga* is absent (Smith 1971; Ledant et al. 1981). Although all three species occupy similar rocky habitats, in northwest Africa *leucopyga* is more restricted to broken ground whereas *leucura* also occurs in flatter country with rock outcrops.

Black-and-white plumage is thought to be primitive within the genus (Mayr & Stresemann 1950), therefore shared black-and-white plumage patterns do not necessarily indicate close relationship, being shared primitive characters. However, the distributional and ecological factors discussed above strongly suggest that these three species do form a superspecies.

O. monticola

This southern African endemic is perhaps the most polymorphic species of wheatear (see Mayr & Stresemann, 1950; Tye in press): the male has two major morph types, one with predominantly black-and-white plumage and the other being mainly grey. The crown and belly colour are also polymorphic, with any combination of crown and belly colour (black, white, two shades of grey, partly black/partly white) possible in black-and-white phase males. Females are plain dark brown.

O. monticola was included by Hall & Moreau (1970) in a superspecies with *leucura* and *leucopyga*, because the dark brown female is similar to that of *leucura*, while black-and-white phase males resemble *leucura* and *leucopyga*. Further, black-and-white phase males always have a black crown when immature, as does *leucopyga*. *O. monticola*, *leucura* and *leucopyga* are also unusual in the genus (and family) in that their juveniles are almost or entirely unspotted. They also share large size and heavy build: *O. monticola* is by far the largest wheatear.

On the other hand, grey-phase *monticola* bear a striking resemblance to immature *O. phillipsi*, and adult *phillipsi* have a combination of the characters of the black-and-white and the grey phases of *monticola. O. monticola, O. phillipsi* and *O. oenanthe* are the only wheatears in which french-grey predominates in at least one plumage phase. Further, *monticola* and *phillipsi* are the only members of the genus to have pale (grey or white) wing-coverts which contrast with the colour of the flight feathers and upperparts. I formerly (Tye 1986) incorrectly stated this to be a character unique to *O. phillipsi*, while Hall & Moreau (1970) considered it unique to *monticola*! It is also a prominent feature of several *Myrmecocichla* species. The size difference between *monticola* and *phillipsi* is probably of little significance: it is paralleled by size differences between subspecies of other *Oenanthe* spp., e. g. *O. bottae frenata* and *O. b. heuglini.*

In view of this it seems unwise to link *O. monticola* very closely with either the *alboniger* or the *phillipsi* group. Range provides no clues, since *monticola* is allopatric with both groups (Figs. 1 & 2). Nor does habitat, as *monticola* occupies a wide variety, from lowland deserts to temperate mountains. If black-and-white plumage is primitive (Mayr & Stresemann 1950), then *O. monticola* possesses an unusual set of derived characters, some (brown female, unspotted young) shared with members of the *alboniger* group, others (french-grey phase, pale wing-coverts) with *phillipsi.* Hence not all of these can indicate close relationship. If *monticola* is closer to the *alboniger* group, then grey plumage evolved twice; alternatively if *monticola* is closer to the *phillipsi* group then dark brown females and unspotted young appeared twice. In addition to these considerations, *monticola* is unique in certain respects, including its polymorphisms and tail pattern. These factors, as well as its geographical isolation, suggest that *monticola* separated comparatively early from its closest relatives, and cannot be linked at the level of superspecies with other wheatears.

O. phillipsi superspecies

I include here the Somali Wheatear *O. phillipsi* and Northern Wheatear *O. oenanthe. O. phillipsi* has previously been regarded as a subspecies of *O. oenanthe* (e. g. Meinertzhagen 1930, 1954; White 1962) though I have attempted to show that the two taxa are not so close (Tye 1986). Differences between *oenanthe* and *phillipsi* include tail pattern, degree of sexual and age dimorphism, pattern of underparts, colour of wing-coverts and underwing-coverts, presence/absence of brown in the plumage and egg colour. This great range of differences probably reflects a not inconsiderable period of evolution in isolation. I have earlier emphasised the differences between *O. phillipsi* and *O. oenanthe* and drawn attention to similarities between *O. phillipsi* and members of the *alboniger* superspecies (Tye 1986). However, the following characteristics of the northwest African *O. o. seebohmi* demonstrate a link between *O. oenanthe* and *O. phillipsi.*

First, although most races of *O. oenanthe* have grey underwing-coverts and axillaries, *O. o. seebohmi* has these features darker grey or near-black, resembling the black underwing of *phillipsi.* Second, most races of *O. oenanthe* have a strong brown wash on the upperparts in most plumage stages, while *phillipsi* has only a faint tinge in immature birds (Tye 1986), but *O. o. seebohmi* males have less of a brown wash, with some individuals having little or none. Finally, although most races of *O. oenanthe* are sexually dimorphic (extent of brown on upperparts) with a pale throat in both

Fig. 2: Breeding ranges of *O. phillipsi* superspecies: dotted areas *O. oenanthe*; cross-hatched *O. phillipsi.*

sexes, while *O. phillipsi* is monomorphic (grey upperparts) with a black throat, *O. o. seebohmi* females often show a tendency towards purer grey, male-type upperparts and a black throat; suggesting either a trend towards sexual monomorphism in *seebohmi* or (perhaps more likely) a trend away from primitive sexual monomorphism in the Eurasian subspecies of *O. oenanthe.*

O. o. seebohmi indicates how a browner species (*oenanthe*) could have evolved from a more contrastingly-coloured ancestor similar in appearance to *phillipsi. O. o. seebohmi* is geographically isolated from the rest of the species and is itself an incipient species (Voous 1977).

O. phillipsi is found only in arid mountains in Somalia and eastern Ethiopia, while *O. o. seebohmi* occurs in temperate mountains of the Atlas, wintering in the west Sahara. The remaining subspecies of *O. oenanthe* breed in temperate grasslands and tundra and winter in African savannas. The geographical range of the superspecies is enormous (Fig. 2), reflecting expansion of *O. oenanthe* from a presumed north African centre of origin.

The members of this superspecies are allopatric (Fig. 2). They are also allopatric with *O. monticola* and nearly so with the *alboniger* superspecies (see Fig. 1). The only sympatry is in northwest Africa and Iberia where *O. oenanthe* overlaps somewhat with *O. leucura.* This, together with the similarities between *phillipsi* and *monticola* (listed above) and between *phillipsi* and the *alboniger* group (Tye 1986) argue for a closeness of relationship not previously recognised. The *alboniger* superspecies, *phillipsi* superspecies and *monticola* form one of several broad groupings of wheatear species which I discuss below.

