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**A REVIEW OF CURRENT CLASSIFICATION METHODS
WITH PARTICULAR REFERENCE TO AFRICAN PASSERIDS (AVES)**

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ABSTRACT

Passerid birds are cosmopolitan, with an African origin that dates back to the Early Tertiary. Whereas primitive representatives were insectivores and frugivores, the Miocene rise and spread of savanna grassland and adaptation to granivory resulted in an explosive radiation that is not reflected in the systematics of the group. Since evolution is complex, a classification that accurately replicates genealogy must be complex also, and far more taxa are required to depict this passerine diversification than are currently admitted. Although most of these names are available, a failure to understand the true purpose of taxonomy has led to their obfuscation by taxonomic lumping and subjective synonymy. So as to determine genealogy, Darwinian (phylogenetic) taxonomy requires identification of primitive and derived characters for correct taxonomic placement, since weighting of these two character-sets greatly influences classification. Moreover it demands cognisance of the phenotypic discontinuities created by extinct and unknown taxa that represent the majority sample (~90%). These form the twigs, stems and branches of the evolutionary tree, and are of paramount importance in replicating ancestry and determining taxonomic rank. Although cladograms are the prevailing method of depicting inferred evolutionary relationships, their use for classification produces incongruous associations. This is because the gaps separating adjacent branches of a cladogram represent phenotypic discontinuities of variable magnitude, that are different for every branch of every cladogram and range from species to families. Equalisation of these internodal gaps draws taxa far closer phylogenetically than they are biologically, so that the use of cladograms and PAUP analysis for classification produces erroneous taxonomic associations. Cladograms provide only an indication of affiliation among the sample under consideration, not close taxonomic bond. Linnaean and Darwinian taxonomy are not different classification systems, they merely draw the cut-off line at different levels in the evolutionary tree; Linnaean taxonomy trims the outer growth whereas Darwinian taxonomy insists on its retention. Since all evolution is a continuum, it is suggested that quantum evolution and punctuated equilibrium are artificial constructs resulting from taxonomic lumping, phenotypic discontinuities and the alternating environmentally-stimulated processes of cladogenesis and anagenesis. The biological species concept is shown to have been fallacious since the day of inception, and the subjectivity of taxa construction is emphasized. Molecular classifications have produced some of the most incongruous taxonomic associations ever to have afflicted avian systematics and, to date, have failed to produce a natural classification. Phenotypic analysis remains the only method capable of tracking close evolutionary relationships and, with due attention to "trifling characters", accurately replicating the finest intricacies of the evolutionary process necessary to achieve a "natural classification".

Key words: African passerids, phylogeny, evolutionary theory, systematics.

INTRODUCTION

Since most African birds were discovered over 100 years ago, for much of the 20th Century few ornithologists concerned themselves with taxonomy, i.e. the identification, description, naming and classification of birds. As a result avian systematics fell into the hands of ecologists, ethologists and twitchers who failed to recognise the true purpose of taxonomy - to accurately replicate genealogy. This left only Dr Hans Wolters (1943-87) to valiantly champion a Darwinian classification that for the most part was met with deaf ears. As a result most of the last 75 years was a lengthy phase of taxonomic rationalisation and simplification in which every canary was returned to *Serinus*, every weaver to *Ploceus* and every sparrow to *Passer* (*cf.* Fry *et al.* 2004; Hockey *et al.* 2005). It represented a failure to recognise living birds as merely the survivors of a much branched evolutionary tree in which "The green and budding twigs may represent existing species; and those produced during former years may represent the long succession of extinct species" (Darwin 1859: 143). Thus extant species represent only a very small portion, guesstimated here at 10%, of the genealogy of any group, with the vast majority of its members extinct. But worse was to follow. Taxonomy fell into the hands of molecular biologists who erroneously saw "The purpose of taxonomy is the identification of species and their assignment to higher level taxa" (Tautz *et al.* 2003: 72). No longer were birds viewed as living entities with a myriad of idiosyncratic biological and behavioural attributes, many unquantifiable, but now they were reduced to scraps of tissue for the extraction of DNA and gene sequencing to be analysed and grouped by computer programs.

DISCUSSION

A natural classification

For most of the last 250 years ornithological classification was "a scheme for arranging together those living objects which are most alike, and for separating those which are most unlike" (Darwin 1859: 372). However in order for a classification to be natural, "the arrangement of the groups in each class … must be strictly genealogical" (Darwin 1859: 378). This guidance, a profound truism, has been ignored (not read) by countless ornithologists who have continued to group like with like (= Linnaean taxonomy), an approach that has persisted into the latest classifications of African birds (Fry *et al.* 2004; Hockey *et al.* 2005). A natural classification is one that *accurately* replicates the evolutionary history of the group, not one air-brushed to satisfy the notions of the taxonomist concerned. Vital to its construct is consideration of the far more numerous extinct species (~90%) that serve to constitute and delineate the branches of the evolutionary tree. Hence the goal of Darwinian taxonomy is to identify all the dichotomies that make up the evolutionary tree and to replicate these in an appropriate taxonomy. It is a phylogenetic taxonomy that searches for evolutionary lineages, groups with "propinquity of descent" (Darwin 1859: 372).

Since evolution is a complex process, natural classifications must be complex also. As a result, to accurately replicate the intricate evolutionary history of passerids requires far more taxa than offered by prevailing classifications. For too long avian systematists have, for reasons known only to themselves, favoured "simple classifications" in which accepted taxa are reduced to a minimum by subjective synonymy, i.e. taxonomic lumping. However, "Simplicity itself is not necessarily virtuous, particularly if it obscures true relationships between entities in the natural world" (Brown in Rudolph 2001: 1). Simplification prunes the youngest growth of the

evolutionary tree to arbitrarily pre-selected levels, and erases the most recent diversification.

Conventionally phenotypic differences are taken as a measure of the degree of evolutionary (genomic) divergence. Thus, once a bird has been identified, described and named it has to be placed into some sort of rational scheme; it has to be classified. Unfortunately most users of classifications are not systematists and simply follow the views of others, thereby adding false credibility to prevailing opinions (Brothers 2021).

The classification of all organisms has proven more an art than a science, philosophically governed by two extremes. "Lumpers" seek to simplify classification by heavy synonymy, often with little justification, and choose to admit only a limited number of taxa. Those that do not fit into preconceived schemes are simply dismissed as "unnecessary" (*cf.* Mayr & Amadon 1951). But always one should guard against "the blindness of preconceived opinion" (Darwin 1859: 434).