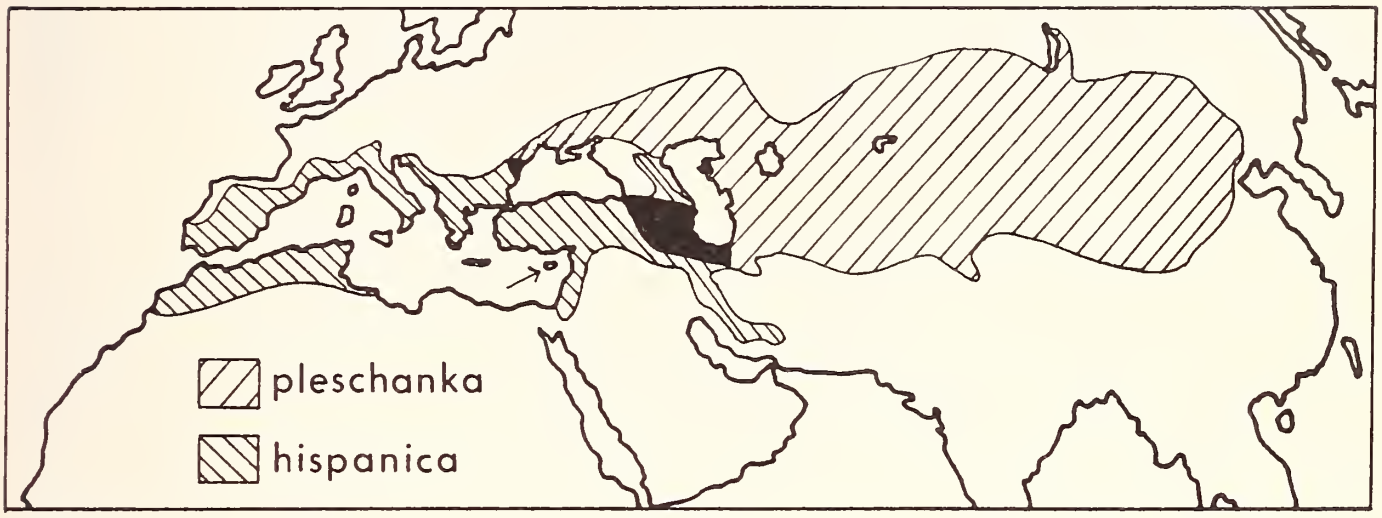

Fig. 3: Breeding ranges of *O. pleschanka* superspecies. Arrow indicates *O. p. cypriaca*; black areas are zones of overlap between *O. pleschanka* and *O. hispanica*.

O. pleschanka superspecies

I include here the Pied Wheatear *O. pleschanka* and Black-eared Wheatear *O. hispanica*, following Vaurie (1949). Each of these species has two subspecies, one of which (*O. p. cypriaca*) has been regarded as a separate species (Sluys & Van den Berg 1982) on the grounds of smaller size, simplified song and reduced sexual dimorphism (see also Christensen 1974). However, these are differences found between geographical races of other wheatear species and *O. p. cypriaca* cannot be treated as more than an incipient species (sensu Hall & Moreau 1970).

O. hispanica and *O. pleschanka* are so closely-related as to have been considered conspecific (Dementiev et al. 1954; but see Grote 1939). The two species have similar size, plumages and polymorphisms (see Mayr & Stresemann 1950). They are almost identical in female and immature dress, and in plumage pattern in the male: the major difference being a greater extent of black (on back and throat) in male *pleschanka*. The eastern race of *hispanica*, *O. h. melanoleuca*, which abuts *pleschanka* in SE Europe and SW Asia, resembles *pleschanka* more closely than the western nominate *hispanica*. *O. h. melanoleuca* has a greater extent of black on the head, and is darker brown on the crown and back in fresh plumage and whiter on the crown when worn (as in *pleschanka*). The throat is polymorphic (black or buff) in both species, and the black-throated form becomes more common further east; this trend includes both races of *hispanica*, and nominate *pleschanka* (in which pale-throated birds are rare).

These two species often live in bushier habitats than most wheatears (Cornwallis 1975; Tye in press), and have morphological adaptations to a more arboreal existence (Leisler et al. 1983). They generally replace one another geographically but overlap in small areas of Bulgaria, Transcaucasia and northern Iran (Fig. 3). Hybrid introgression occurs around zones of near-parapatry (in north-west Iran: Haffer 1977) and sympatry (in Transcaucasia and the Mangyshlak Peninsula: Loskot 1986; Panow 1986) but Haffer (1977) considered the degree of introgression insufficient to warrant merging the two into a single species.

The present superspecies appears to stand between species which are mainly black-and-white and those which are mainly sandy-brown. It is perhaps most closely-related to the *O. picata* species-group: male *pleschanka* in worn dress closely resemble *O. lugens*, a member of the *picata* group.

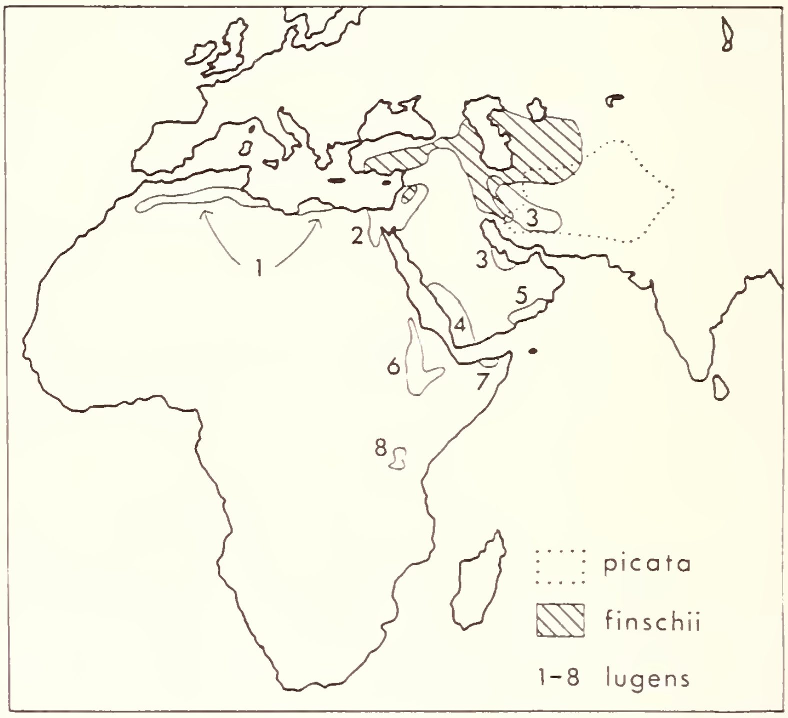

Fig. 4: Breeding ranges of *O. picata* species-group. Numbers indicate subspecies of *O. lugens* as follows: 1 *halophila*, 2 *lugens*, 3 *persica*, 4 *lugentoides*, 5 *boscaweni*, 6 *lugubris*, 7 *vauriei*, 8 *schalowi*.

O. picata species-group

I include here the Eastern Pied Wheatear *O. picata*, the Mourning Wheatear *O. lugens*, and Finsch's Wheatear *O. finschii*. *O. picata* and *O. lugens* have previously been associated as a superspecies (Mayr & Stresemann 1950; Hall & Moreau 1970), or even as members of a single species (Stresemann 1925), while *O. finschii* has been regarded as a subspecies of *O. lugens* (e. g. by Dementiev et al. 1954). In fact, the breeding ranges of *O. lugens* and *O. finschii* overlap in Jordan and the Zagros Mountains of western Iran (Fig. 4), so these two are good species, although evidently closely-related (see Cramp 1988). Further, the range of *O. picata* overlaps those of *lugens* in eastern Iran and *finschii* in northern Iran and Afghanistan (Fig. 4).

O. picata is one of the most variable species of wheatear (see Mayr & Stresemann 1950, Panow 1980), while *O. lugens* is certainly the most polytypic and also shows polymorphism in some of its races. In contrast *O. finschii* is not polymorphic (although it has sexual dimorphism) and geographical variation in it is slight (see Ticehurst 1927).

O. picata has three major plumage types, *capistrata*, *opistholeuca* and *picata*, which have been regarded as three morphs of a monotypic species (Mayr & Stresemann 1950). However, Panow (1980) presents data on ranges, plumage variation, breeding biology and hybridisation which suggest that they are in fact three subspecies which are at present introgressing through dispersal into one another's ranges. The variation, which is discussed more fully by Stresemann (1925), Mayr & Stresemann (1950) and Panow (1980), involves mainly the colour of the crown and belly, both of which can be black or white. Intermediates occur, some with a grey crown.

O. lugens has eight geographical races (see Fig. 4), which may be divided into three groups: "*lugubris*" group (comprising *O. l. lugubris*, *O. l. vauriei* and *O. l. schalowi*), "*lugentoides*" group (*O. l. lugentoides* and *O. l. boscaweni*) and "*lugens*" group (*O. l. lugens*, *O. l. halophila* and *O. l. persica*). The *lugubris* group is restricted to Africa, with three isolated, montane subspecies. All three are sexually dimorphic and one (*O. l. lugubris*) polymorphic in the male. The *lugentoides* group is restricted to the southern part of the Arabian peninsula, and contains sexually dimorphic subspecies with monomorphic males. The *lugens* group ranges across north Africa to the Levant, north-west Arabia and Iran. These are monomorphic except in a small part of the range of *O. l. lugens* in southern Syria and northern Jordan, where a largely-black morph exists (see Cramp 1988). Another of the subspecies of this group (*O. l. halophila*) is sexually dimorphic, but males are monomorphic. The *lugens* group is partially migratory, overlapping in winter with other subspecies.

The subspecies groups of *O. lugens*, and even some of its individual subspecies (e. g. *O. l. schalowi*) are incipient species, being geographically isolated (Fig. 4) and with distinctive plumages. Although *O. l. schalowi* at one extreme appears strikingly different from *O. l. halophila* at the other, these extremes are linked by a chain of subspecies along which characters change gradually or one by one, so that it is probably best to regard all as members of a single species.

O. picata is morphologically most similar to the members of the *lugubris* group, though it is much smaller. These taxa have the greatest amount of black in the plumage, and may represent the primitive plumage type, preserved at the extremes of the species-group's range (see Vaurie 1949; Patterson 1981).

Males of *O. finschii* closely resemble the members of the *lugens* group, differing only in the colour of the back (uniform with the grey crown in *finschii*, black in *lugens*). Female *O. finschii* are very similar to females of *O. l. halophila* (*lugens* group) and similarly show a tendency towards a black throat, which is pronounced in some individuals.

The members of this species-group occur in a variety of desert and sub-desert habitats through north Africa, Arabia and west-central Asia (Fig. 4). *O. lugens* is associated with broken, rocky country on steep slopes, often in mountains. *O. finschii* and *O. picata* are found in similar habitats in Asia, though perhaps more frequently on flatter ground (Dementiev et al. 1954; Cornwallis 1975; Cramp 1988; Tye in press). Their ranges are mutually exclusive but for the marginal overlaps described above. This species-group and the *alboniger* superspecies occupy similar habitats and ranges in north Africa and the middle East. Where ranges overlap, the two groups are perhaps largely ecologically separated as a consequence of size differences (*alboniger* group large, *picata* group small).

O. monacha

The male Hooded Wheatear *O. monacha* resembles the members of the *alboniger* superspecies, in its large size and sharp black and white coloration and it has previously been suggested that it may be closely related to them (Hall & Moreau 1970). However, other factors suggest that it may actually be closer to the *picata* species-group.

O. monacha differs from the *alboniger* group in its slighter build, much longer tail and long, narrow bill. As a result of these features, *O. monacha* appears a slimmer bird than the heavily-built members of the *alboniger* superspecies. *O. monacha* also has weaker feet, with short, slender tarsus and toes. In these characteristics *monacha* more closely resembles the *picata* group.

The plumage of male *monacha* resembles *alboniger* and *leucopyga* but the black feathers of the upperparts are often fringed grey, which is not a feature of the *alboniger* superspecies but is found in most members of the *picata* species-group. Details of plumage pattern also differ between *monacha* and the *alboniger* group, for example the white on the crown of *monacha* extends to the bill while in *leucopyga* there is a black forehead. The female of *monacha* has an unusual pale buff plumage with a distinctive pinkish tail, very unlike the *alboniger* group but resembling pale females of the *picata* group.

O. monacha and the *alboniger* superspecies occupy similar desert habitats, but *monacha* is adapted to feeding on aerial insects whereas the *alboniger* superspecies comprises primarily terrestrial foragers. This feeding technique enables *monacha* to occupy more hostile terrain than *alboniger* and *leucopyga* (Cornwallis 1975; Cramp 1988; Tye in press).