In an attempt to better understand relationships "splitters" recognize many taxa and create a complex taxonomy. Unfortunately for most of the last century avian systematists have failed to appreciate the importance of genealogy to taxonomy and the thoughtful work of Austin Roberts (1922, 1947) and Hans Wolters (1943, 1950, 1954, 1957, 1966, 1970, 1979, 1987) was dismissed in favour of "simple classifications", very often to satisfy bird watchers and laypersons. In a group as diverse as the order Passerida, with more than 6,000 living species, representing more than 60% of avian diversity (Oliveros *et al.* 2019), taxonomic splitting is mandatory if genealogy is to be replicated accurately and a natural classification achieved. Moreover, contrary to prevailing opinion, in phylogenetic taxonomy rank is not discretionary and cannot be preconceived; it is predetermined by evolutionary position (Cooper 2015). Unfortunately "Numerous apparently rapid divergence events within passerines have hindered reconstruction of their evolutionary interrelationships" (Oliveros *et al.* 2019: 7917).

Primitive and derived characters

The defining characters of all organisms are biological isolating mechanisms that serve to facilitate recognition by their own kind, and to inhibit interbreeding with their closest relatives. Thus consistent disparity can be established and maintained only where interbreeding is averted and gene flow inhibited, i.e. when breeding populations are genetically isolated. But this is not instantaneous, for "species have been modified … by the preservation or the natural selection of many successive slightly favourable variations" (Darwin 1859: 432). In determining relationships therefore it is important to appreciate that all the biological attributes of an organism fall into two fundamental categories - primitive characters inherited unchanged from the ancestor (plesiomorphies), and derived characters (slightly favourable variations) that distinguish an organism from its predecessor (apomorphies). In any organism inherited characters are overwhelmingly predominant and betray "the hidden bond of community of descent" (Darwin 1859: 462). Since they have been passed down through many generations, often for millions of years, plesiomorphies are indicative of affiliation (distant relationship), not close taxonomic bond, for when "one group of animal exhibits an affinity to a quite distinct group, this affinity in most cases is general and not special" (Darwin 1859: 386). Plesiomorphies are identified by the Commonality Principle - the most widespread characters are likely to be the most primitive. As a result apomorphies constitute only a small portion of the attributes of any organism and, since they are more recently acquired, record the latest

evolutionary novelties. It is only they that can reveal close biological relationships and recent evolutionary history. Often however, so as to deceive, they may be analogous characters that have arisen in unrelated organisms as an adaptation to similar conditions. Such convergence (homoplasy) is so common and widespread that one must not "in classifying, trust to resemblance" (Darwin 1859: 373). Moreover one should also guard against recapitulation since "it is a very surprising fact that characters should reappear after having been lost for many, probably for hundreds of generations".

Since evolution is "descent with modification" (Darwin 1859: 112), Darwinian taxonomy is a search for "acquired characteristics", derived traits (apomorphies) that distinguish an organism from its progenitor. Hence for any classification to be "strictly genealogical" the prime task of the taxonomist is to unravel the evolutionary history (phylogeny) of the group by discriminating primitive and derived characters, and then to assemble these into higher taxa on the basis of shared derived characters (synapomorphies). It is a bottom up process. Unfortunately most avian classifications currently on offer have been predetermined from the top downwards, cramming birds into preconceived taxa that have not been vetted by thorough Darwinian/Hennigian analysis. Hence, in reality, "the universality and unambiguous meaning afforded by available naming systems do not have phylogeny or evolution as their foundation" (Fitzhugh 2008: 79).

For those schooled in Linnaean taxonomy (unification on the basis of primitive characters), Darwinian taxonomy produces a very different classification that, understandably, has encountered much resistance. Thus Fry *et al.* (2004: xv) maintained that "There are theoretical and practical difficulties with the PSC (phylogenetic species concept), however, and it has been argued persuasively that the BSC (biological species concept) appeals better to common sense, serves ornithology best, and is likely to remain the most valuable and popular species concept among field ornithologists for a good many years to come". Erudite words, but in ignorance of Darwin's wise council. Snow's (1997: 110) query, "Should the biological be superceded by the phylogenetic species concept?" is equally rhetorical. Biological classifications not strictly rooted in genealogy are no more than "convenient fiction, a pandering to our own limitations" (Dawkins 2004: 109). We must however "question the efficacy of promoting the development and implementation of the PN [phylogenetic system of nomenclature] as an entirely separate system from the LN [Linnaean system of nomenclature]" (Fitzhugh 2008: 79) since the difference, actually, is merely the level at which the evolutionary tree is pruned. Linnaean taxonomy is invaluable for detecting suprageneric categories, trimming the evolutionary tree to pre-selected basal levels, thereby revealing distant relationships (affiliation). Darwinian taxonomy on the other hand rejects pruning entirely, and is mandatory for identifying the most recent evolutionary dichotomies and closest taxonomic bonds.

Character weighting

Species are a mosaic of primitive and derived traits, and the taxonomic weighting of these two character-sets greatly influences classification. Since primitive characters dominate the attributes of all species, grouping like with like (Linnaean taxonomy) assigns plesiomorphies greatest taxonomic weight. The result is grouping of distantly related birds by affiliation, and ignoring the finer more recent branches of the evolutionary tree - it results in taxonomic lumping. Since evolution is "descent with modification" however, only derived traits expose the most recent dichotomies in the

evolutionary tree. Consequently, in order to achieve a natural classification, one that accurately replicates genealogy, apomorphies must carry the greatest taxonomic weight in phylogenetic assessment.

Phenotypic discontinuities

Charles Darwin (1859: 388) appreciated that "if every form which has ever lived on this earth were suddenly to reappear ... it would be quite impossible to give definitions by which each group could be distinguished from other groups, as all would blend together by steps as fine as those between the finest existing varieties".

Fortunately for biologists this unbroken evolutionary continuum is compartmentalised by phenotypic discontinuities resulting from large parts of the evolutionary record not having been preserved, or remaining to be discovered (Cooper 2015). Such discontinuities are a measure of the number of taxa missing (extinct/not found), the quantity to be inferred by the magnitude of the discontinuity: "The more aberrant any form is, the greater must be the number of connecting forms which .... have been exterminated and utterly lost" (Darwin 1859: 386).