The breeding range of *monacha* broadly overlaps those of *leucopyga* (in Arabia) and *alboniger* (in Iran and Baluchistan) (Figs. 1 & 5). For this reason alone, *monacha* cannot be included in the *alboniger* superspecies and, given the morphological and ecological differences discussed above, it seems unlikely that it is closely related to them. Its range also overlaps those of *lugens* and *picata* and it differs morphologically from the members of the *picata* group more than the latter do amongst themselves. Its precise relationships are thus unclear but perhaps most credible is that *monacha* represents an earlier divergence from the line which later gave rise to the *picata*

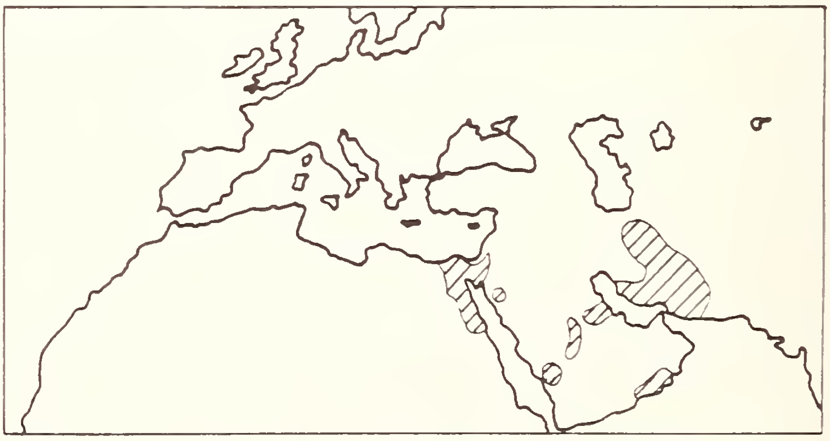

Fig. 5: Breeding range of *O. monacha*.

species-group. Judging by its present distribution and habitat preferences it may have originated as a montane or extreme desert isolate, specializing in capturing aerial prey from rocky perches.

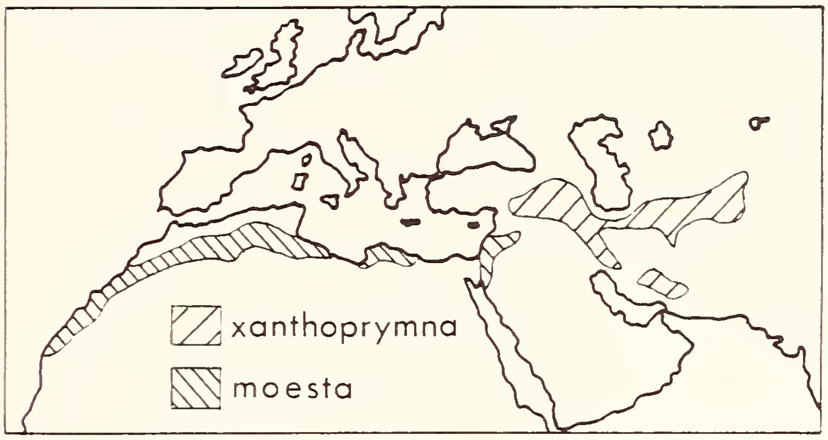

Fig. 6: Breeding ranges of *O. moesta* and *O. xanthoprymna.*

O. moesta, *O. xanthoprymna* and *O. deserti*

These three species appear to be closely-related to one another and to the *picata* species-group. Tristram's Wheatear *O. moesta* and the Red-tailed Wheatear *O. xanthoprymna* are generally regarded as forming a superspecies (Mayr & Stresemann 1950; Heim de Balsac & Mayaud 1962). Voous (1977) went further in suggesting that these two were close to *O. finschii.* However, this seems unlikely if *finschii* is a member of the *picata* group as outlined above, because the range of *moesta* broadly overlaps that of *lugens* in north Africa and the Middle East and the range of *xanthoprymna* overlaps *finschii* and *lugens* in eastern Turkey and northern Iran. Given this extensive geographical overlap between the *picata* group on the one hand and *moesta-xanthoprymna* on the other (Figs. 4 & 6), it is unlikely that the five species involved are the result of a single recent isolation event at the level of superspecies.

Vaurie (1949) regarded the Desert Wheatear *O. deserti* as forming a species-group with *O. finschii*, but did not present reasons for his opinion, while Cramp (1988) placed *deserti* in a species-group with *finschii* and *lugens*, again without giving reasons and without including *picata* with these species.

The above statements reveal considerable uncertainty about the relationships of *moesta*, *xanthoprymna* and *deserti*, both among themselves and with other wheatears.

The most obvious character shared by *moesta* and *xanthoprymna* is the rufous colour of the rump and (in *moesta* and *O. x. chrysopygia* only) tail. It is perhaps this character which led Heim de Balsac & Mayaud (1962) to suggest that they were conspecific. However, all members of the *picata* species-group also show a tendency towards rufous near the tail: least obvious in *finschii* and most developed in the *lugubris* group.

Further, *moesta* stands mid-way between the *picata* group and *xanthoprymna* in several other respects. The colour of the crown and nape of male *moesta* is virtually identical with that of pale-crowned members of the *picata* group: a distinctive, pale, pink-tinged greyish-white which is found in no other wheatear but these four species. The back of male *moesta* is black or greyish-black, like that of most of the *picata* group. These patterned upperparts stand in apparent contrast to the uniform dull grey-brown of *xanthoprymna*. The latter approaches most closely two members of the *pileata* superspecies (see below). However, some *xanthoprymna* show a slight pinkish cast on the crown, and the back of some *moesta* approaches the colour of *xanthoprymna* in having a dusky-brown wash.

These factors seem to indicate a degree of relationship between *moesta* and the *picata* group. As pointed out above, geographical considerations prevent *moesta* and *xanthoprymna* from being included in the *picata* group, but *moesta* seems morphologically at least as close to the *picata* group as to *xanthoprymna* and can certainly not be considered conspecific with the latter. *O. moesta* and *O. xanthoprymna* may be a true superspecies or they may represent two successive isolations (*moesta* later) from the stem which gave rise to the *picata* group. The *picata* group is largely adapted to rocky habitats, while *moesta* has become more or less restricted to flat plains, avoiding broken ground (Tye in press). Hence, where its range overlaps that of *lugens*, the two are largely separated by habitat. In contrast, *xanthoprymna*, which may have originated as a south-west Asian montane isolate, remains a species of rocky mountains.