Since extant organisms represent merely the most recent members of the evolutionary tree, they preserve only a very small portion of the genealogy of any group, guesstimated here as little as 10%, from which "many a limb and branch has decayed and dropped off; and these fallen branches of various sizes may represent those whole orders, families, and genera which have now no living representatives, and which are known to us only in a fossil state" (Darwin 1859: 143). It is impossible therefore to construct a natural classification, one that accurately replicates genealogy, by ignoring 90% of the sample since, from a systematic perspective, this draws living birds much closer together than they really are, thereby leading to incongruous taxonomic associations. Consequently, consideration of extinct and undiscovered species is imperative if genealogy is to be replicated accurately and a natural classification achieved. As a result every taxon should include all its members down to the most recent evolutionary dichotomy. The stems and branches, where most evolution occurs, comprise the extinct or undiscovered species, and the extant species the outermost twigs and leaves. The importance of this Darwinian interpretation is that almost every surviving taxon comprises a stem of more numerous antecedents that are extinct, with "the amount of modification which the different groups have undergone … to be expressed by ranking them under different so-called genera, sub-families, families, sections, orders, and classes" (Darwin 1859: 459). Thus the magnitude of phenotypic discontinuities is fundamental in determining taxonomic rank. A failure to appreciate this guidance has led some to allocate 22 families to the superfamily Passeroidea (https://animaldiversity.org/accounts/Passeroidea).

Since phenotypic discontinuities range from a species to hundreds of species, not every one of which can be categorized, it is proposed to recognise only three (Cooper 2015). Minor phenotypic discontinuities involve extinct subspecies, species and perhaps a few genera, with ancestral relationships remaining discernible and obvious. Such discontinuities separate all extant genera and, where there is a sole survivor (isospecies), are the bases for recognition of monotypic genera. Very many living species fall into the latter category, but have been deemed "unnecessary" and expunged from consideration by taxonomic lumping. They are vital however to the accurate replication of genealogy, and refute the claim that "Monotypic supraspecific hypotheses have no epistemic basis" (Fitzhugh 2008: 52).

Moderate phenotypic discontinuities involve a number of extinct genera, subtribes and tribes, and ancestral relationships may be reasonably inferred. Commonly they separate subfamilies and families.

Major phenotypic discontinuities involve extinct superfamilies and other higher taxa, so that extant members are phenotypically so different that ancestral relationships are obscure. They result in cryptogenic taxa of conjectural ancestry and rank.

Quantum evolution and punctuated equilibrium

Compartmentalisation of the evolutionary record led to the hypotheses of quantum evolution (Simpson 1944) and punctuated equilibrium (Eldredge & Gould 1972). However all life is an evolutionary continuum (Hotton 1968), from the appearance of the first bacterium to Man. A sparrow cannot give rise to a weaver without numerous intermediates, and all evolutionary relationships are naturally paraphyletic, "with lines of gradual continuity linking literally every species to every other" (Dawkins 2004: 108). Every child has a father, a grandfather, a great grandfather and this "daisy chain" continues back to the beginning of life, leading to "the old canon in natural history, *Natura non saltum facit*" (Nature does not make leaps) (Darwin 1859: 218). Hence one "ought to be extremely cautious in saying that any organ or instinct, or any whole being, could not have arrived at its present state by many graduated steps" (Darwin 1859: 460). Within this evolutionary continuum, in every lineage, there is a child that is a different species to its parents. It is only phenotypic discontinuities that make discrimination and identification possible, for "In a world of perfect and complete information, fossil information as well as recent, discrete names for animals would become impossible" (Dawkins 2004: 108). It is no coincidence therefore that the hypothesis of punctuated equilibrium emerged in the wake of the "new systematics" whose main accomplishment was "a vast condensation and elimination of spurious taxa established on typological criteria" (Eldredge & Gould 1972: 92). While this approach may have been necessary at the species level, it was carried over mercilessly to the genus level, and taxonomic lumping controlled biological systematics for most of the last half of the 20th Century. Its effect was to erase the finer branches of the evolutionary tree, thereby automatically and artificially increasing the size of the evolutionary "steps" separating taxa. Subjective synonymies became lengthy, the "importance, for classification, of trifling characters" (Darwin 1859: 375) was ignored, minor phenotypic changes were overlooked, and differences separating taxa became leaps. Such quantum shifts characteristically accompany, and are accentuated by, the alternating processes of cladogenesis (adaptive radiation) and anagenesis (species replacement) (Ricklefs 2004) that partner the major environmental shifts that are so well documented in the fossil record.

Evolutionary relationships

Biological evolution is the story of life, and Darwin (1859: 117) recognized that life's relationships could be "represented by a great tree", an evolutionary tree, what has come to be known as a "tree of life", with the leaves and twigs the most recent dichotomies, and the trunks the most distant. Hence evolutionary relationships may be depicted by a phylogenetic tree (dendrogram), or by a phenogram that depicts "taxonomic relationships among organisms based on overall similarity of many characteristics without regard to evolutionary 'history' or assumed significance of specific characters" (Rohlfe 2013: 293) for which the computer program PhenoGram is available.

Cladograms are branching diagrams that have long been the preferred basis of depicting inferred evolutionary relationships and, as a result, have been used for the grouping and classification of organisms. With the advent of DNA sequencing they are now used in molecular phylogenetics to construct phylogenetic trees that arise from molecular evolution. Taxa are grouped on the basis of synapomorphies, but it is during the internodal gaps of a cladogram that most evolution occurs, "when the individual unit becomes part of a chain … an intermediary, a link …. no longer existing but transmitting" (Chardin 1959: 162). The number of taxa within every internodal gap is, however, inherently unequal for every branch of every cladogram, and can span anything from one species to many genera, and even families or more. Hence equalisation of the internodal gaps (phenotypic discontinuities) of cladograms draws taxa adjacent that biologically are well removed phylogenetically.

A natural classification cannot be achieved by alliances inferred solely on the basis of extant members, by ignoring ~90% of the sample, for "inadequate taxon sampling and limited choice of outgroup(s) can lead to spurious inferences of phylogeny" (Torre-Bárcena *et al.* 2009: 1). Indeed, "The choice of an outgroup is a crucial step in cladistic analysis because different outgroups can produce trees with profoundly different topologies" (Wikipedia).

Cladograms provide only a semblance of affiliation among the sample under consideration; they do not necessarily, and mostly do not, depict close ancestor-descendant relationships. In fact they can be highly deceptive, for "what they reveal are suggestive, but what they conceal are vital" (Levenstein in Ratcliffe 2016). Certainly the insistence that "cladograms, should be reflected as accurately as possible in a nomenclatural system" (Fitzhugh 2008: 54) is a grave error. The genealogy of living organisms is like a fishing net, the extant members representing the fine threads and the extinct/unknown species the gaps between. It is the latter that are fundamental in determining taxonomic associations and the rank of survivors.

Since 2003 it has become common to use the computer program PAUP (Phylogenetic Analysis using Parsimony) to generate evolutionary relationships and reclassify organisms, particularly where direct evidence for genealogy (the fossil record) is scant or absent.

Species are a mosaic of primitive and derived characters, and evolution is fastest where the need is greatest. Consequently, although many of the attributes of a species are evolving, they are all doing so at different rates. Thus, while primitive characters are undergoing stasis or very slow rates of evolution (bradytely), derived characters are evolving at faster but disparate rates (horotely, tachytely) (Simpson 1944). Hence all the taxonomic characters of an organism are evolving at independent rates, each with a different taxonomic value within the lineage concerned. This value cannot be presumed or pre-guessed and, most importantly, cannot be equalised from one lineage to the next. Consequently, by unifying phenotypic discontinuities, PAUP generates the same erroneous associations produced by the use of cladograms.

Molecular classifications

In 1990 Charles Sibley and Jon Ahlquist offered a phylogenetic classification of the birds of the world based on DNA-DNA hybridization studies that, purportedly, calculated the percentage similarity between different species. It resulted in a revolutionary re-arrangement of bird classification which, at lower taxonomic levels (family and below), produced some of the most incongruous and even outrageous taxonomic associations ever to have afflicted avian systematics. It led to critically

important non-quantifiable phenotypic attributes such as behaviour, vocalization and nest construction, that are of paramount importance in avian speciation, being ignored.

In complete disregard of genealogy, and countless extinct antecedents, Sibley & Munroe (1990) assigned 45 genera of birds to the family Passeridae, including such phenotypically divergent genera as *Passer*, *Macronyx*, *Motacilla*, *Bubalornis* and *Estrilda*. By using mitochondrial DNA, an inherited primitive character, they detected very distant affiliations not close taxonomic bonds, uniting avian genera whose last common ancestor was tens of millions of years ago. Moreover their systematic grouping implied, phylogenetically, that all these genera were the product of an evolutionary fan, sharing the same common ancestor, an obvious absurdity. Secondly they seem not to have appreciated that living genera are simply the survivors of long lineages of extinct antecedents, the number different for every genus. Non-recognition of phenotypic discontinuities resulted in the bizarre grouping of Hawaiian honeycreepers (Drepanidinae) with canaries (Fringillinae) (*cf.* Johnson *et al.* 1989). Using other genes it has since been shown that Drepanidinae are "disparate members of a larger radiation of tanagers and finches" (Burnes *et al.* 2003: 360). Likewise the taxonomic folly of grouping *Estrilda* with *Macronyx* is patent and, clearly, "major revisions to the widely accepted classification of Sibley & Ahlquist (1990) are necessary" (Beresford *et al.* 2005: 849).

Since 1990 the literature has been replete with papers offering new classifications and groupings relying on molecular analysis (Groth 1998, Klicka *et al.* 2000, Barker *et al.* 2002, Ericson & Johansson 2003, Cracraft *et al.* 2004, Ryan *et al.* 2004, Beresford *et al.* 2005, Irestedt *et al.* 2006, Nguembock *et al.* 2009, Zuccon *et al.* 2012, De Silva *et al.* 2017, 2019, Kuhl *et al.* 2020), with Miller (2007) regarding DNA barcoding as the "saviour" of taxonomy. All have fallen, however, into the same trap as Sibley and his co-workers and, to date, no molecular classification of passerines can be said to accurately replicate genealogy.

Molecular suggestions that motacillids are closer to *Passer* than *Ploceus* (Beresford *et al.* 2005, fig. 1), and the genomic placement of *Motacilla* between *Passer* and *Fringilla* (Kuhl *et al.* 2020) is, to anyone familiar with the genera involved, phenotypically and phylogenetically untenable. Comparison of *Motacilla* with the most primitive ploceoid *Bubalornis* reveals a major phenotypic discontinuity, as does its phenotypic comparison with any fringillid. A recent genomic study of motacillids (Alström *et al.* 2015) suggests an evolutionary radiation in parallel with ploceoids with any common ancestry dating back 20 million years or more. The nesting of *Erythrura* with *Vidua* (Beresford *et al.* 2005; Yuri & Mindell 2002), or *Vidua* with *Corvus* (Cracraft *et al.* 2004. fig. 27.5) are outrageous, as is placing *Symplectes* (= *Ploceus bicolor*) with its highly evolved nest before *Passer* (Beresford *et al.* 2005).

Zuccon *et al.* (2012), while recognizing the genus *Serinus* was polyphyletic, which is phenotypically obvious, proposed to restrict it to the species *alario* (Linné), *canicollis* (Swainson), *canaria* (Linnaeus), *pusillus* (Pallas), *serinus* (Linnaeus) and *syriacus* Bonaparte. Both *alario* and *canicollis* however form clades ("superspecies") with other species and thus are phyletically distinct, as well as being sufficiently different phenotypically to be assigned to different genera. Moreover to claim that the remaining African and Arabian species of *Serinus* formed a "clade", for which they resurrected the genus *Crithagra*, required admitting that, although "some African species have never been subject to a molecular analysis, they are included here on grounds of morphological similarity to the analyzed species and biogeography" (Zuccon *et al.* 2012: 594). Importantly, their conclusion exposes the point that the

further down the evolutionary tree cut-off lines are drawn, the more plesiomorphic characters come into play, the more grouping is by affiliation not close taxonomic bond, and the more disparate branches become "monophyletic." Their interpretation of *Crithagra* as a "clade" actually groups a highly divergent assemblage of phenotypically distinct canaries, including *Serinops*, *Poliospiza* and *Dendrospiza*, that do not all share the same common ancestor, and hence involves a number of distinct genera (clades). Certainly their proposal to synonymize the large island endemic *Neospiza* with *Crithagra* is unsupportable. The small degree of phenotypic divergence in the creation of serinine species, as exemplified by the differences between *Serinus serinus* and *S. canaria*, *Pronospiza canicolla* and *P. flavivertex*, *Alario alario* and *A. leucolaema*, among many other examples, indicates that a moderate phenotypic discontinuity separates the very large frugivorous *Neospiza* from any common ancestor with *Crithagra*, and it is at the very least generically distinct (*cf.* Melo *et al.* 2017), more so since its closest affinities seem to be with São Tomé *Phaeospiza*.