The relationships of *O. deserti* are even more obscure. It shows a mixture of characteristics which indicate some degree of linkage to the *picata* group and to *moesta-xanthoprymna* but its precise position relative to these species is unclear. It has a similar plumage pattern (but not tail pattern) to that of *O. finschii*, although the general body colour is different; plumage details also differ, e. g. *deserti* has pale scapulars, uniform with the upperparts, while in *finschii* the scapulars are black, uniform with the wings. The range of *deserti* also overlaps with that of all three members of the *picata* group, over almost the entire range of *deserti* (Figs. 4 & 7), so it does not seem justifiable to include *deserti* in a species-group with *finschii* or the *picata* group as a whole (contra Cramp 1988).

O. deserti and *O. moesta* are the two wheatears with the largest amount of black in the tail (excepting *O. monticola nigricauda*). They are also ecologically similar, oc-

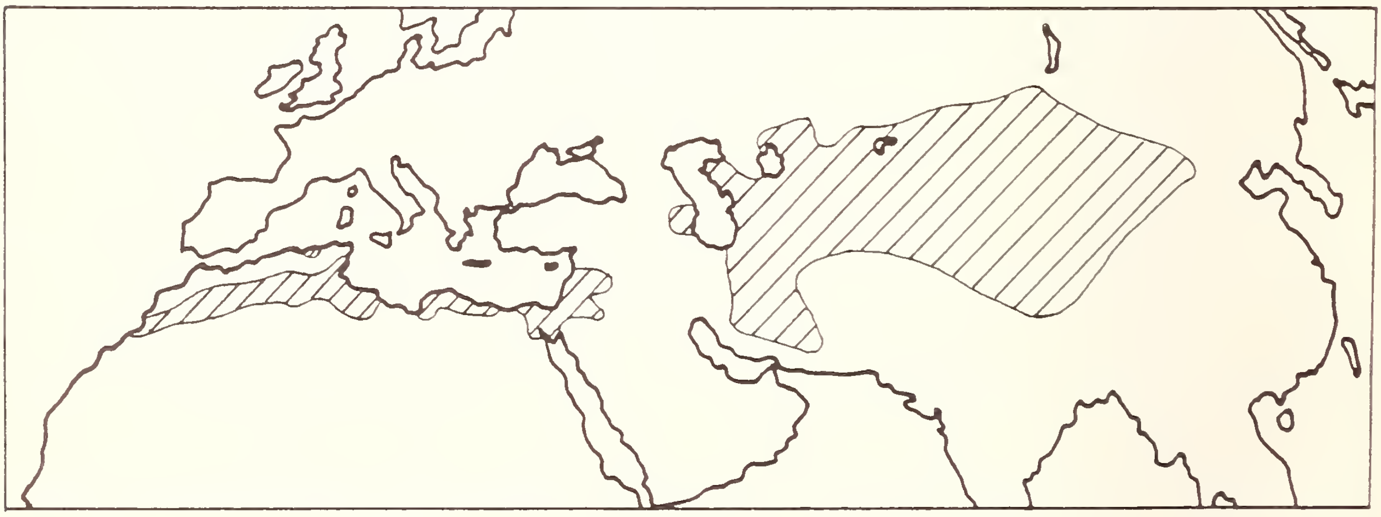

Fig. 7: Breeding range of *O. deserti*.

curring in almost identical habitats in approximately coincident ranges in north Africa (Whitaker 1905; Heim de Balsac & Mayaud 1962; Tye in press; cf. Figs. 6 & 7). These factors suggest that *deserti* does not form a species-group with *moesta*. It seems most likely that *deserti* represents an earlier isolate from the line which later gave rise to the *picata* group and *moesta-xanthoprymna*, but it is conceivable that an earlier superspecies split produced these three lines simultaneously. *O. deserti* is a primarily Asian plains-dwelling derivative of this predominantly rocky-habitat group, while *moesta* seems to be a later, African plains derivative. *O. deserti* may have spread into Africa subsequently, where it and *moesta* now have almost identical habitat and ranges.

O. pileata superspecies

I include here the remaining three species: the Capped Wheatear *O. pileata*, Red-breasted Wheatear *O. bottae* and Isabelline Wheatear *O. isabellina*. *O. pileata* was first linked in a superspecies with the other two by Hall & Moreau (1970), although *bottae* and *isabellina* had previously been regarded as forming a superspecies (Mayr & Stresemann 1950) or even a single species (Ripley 1952; Meinertzhagen 1954). I follow Hall & Moreau's (1970) treatment. *O. bottae* includes two incipient species: one comprises the large, pale *O. b. bottae* and *O. b. frenata*, which are very different in size (almost no overlap) and habitat from the small, dark *O. b. heuglini*. The latter is parapatric with *frenata* in Ethiopia, where *heuglini* occupies the lowlands and *frenata* highlands.

O. pileata is distinguished by its black breast-band, which is unique in the genus, but other aspects of its plumage closely match those of *bottae* and *isabellina*. *O. bottae heuglini* and *O. pileata* share dark brown upperparts and dark eye-line, and *O. b. heuglini* occasionally shows traces of a breast band (Hall & Moreau 1970).

O. pileata and *isabellina* are similar in size and build to the larger races of *bottae* (nominate and *frenata*), while *isabellina*, *b. bottae* and *b. frenata* often have traces of a dark eye-line like that of *pileata*. All three species have a similar tail-pattern with a broad terminal black band.

All three species are similar in ecology (with the possible exception of the montane *O. b. frenata*), preferring bare, overgrazed or burnt steppes and savannas (see Tye in press). They have mutually-exclusive breeding ranges in the semi-arid regions of Africa and Asia (Fig. 8); the marginal overlap suspected to occur by Hall & Moreau (1970) between *pileata* and *b. heuglini* in east Africa does not apparently exist (see Tye in press). The members of this superspecies form a chain from the comparatively dark-plumaged *O. pileata* and *O. b. heuglini* through the other, paler races of *bottae* to *isabellina*, the palest wheatear of all.

The present superspecies shows similarities with *xanthoprymna* and *deserti* which may suggest a degree of relationship. The *pileata* superspecies has a tail pattern like that of *deserti* and *xanthoprymna* (and *moesta*), with a broad terminal band. The general body colour of *deserti* is similar to that of *isabellina*, though this may be independently derived. *O. xanthoprymna* has dark brownish-grey upperparts, resembling *pileata* and *O. b. heuglini* in this respect. It is conceivable that the *pileata* superspecies represents a fourth branch of the postulated early split which gave rise to *deserti*, *xanthoprymna*, *moesta* and the *picata* group.

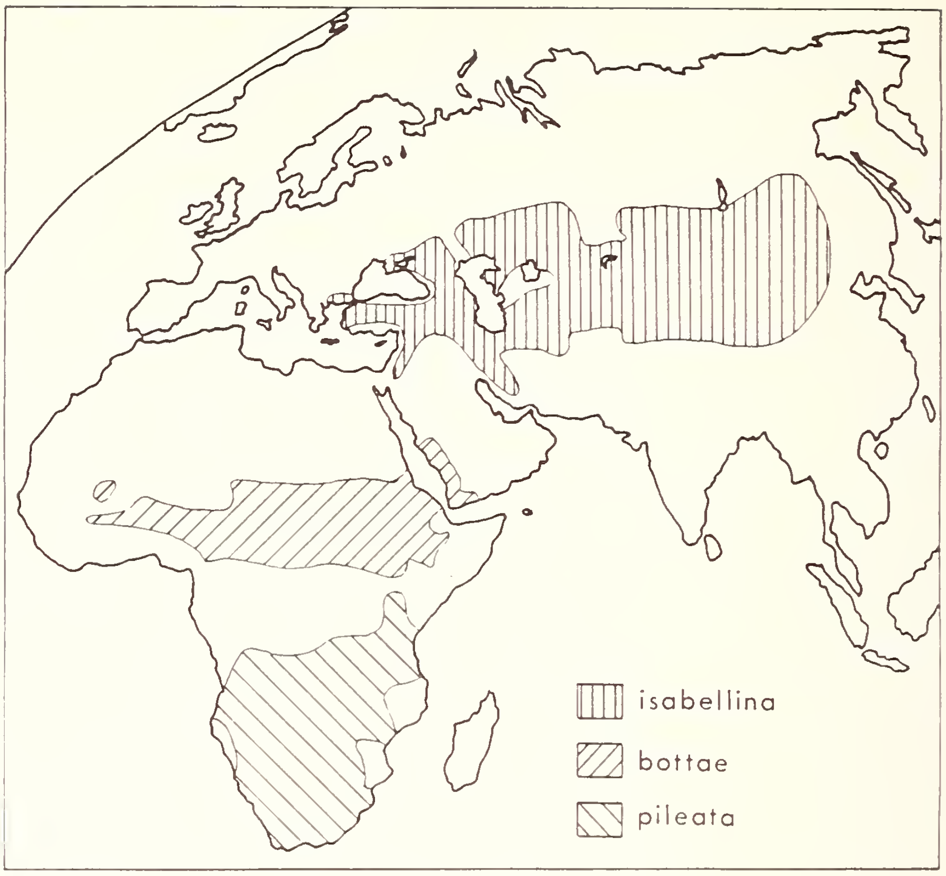

Fig. 8: Breeding ranges of *O. pileata* superspecies.

Relationships between superspecies

Wheatears fall into three broad assemblages: the black-white-grey species *alboniger* to *oenanthe* form one group, the *pleschanka* superspecies a second and the *monacha* to *isabellina* sequence the third (Fig. 9).

Black-and-white monomorphic plumage is probably primitive (Mayr & Stresemann 1950, and see above), and a plausible evolutionary progression leads in three directions from highly-contrasting black-and-white ancestors, resembling the *alboniger* group, to the grey-brown of *oenanthe* and to the sandy coloration of *hispanica* and the *pileata* group. All three branches progress towards paler, less contrasting plumages with more sandy-brown while the *alboniger* superspecies retains the primitive black-and-white. Although the *pleschanka* and *picata* groups include one or more black-and-white plumage phases, in their other phases (e. g. female, non-breeding) they are predominantly brown, or the black-and-white is accompanied by a tendency to pink, buff or grey (e. g. *picata* group). Even in the *alboniger* group, *O. leucura* has a tendency to brown. These developments, along with relationships within species-groups as discussed above, are represented in Fig. 9.

The precise details of the origins of the main lines from the ancestral *Oenanthe* stem are not clear: particular areas of uncertainty are indicated in Fig. 9 by dotted lines. In the sequence *alboniger* — *oenanthe*, *O. monticola* forms a bridge and may suggest that the *phillipsi* superspecies is more closely linked to the *alboniger* superspecies than indicated. The french-grey plumage colour strongly suggests community of origin for *monticola* and the *phillipsi* superspecies, but *monticola* differs from the latter in many details of plumage pattern.

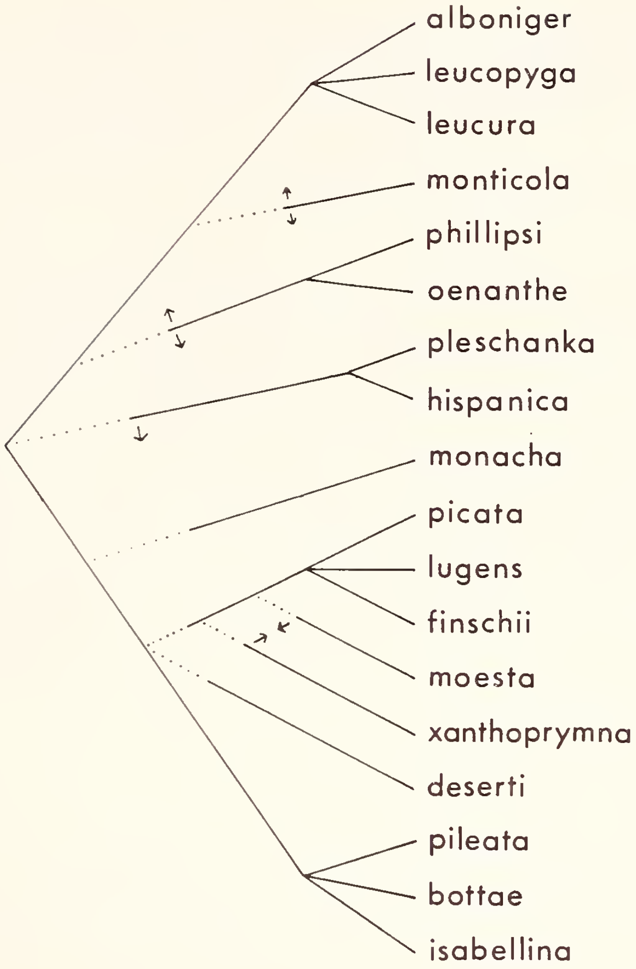

Fig. 9: A suggested phylogeny for the genus *Oenanthe*. Areas of particular uncertainty indicated by dotted lines; plausible alternatives by arrows (see text).