Recently De Silva *et al.* (2017: 21) offered phylogenetic relationships purported to represent "A first robust phylogeny based on mitochondrial and nuclear markers", and "a first extensive phylogeny for the family Ploceidae, based on a multilocus dataset of three mitochondrial loci and four nuclear markers. Analysis of these data offered strong support for monophyly of the family and revealed seven distinct clades within Ploceidae. A major feature of our results is broad polyphyly of *Ploceus*: Asian *Ploceus* species should retain the generic name, whereas African *Ploceus*, together with *Anaplectes*, should be placed in *Malimbus*. In light of deep divergence, we assign the Malagasy *Ploceus* species to their own genus, *Nelicurvius*."

Despite detecting seven distinct clades, they arbitrarily choose to recognise only three genera, *Ploceus*, *Malimbus* and *Nelicurvius*. To suggest that the evolutionary history of such a diverse group as the African ploceoids can be accurately replicated by recognition of only three genera is a gross simplification of the complex evolutionary history of the group. Phenotypically the taxonomic error of assigning *Textor cucullatus* to the genus *Malimbus* is patent. Juxtaposition of the nests of *Bubalornis* and *Euplectes* highlights the flaw of assigning them to a single genus. Comparison of the nuptial displays of *Diatropura* and *Hyphanturgus* further emphasizes an error in classification. Contrasting the call of *Plocepasser* and *Symplectes* underscores a serious taxonomic error, as does comparison of the diets of *Quelea* and *Hyphantornis*. Their "robust phylogeny" represents an error in the taxonomic interpretation of genomic information, an egregious genus concept, a selective recognition of "clades", and a serious failure to accurately replicate genealogy.

Subsequently De Silva *et al.* (2019) claimed, without supporting the assertion, that plumage traits and morphology of ploceids exhibited high plasticity and phenotype did not always reflect phylogeny. They recommended uniting African *Ploceus*, *Malimbus*, *Anaplectes* and *Notiospiza* in the genus *Malimbus*, retaining the monotypic genus *Pachyphantes*, and placing *Brachycope* with *Euplectes*. As their phylogram of relationships showed however, their interpretation of *Malimbus* represented an arbitrary lumping of numerous phenotypically and phylogenetically distinct clades and, like the earlier study of De Silva *et al.* (2017), their concept of a genus is so all-embracing that their taxonomic conclusions are a calamitous reflection of genealogy. The error of assigning such a phenotypically distinct genus as *Notiospiza* to *Malimbus* is obvious. Equally egregious is allotting *Textor cucullatus*, *Hyphanturgus ocularis*, *Bensonhyphantes oliveiceps* and *Sitagra luteola* to *Malimbus*, with *Microploceus velatus* appearing in two well separated clades.

Molecular classification is not a taxonomic panacea and to date has proven just the opposite, a serious impediment to the achievement of a natural classification. For many, phylogenetics has become a process of dismissing the living organism, discarding all the valuable biological information gathered over many centuries, plugging sequences into a computer program, and ignoring the " empirical data that have demonstrated that DNA barcoding is much less effective for identification in taxa where taxonomic scrutiny has not been thorough' and that the 'promise of barcoding will be realized only if based on solid taxonomic foundations (Meyer & Paulay 2005: 2229". And yet "there is no credible reason to give DNA characters greater stature than any other character type" (Lipscomb *et al.* 2003: 65), especially since "barcoding genes are typically very few and often consist of organellar (e.g., mitochondrial) markers, which can be misleading when hybridization and/or ancestral polymorphism result in cytonuclear discordance (Bonnet *et al.,* 2017; Toews & Brelsford, 2012) - and more generally restrict the testing of taxonomic hypotheses to a tiny portion of the genome (Chan, Hartwig *et al.,* 2022; Rubinoff *et al*., 2006)" (Vences *et al.* 2024: 3). In addition, since molecular classification relies on sequestering "an infinitesimally tiny fraction of an organism's genome ... both to classify and identify the organism in question [and thus] produces what is at best a caricature of real taxonomy ... The supposed advantages of DNA taxonomy do not stand up to rigorous scrutiny" (Lipscomb *et al.* 2003: 65). In fact "the arguments against 'traditional' taxonomy in favour of molecular identification methods are illusory even for proponents of barcoding. Phylogenies produced by 'point-and-click' biologists who lack a theoretical background in phylogenetic inference and a solid empirical knowledge of the organisms under study will simply not withstand scrutiny (Grant *et al.,* 2003). Moreover, by so casually dismissing 'traditional' taxonomy as a means of independently testing molecular hypotheses, we constrain our ability to identify artefacts and errors in sampling, voucher identification, and sequencing" (Carvalho *et al.* 2007: 142).

Brothers (2021: 4-5) found that "The accuracy with which molecular approaches estimate the true evolutionary sequences is … questionable, especially since different types of molecular analyses often produce different results. Given the different emphases on modes of analysis … it is not surprising that the results of molecular analyses mostly differ from those based on phenotypic characters ... The limited availability of suitable specimens (and funding) for molecular studies has often meant that sampling has been inadequate to produce convincing results, so that consecutive phylogenetic estimates of the same groups may differ considerably".

The reality, therefore, is that "Despite tremendous efforts in the past decades, relationships among main avian lineages remain heavily debated without a clear resolution. Discrepancies have been attributed to diversity of species sampled, phylogenetic method, and the choice of genomic regions" (Stiller *et al.* 2024: 581).

Yet another problem with molecular classification is the assumption that new species are created by the acquisition of new genes when, in fact, very many are likely to be the product of already present neutral genes being activated to become advantageous by changed circumstances, and so "characters and structures, which we are apt to consider as of very trifling importance, may thus be acted on" (Darwin 1859: 77), for "Under nature, the slightest differences of structure or constitution may well turn the nicely-balanced scale in the struggle for life, and so be preserved" (Darwin 1859: 76). Since demes/varieties arise in the periphery of a species range, clustered like satellites "round their parent-species" (Darwin 1859: 53), it seems likely that the genes distinguishing many species first appeared in the satellite populations around the

periphery of the mother species, *before* allopatric isolation gave rise to new species. Certainly it is an error to believe that the type species of every genus came from the centre of a species distribution.

Crair (2021: 3, 6) reported on the studies of Poelstra *et al.* (2014) and how, after the last glacial 12 kyr ago, "Carrion and hooded crows sometimes interbred and produced fertile and healthy offspring in a narrow hybrid zone running through cities such as Dresden and Vienna. But the birds retained distinct identities on both sides of this feather curtain …. only 0.28 per cent of the crows' genomes could be used to sort the individuals into carrion and hooded populations. In fact, German carrion crows shared more of their DNA with German hooded crows than they did with other carrion crows from Spain. There were only eighty-two base pairs that never matched - less than one ten-millionth of a per cent of the total genome, a fraction so tiny that it should be statistically irrelevant".

Then there is the issue of recapitulation, "When a character which has been lost in a breed, reappears after a great number of generations, the most probable hypothesis is … that in each successive generation the character in question has been lying latent, and at last, under unknown favourable conditions, is developed" (Darwin 1859: 169). Pigeons have radiated into over 322 living species and, by contrasting the morphological differentiation displayed by domesticated pigeons with that displayed by extant genera of wild pigeons, Baptista *et al.* (2009: 721) found that "morphological and behavioral similarities between extant columbiform species and domestic pigeon breeds result from the action of genes found in the (ancestral) protocolumbiform that are normally suppressed and are recalled from time to time by natural or artificial selection".

Finally there is the problem of hybridisation that Abbot *et al.* (2013: 229) have implicated in speciation; "If hybridization is defined as reproduction between members of genetically distinct populations (Barton & Hewitt, 1985), producing offspring of mixed ancestry, then it occurs in almost all proposed processes of speciation … the consequences of hybridization and the role it might play in promoting or retarding speciation can be expected to vary widely both between different hybridizing taxa and at different stages of divergence … Hybridization may contribute to speciation through the formation of new hybrid taxa, whereas introgression of a few loci may promote adaptive divergence and so facilitate speciation." Stiller *et al.* (2024: 857), after analysing the genomes of 363 bird species (218 taxonomic families) found that "several recalcitrant relationships remain, even with this wealth of data, due to challenges imposed by biological processes such as hybridization that are hard to model in deep time using phylogenetics."

Genetic analyses showed that Steller's Eider (*Polysticta stelleri*) "contains genetic ancestry from Long-tailed Ducks and several eider species. Specifically, 94-98% of genetic variation in the Steller's Eider came from three other eider species, while the remaining 2-6% was assigned to Long-tailed Ducks.

These patterns raise the possibility that the Steller's Eider is a hybrid species" (https://avianhybrids.wordpress.com/2022/03/12/recent-and-ancient-hybridization-among-sea-duck-species).

Although phenotype is an explicit expression of genotype, and paramount in tracking evolution, particularly when attention is paid to "trifling characters", ontogeny should not be neglected, for natural selection "can modify the egg, seed or young, as easily as the adult" (Darwin 1859: 115). In many species of birds the juvenile plumage is very different to that of adults. This is well shown by the Bateleur (*Terathopius ecaudatus*), a gloriously short-tailed black eagle with rubicund face and legs, and no obvious

living relative. The immature Bateleur is a very different bird, uniformly brown with grey reticulate tarsi, closely resembling an adult Brown Snake Eagle (*Circaeetus cinereus*). This affiliation indicates that the Bateleur is a highly derived snake eagle with an origin close to the Brown Snake Eagle.

With an understanding of the evolutionary process, and the true purpose of taxonomy, natural classifications can best be achieved by tracking genealogy from the bottom upwards, deme by deme, subspecies by subspecies, species by species and so on, but only after having verified the species present by using Darwinian/Hennigian principles. Such considerations should be guided by the intuition resulting from experience with a group as a living biological entity, a familiarity that allows more appropriate character weighting, better estimation of the magnitude of phenotypic discontinuities, and recognition of some of the convergences that are an inherent feature of the evolutionary history of all groups. Refreshingly exemplary studies of this type are those of Poelstra *et al.* (2014) and Vázquez-López *et al.* (2020) who have combined molecular information with phenotype, vocalisation and other attributes to first determine species identity. Further long-term hope may be provided by "The understanding that species are independently evolving segments of population-level lineages, the rise of integrative approaches to delimit such lineages, and the advent of high-throughput sequencing have considerably renewed the discipline of taxonomy. Using genome-scale molecular datasets, the extent of admixture across hybrid zones can now be effectively assessed and the evolutionary independence of lineages inferred, leading to more reliable and comparable species delimitation criteria" (Vences *et al.* 2024: 1).

Taxonomic categories
According to the ICZN (2000) the only taxonomic units formally recognised below the genus level are subgenus, species and subspecies. But, in an attempt to reflect finer stages in the speciation process, ornithologists have introduced a number of categories, mostly unique to ornithology, that have entered into the literature and gained widespread usage (Rensch 1929; Mayr 1931; Amadon 1966; Amadon & Short 1976, 1992; Siegfried 1998; Mallet 2007).

Once a bird population is identified as different, the first issue to resolve is the nomenclatural significance (rank) of this disparity; what to name and how to name it (Pleijel & Rouse 2003). A perusal of the literature shows a lack of consensus and, more importantly, very inconsistent application.

Demes
Moving from one region to another the astute observer will notice more or less obvious differences between bird populations that are a result of the evolutionary process. These are demes - discrete naturally occurring populations, the members of which inhabit a particular area, recognise one another, and which prefer to breed among themselves. To a large degree demes conform to the "permanent varieties" of Darwin (1859), and as "small clades tend to be marginal geographically and/or ecologically" (Ricklefs 2005: 121). Although Darwin's famous book was entitled "On the origin of species", in fact it was mostly about "the preservation of favoured races", i.e. demes/subspecies, since these "are in several respects the most important" (Darwin 1859: 62), and "there is no fundamental distinction between species and varieties" (Darwin 1859: 240) so that, "according to my view, varieties are species in the process of formation, or are, as I have called them, incipient species" (Darwin 1859: 122).

Demes are genetically distinct local populations that record the first step in evolutionary divergence (Darwin 1859: 68). Their differences are slight; they occur in close geographical proximity and, where they come in contact, hybridise freely (Wright 1955). However Darwin (1859: 142) suggested that "the small differences distinguishing varieties of the same species, steadily tend to increase, till they equal the greater differences between species of the same genus, or even of distinct genera". Although they constitute *the only objective biological taxon*, incongruously demes are not recognised by formal zoological nomenclature, and the term has been discounted by most avian systematists. However, since a species is a population of individuals, the recognition of demes is requisite for proper population analysis and species discrimination.