Alternatively, the *phillipsi* superspecies could conceivably be closer than indicated to the *pleschanka* superspecies. *O. oenanthe* resembles the *pleschanka* group in general plumage pattern, though not in general ground colour. They also show similar sexual dimorphisms and non-breeding and immature plumages. However, these similarities probably represent convergence, and *phillipsi* differs more strongly than *oenanthe* from the *pleschanka* group. *O. deserti* also resembles *oenanthe* and the *pleschanka* group in plumage pattern, while *O. oenanthe* in its browner female, immature and non-breeding plumages is extremely similar to females of the *picata-isabellina* sequence. It is possible that the *phillipsi* superspecies and/or *pleschanka* species-group are more closely linked to *deserti* and the *picata-isabellina* sequence than indicated in Fig. 9. As might be expected, these areas of greatest uncertainty occur with respect to the earliest divisions within the genus.

At the opposite extreme, the most recent splits are those about which one can be most certain. *O. pleschanka* and *hispanica* have obviously diverged very recently, or at any rate did not drift far apart genetically when in isolation from one another. They might now almost be regarded as a single species. Similarly *picata*, *lugens* and *finschii* have been regarded as conspecific and are obviously extremely close. Indeed, the difference between subspecies of some species (e. g. *O. oenanthe oenanthe* and *O. o. seebohmi*; *O. b. bottae/frenata* and *O. b. heuglini*; the *lugens*, *lugentoides* and *lugubris* groups of *O. lugens*) is comparable with those separating *pleschanka* from *hispanica* or *picata* from the *lugubris* group or *finschii* from the *lugens* group. The recent evolution of the genus has evidently been complex, with some recently-isolated populations (e. g. members of the *picata* species-group) quickly diverging, and some of their daughter populations (e. g. *lugens* species) spreading and themselves splitting into isolated populations.

Wheatears and the history of the Saharo-Sindian arid zone

Harrison (1986) includes several wheatears (viz *alboniger*, *leucopyga*, *lugens*, *moesta*, *deserti* and tentatively *monacha*) in what he recognizes as a distinct Saharo-Sindian arid-belt avifauna which his analysis suggests has shown little evidence of recent speciation or subspeciation. Harrison suggests this points to expansion-contraction of ranges in recent geological time, rather than fragmentation. However, if one takes fragmentation at the level of superspecies, this seems to hold true for rather few of the wheatears which inhabit this arid zone. *O. alboniger*, *leucopyga*, *lugens* and probably *moesta* are all members of superspecies or species-groups. Three of these species have themselves subspeciated; two weakly, but *lugens* is the most polytypic wheatear with eight subspecies. *O. xanthoprymna*, which was not considered by Harrison (1986), is another arid-zone species with two well-marked subspecies. *O. monacha* and *O. deserti* are the only arid-zone wheatears which might support Harrison's thesis. In general, most wheatears can be included in superspecies (or in species-groups which show evidence of recent range expansions) and many have split recently into well-marked subspecies or incipient species. Wheatears thus show marked evidence of recent fragmentation of distributions, as well as of expansion and contraction. Since wheatears are a primarily arid-zone group of birds, they suggest that the Saharo-Sindian arid belt has itself been subject to fragmentation in recent geological time.

The place of origin of each wheatear group is obscure, since all superspecies and species-groups have spread to occupy almost the entire north African and southwest and central Asian arid belt, and sometimes further. However, species density is highest in north Africa and the Middle East, and this may mark a centre of origin. A plausible sequence of events involves first the spread and fragmentation of the *Oenanthe* ancestor, forming populations from which were derived the three broad groupings discussed above. Each of these ancestral species again spread to occupy the whole of the Afro-Asian arid belt and was subject to further fragmentation. Today's superspecies show evidence of at least one, and in some cases up to three, such waves of spread and fragmentation. If, as hypothesised earlier, *Cercomela*, *Myrmecocichla* and *Oenanthe* are not monophyletic genera but are interlinked, then the former two groups must be considered as part of this arid-zone chat radiation.

Acknowledgements

I thank the staff of the British Museum (Natural History) Sub-department of Ornithology, particularly P. R. Colston, G. S. Cowles and M. P. Walters, for permission to examine specimens in their care, and for cordial discussions. Additional material was kindly supplied by G. S. Keith (American Museum of Natural History) and M. A. Traylor (Field Museum of Natural History, Chicago). K. E. Joysey permitted use of facilities and specimens in the Cambridge University Museum of Zoology. M. C. Jennings graciously provided draft distribution maps from the forthcoming Atlas of the Breeding Birds of Arabia, while the editors of Birds of the Western Palaearctic provided pre-publication drafts of the articles on wheatears. Hilary Tye helped design, and drew, the Figures, and Margaret Clements processed the words. J. Haffer constructively reviewed the manuscript.

Zusammenfassung

Die Beziehungen innerhalb der Steinschmätzer (Gattung *Oenanthe*) sind umstritten; eine gründliche Revision der gesamten Gruppe fehlt. In der vorliegenden Arbeit werden alle Arten (Paläarktis und Afrotropis) behandelt; unter Berücksichtigung ökologischer, geographischer und morphologischer Faktoren wird eine Phylogenie und ein System von Superspezies oder Artengruppen vorgeschlagen. Die Stellung der Gattung wird in Bezug auf ihre nächsten Verwandten *Cercomela*, *Myrmecocichla*, *Thamnolea* und *Saxicola* erörtert. Steinschmätzer lassen sich in fünf Superspezies oder Artengruppen (mit 13 Arten) gruppieren; für fünf Arten sind die Beziehungen weniger gesichert. Steinschmätzer des Saharo-Sindischen (Nordafrika bis Zentralasien) Trockengürtels lassen eine sehr junge Zersplitterung der Populationen erkennen, was dafür spricht, daß der Trockengürtel selbst in junger geologischer Zeit in Teilareale zersplittert war. Die heutigen Verbreitungsmuster sprechen dafür, daß es mehrere Wellen von Speziation und anschließender Ausbreitung durch, gelegentlich darüber hinaus, diese Trockenzone gegeben hat.

References

Amadon, D. (1966): The superspecies concept. — Syst. Zool. 15: 245—249.

Christensen, S. (1974): Notes on the plumage of the female Cyprus Pied Wheatear *Oenanthe pleschanka cypriaca*. — Ornis Scand. 5: 47—52.

Cornwallis, L. (1975): The comparative ecology of eleven species of Wheatear (genus *Oenanthe*) in S. W. Iran. — D. Phil. thesis, University of Oxford.

Cramp, S. (ed.) (1988): The birds of the western Palaearctic, Vol. 5. — Oxford University Press, Oxford.

Dementiev, G. P., N. A. Gladkov, K. N. Blagosklonov, I. B. Volchanetskii, R. N. Meklenburtsev, E. S. Ptushenko, A. K. Rustamov, E. P. Spangenberg, A. M. Sudilovskaya & B. K. Shtegman (1954): Birds of the Soviet Union, Vol. 6. — Israel Programme for Scientific Translations (1968), Jerusalem.

Glutz von Blotzheim, U. N. & K. M. Bauer (1988): Handbuch der Vögel Mitteleuropas, Vol. 11. — AULA, Wiesbaden.

Greig-Smith, P. W. (1982): Interspecific aggression between chats. — Bird Study 29: 162—164.

Grote, H. (1939): Ist *Oenanthe pleschanka* (Lepech.) eine Rasse von *Oenanthe hispanica* (L.)? — Orn. Monatsber. 47: 54—57.

Haffer, J. (1977): Secondary contact zones of birds in northern Iran. — Bonn. zool. Monogr. 10: 1—64.

Hall, B. P. & R. E. Moreau (1970): An atlas of speciation in African passerine birds. — British Museum (Natural History), London.

Harrison, C. J. O. (1986): The Saharo-Sindian arid zone birds. — Sandgrouse 7: 64—70.

Heim de Balsac, H. & N. Mayaud (1962): Les oiseaux du nord-ouest de l'Afrique. — Lechevalier, Paris.

Ledant, J.-P., J.-P. Jacob, P. Jacobs, F. Malher, B. Ochando & J. Roché (1981): Mise à jour de l'avifaune algérienne. — Gerfaut 71: 295—398.

Leisler, B., G. Heine & K. H. Siebenrock (1983): Einnischung und interspezifische Territorialität überwinternder Steinschmätzer (*Oenanthe isabellina*, *O. oenanthe*, *O. pleschanka*) in Kenia. — J. Orn. 124, 393—413.

— & H. Winkler (1985): Ecomorphology. — In: Johnston, R. F. (ed.): Current Ornithology, Vol. 2, 155—186. — Plenum, London.

Loskot, V. (1986): Morphism and hybridisation of wheatears *Oenanthe hispanica* and *O. pleschanka*. — Proc. 18 Int. Orn. Congr.: 1031.

Lynes, H. (1924—26): On the birds of North and Central Darfur, with notes on the West-Central Kordofan and North Nuba Provinces of the British Sudan. — Ibis (11) 6: 399—446, 648—719; (11) 7: 71—131, 344—416, 758—797; (11) 8: 346—405.

Mayr, E. & E. Stresemann (1950): Polymorphism in the chat genus *Oenanthe*. — Evolution 4: 291—300.

Meinertzhagen, R. (1930): Nicoll's birds of Egypt. — Hugh Rees, London.

— (1954): Birds of Arabia. — Oliver & Boyd, Edinburgh.

Moreno, J. (1984): Search strategies of Wheatears (*Oenanthe oenanthe*) and Stonechats (*Saxicola torquata*): adaptive variation in perch height, search time, sally distance and inter-perch move length. — J. anim. Ecol. 53: 147—159.

Panow, E. N. (1974): Die Steinschmätzer. — Ziemsen-Verlag, Wittenberg Lutherstadt.

— (1980): Divergenzen und Hybridisation in der Gruppe der Elstersteinschmätzer (*Oenanthe picata*). — Mitt. zool. Mus. Berlin 56 Suppl. Ann. Orn. 4: 2—23.

— (1986): [New data on hybridization of *Oenanthe pleschanka* and *O. hispanica*]. — Zool. Zh. 65: 1675—1683.

Patterson, C. (1981): The development of the North American fish fauna — a problem of historical biogeography. — In Forey, P. L. (ed.): The Evolving Biosphere, 265—281. — British Museum (Natural History), London.

Ripley, S. D. (1952): The thrushes. — Postilla 13: 1—48.

— (1962): Brief comments on the thrushes. — Postilla 63: 1—5.

Short, L. L. (1976): The contribution of external morphology to avian classification. — Proc. 16 Int. Orn. Congr.: 185—195.

Sluys, R. & M. Van den Berg, (1982): On the specific status of the Cyprus Pied Wheatear *Oenanthe cypriaca*. — Ornis Scand. 13: 123—128.

Smith, K. D. (1971): Notes on *Oenanthe* species in winter in Africa. — Bird Study 18: 71—79.

Snow, D. W. (1978): An atlas of speciation in African non-passerine birds. — British Museum (Natural History), London.

Stresemann, E. (1925): *Oenanthe opistholeuca* (Strickland) — eine melanistische Mutante von *Oenanthe picata* (Blyth). — Orn. Monatsber. 33: 178—181.

Ticehurst, C. B. (1927): On *Oenanthe hispanica*, *Oenanthe finschii* and *Oenanthe picata*. — Ibis (12) 3: 65—74.

Tye, A. (1986): Plumage stages, moults, sexual dimorphism and systematic position of the Somali Wheatear *Oenanthe phillipsi*. — Bull. Br. Orn. Club 106: 104—111.

— (1988): Foraging behaviour and selection of prey and perches by the Buffstreaked Chat *Oenanthe bifasciata*. — Ostrich 59: 105—115.

— (1989): The systematic position of the Buff-streaked Chat *Oenanthe/Saxicola bifasciata*. — Bull. Br. Orn. Cl. 109: 53—58.

— (In press): The wheatears, *Oenanthe* spp. In: Keith, G. S., E. K. Urban & C. H. Fry (eds.): The Birds of Africa, vol. 4. — Academic Press, London.

Vaurie, C. (1949): Notes on the bird genus *Oenanthe* in Persia, Afghanistan and India. — Amer. Mus. Novit. 1425: 1—47.

Voous, K. H. (1977): List of recent Holarctic bird species: passerines. — Ibis 119: 223—250, 376—406.

Whitaker, J. S. (1905): The Birds of Tunisia. — R. H. Porter, London.

White, C. M. N. (1962): A revised checklist of African shrikes, orioles, drongos, starlings, crows, waxwings, cuckoo-shrikes, bulbuls, accentors, thrushes and babblers. — Government Printer, Lusaka.

Alan Tye, British Ornithologists' Union and Edward Grey Institute of Field Ornithology, Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, England.

Zeitschrift/Journal: Bonn zoological Bulletin - früher Bonner Zoologische Beiträge.

Jahr/Year: 1989

Band/Volume: 40

Autor(en)/Author(s): Tye Alan

Artikel/Article: Superspecies in the genus Oenanthe (Aves, Turdidae) 165-182