Subspecies

Subspecies (= races) are the smallest formally recognised taxonomic unit and, since however, they represent subdivisions of a species, cannot stand alone and must be linked to the nominate species. As they are of lower taxonomic rank to species, traditionally the differences are deemed to be more trivial. It is as true today as when first penned that "no certain criterion can possibly be given by which variable forms, local forms, subspecies, and representative species can be recognised ... Certainly no clear line of demarcation has as yet been drawn between species and subspecies ... or, again, between subspecies and well-marked varieties, or between lesser varieties and individual differences. These differences blend into each other by an insensible series" (Darwin 1859: 64-68). Consequently Darwin was forced to bemoan how entirely vague was the difference between varieties and species, and he found it necessary "to leave it to the judgment of the individual systematist, whether or not he considers two particular forms ... species or subspecies". In fact "no certain criteria can possibly be given by which variable forms, local forms, sub-species, and representative species can be recognised" (Darwin 1859: 64). He concluded however that subspecies are "forms which in the opinion of some naturalists come very near to, but do not quite arrive at, the rank of species" (Darwin 1859: 64). Thus, traditionally, it has been left to the subjectivity of the taxonomist concerned to decide which demes will be accorded varietal, subspecific or specific status.

Almost 100 years later this same ambiguity was echoed by Mayr (1963: 106) who observed that "Every subspecies that was ever carefully analyzed was found to be composed of a number of genetically distinct populations [= demes]. It is in many cases, entirely dependent upon the judgment of the individual taxonomist how many of these populations [demes] are to be included in one subspecies. The limits of most subspecies are therefore subjective".

Mayr (1963: 106) defined a subspecies as "a geographically localized subdivision of the species, which differs genetically and taxonomically from other subdivisions of the species", a definition repeated by O'Brien & Mayr (1991). He did not offer advice as how to recognise subspecies however and very many demes, especially those with disjunct distributions, tend to be accorded subspecific or even specific rank. At the other end of the scale their status vacillates subjectively. During phases of taxonomic "splitting", many subspecies are upgraded to species and during phases of "lumping" many species are downgraded to subspecies. In this respect the subspecies has been invaluable in preserving the biological species concept, by downgrading species wherever hybridisation is encountered, without concern of ancestry. Hardly surprisingly Wilson & Brown (1953: 100) regarded the subspecies concept as "the most critical and disorderly area of modern systematic theory".

Besides ambiguity of definition and recognition, there are other problems surrounding the subspecies concept. ICZN (2000) rules demand that all subspecies be attached to the nominate species regardless of ancestry. As a result subspecies are added to the nominate species, sometimes to an extraordinary degree. Howard & Moore (1984) listed 37 subspecies of *Troglodytes troglodytes*, 38 of *Tyto alba*, 41 of *Coereba flaveola* and 67 of *Pachycephala pectoralis*. Phylogenetically such taxonomic groupings imply all the subspecies evolved independently from the same (nominate) ancestor, i.e. they form an enormous evolutionary fan, which even a cursory analysis shows to be untrue. Many subspecies are closer to other subspecies than to the nominate subspecies, and some subspecies are closer to the descendent species than to the nominate species, and hence are allocated to the wrong species. Unsurprisingly "Analyses of mtDNA data reveal historical divisions in many species, which have an inconsistent relationship with subspecies boundaries … [and that] … Mitochondrial DNA sequence data reveal that 97% of continentally distributed avian subspecies lack the population genetic structure indicative of a distinct evolutionary unit … Although sequence data show that species include 1.9 historically significant units on average, these units are not reflected by current subspecies nomenclature. Yet, it is these unnamed units and not named subspecies that should play a major role in … identifying biological diversity. Thus, a massive reorganization of classifications is required so that the lowest ranks, be they species or subspecies, reflect evolutionary diversity. Until such reorganization is accomplished, the subspecies rank will continue to hinder progress in taxonomy, evolutionary studies and especially conservation" (Zink 2004: 561).

Many avian subspecies are discriminated morphometrically, based on the relative lengths of wing, tail, culmen and tarsus (*cf.* McLachlan & Liversidge 1981). Geist (1991) argued that "The use of morphometry to detect genetic differences, how ever, is like using a rubber band to measure distance. While morphometry is a good tool to segregate populations (where factors of individual variation such as genetic relatedness, resource abundance, behavioural traditions, climatic effects, etc., vary in the same direction), it is an inadequate tool to segregate taxa. Comparative morphometry confounds genetic, epistatic, environmental and statistical variation, and thus confuses phenotype with genotype and homology with analogy".

Moreover it has also been a fallacy to believe that morphological differences between species and subspecies are an order of magnitude when, in fact, there is no difference, merely their position in the evolutionary scheme. Phylogenetically a subspecies is a group of demes that share the most recent common ancestor, and are separated by a minor phenotypic discontinuity from other related demes.

It is hardly surprising therefore that "the use or rejection of the subspecies category at present is to a considerable degree determined by the theoretical views of the individual taxonomist, making it contextually dependent and, provided the total dominance of PSC and similar concepts, destined for gradual extinction in the future. A harbinger of this is the complete absence of a subspecies section in some of the newest taxonomy guidelines (Wiley and Lieberman, 2011; Wheeler, 2012)" (Vinarski 2015: 406).

Since, by the Darwinian definition, a subspecies has undergone sufficient genomic change to be almost another species, one cannot keep adding subspecies to subspecies without quickly crossing the species threshold. In any one evolutionary direction a species can consist of only a very limited number of subspecies. The perseverance of this misconstruance has led to the "ring-species concept" (Mayr 1942; Irwin *et al.* 2001; Moritz *et al.* 1992; Liebers *et al.* 2004; Kuchta & Wake 2016) whereby

subspecies give rise to a succession of subspecies until eventually they reconnect and are specifically distinct.

Semispecies
Semispecies were introduced for "forms believed to be subspecies, but approaching, or possibly of, species status" (Amadon 1966). Astonishingly this definition precisely mirrors Darwin's (1859: 47-48) definition of a subspecies as "forms which in the opinion of some naturalists come very near to, but do not quite arrive at, the rank of species". Mayr (1963: 671) regarded semispecies as "borderline cases between species and subspecies". They are inferred to be closer to species than subspecies, and have been described also as "emergent interspecies" (Ripley 1945: 340) and "emerging species" (Summers-Smith 2010). All these definitions conform to the "incipient species" of Darwin (1859), and are thus equivalent to subspecies. It may be, however, that if constructed from the base (demes) upwards, they could be resurrected as a formal taxonomic unit since "Molecular taxonomy possesses the tools to more precisely define the meaning ascribed to particular terms and guarantee that none of the biodiversity aspects are missed by systematics" (Vinarski 2015: 412).

Megasubspecies
These were defined as "well-marked forms approaching the level of species, but nonetheless judged to be conspecific" (Amadon & Short 1976). Again this definition replicates Darwin's definition of a subspecies but, also, is very similar to what he termed "doubtful species", that is "forms which possess in some considerable degree the character of species, but which are so closely similar to other forms, or are so closely linked to them by intermediate gradations, that naturalists do not like to rank them as distinct species" (Darwin 1859: 43). Purportedly megasubspecies are closer to species than semispecies but this judgment is so subjective as to make them meaningful only to their instigator.

The biological species concept
Stresemann (1919: 64; translated and cited by Mayr 1942: 119) was the first to link the definition of a species to breeding efficacy; "Forms which have reached the species level have diverged physiologically to the extent that, as proven in nature, they can come together again without interbreeding." This led to "The view generally entertained by naturalists … that species, when intercrossed, have been especially endowed with the quality of sterility" (Darwin 1859: 220). As a result, championed by Ernst Mayr, the biological species concept rose to the fore in the last half of the 20th Century, according to which species are "groups of actually or potentially interbreeding natural population, which are reproductively isolated from other such groups" (Mayr 1963: 120). This definition emphasised a shared gene pool and reproductive (genetic) isolation. Unfortunately the cornerstone of this hypothesis, reproductive isolation, was demonstrably erroneous from the day of inception.
Darwin (1859) recorded how hybrids between the Capercaillie (*Tetrao urogallus*) and the Black Grouse (*T. tetrix*) were so common in the wilds that Scandinavian hunters had given them a special name. Today the Western Black Grouse and Capercaillie are not only regarded as specifically distinct but are assigned to different genera (*Tetrao* and *Lyrurus*), providing evidence of bigeneric hybridisation.
Ducks too are notorious hybridisers, even at the generic level and above (Johnsgard 1960; Mank *et al.* 2004; Lavretsky *et al.* 2021). Darwin (1859: 227-228) found that "hybrids from the common and Chinese geese (A. cygnoides), species which are so

different that they are generally ranked in different genera, have often bred in this country with either pure parents … [and] … whole flocks of these crossed geese, are kept in various parts of the country [India]". Perspicaciously Darwin (1859: 220) showed "that sterility is not a specially acquired or endowed quality, but is incidental on other acquired differences", and that "neither sterility nor fertility affords any clear distinction between species and varieties" (Darwin 1859: 223). Indeed Darwin (1859: 110) believed it to be "a general law of nature that no organic being fertilises itself for a perpetuity of generations; but that a cross with another individual is occasionally - perhaps at long intervals of time – indispensable".

Johnsgard (1960) commented on the abundance of swan x goose hybrids and listed many other examples of intergeneric fertile hybrids. These led him to the erroneous taxonomic conclusion that their abundance "vindicates the submerging of the previously upheld subfamilies Cygninae and Anserinae, and the numerous goose hybrids also provides justification for discarding several monotypic genera" (Johnsgard 1960: 28) The reality however is that "Waterfowl hybridize like there is no tomorrow. Between 30% and 40% of ducks, geese and swans are known to interbreed. For some species combinations, hybrids are regularly observed because they are easy to recognize and occur close to humans. A nice example concerns Greylag Goose (*Anser anser*) x Canada Goose (*Branta canadensis*) hybrids in the Netherlands"   (https://avianhybrids.wordpress.com/2022/03/12/recent-and-ancient-hybridization-among-sea-duck-species). Moreover observational data "suggest that Mallard Ducks are able to hybridise with numerous native South African *Anas* species, notably Cape Shovelers (*A. smithii*), Cape Teal (*A. capensis*), African Black Ducks (*A. sparsa*), and especially, Yellow-billed Ducks (*A. undulata*)" (Stephens *et al*. 2019: 2), although it should be noted that phylogenetically there is more than one genus among the "South African *Anas* species".

Since Darwin's time countless studies have shown, both in captivity and in the wilds, that "good species" can and do interbreed and that hybridisation is widespread and common (Mayr 1963; Grant & Grant 1992; Grant 1993; Grant *et al*. 2004, McCarthy 2006; Stephens *et al*. 2019). In the Palearctic there are well established "hybrid zones" between the Yellowhammer (*Emberiza citrinella*) and Pine Bunting (*E. leucocephalos*), the Black-headed (*Emberiza melanocephala*) and Red-headed Bunting (*E. bruniceps*) and the Collared (*Pipilo ocai*) and Rufous-sided (*P. erythrophthalmus*) Towhees (Byers *et al*. 1995). In Southern Africa the Red-headed Finch (*Amadina erythrocephala*) is a "good species" that hybridises both in the wilds and in captivity with the Cut-throat Finch (*A. fasciata*) and produces fertile offspring. Natural hybridisation is also recorded between *Passer domesticus* and *P. hispaniolensis* (Belkacem *et al*. 2016).

Many naturally occurring bigeneric hybrids have been recorded among African passerids (*cf.* Colahan & Craig 1981) but obviously, without exception, have been obfuscated by taxonomic lumping. These include *Passer* x *Caffropasser, Quelea* x *Queleopsis, Xanthoplectes* x *Microploceus, Melanopteryx* x *Textor, Tachyplectes* x *Euplectes, Euplectes* x *Taha, Urobrachya* x *Xanthomelana, Urobrachya* x *Coliostruthus, Steganura* x *Hypochera, Vidua* x *Hypochera, Amauresthes* x *Pseudospermestes* and *Pytilia* x *Marquetia.*

Mayr's (1963: 120) definition of species as reproductively isolated "natural populations" was designed to precluded evidence of cross-breeding in captivity, since these are contrived populations. As so little information is available about hybridisation under "natural conditions" (in the wilds) for the vast majority of species, and will never be known for extinct species, the biological species concept was an

untestable hypothesis, that left species recognition to "the opinion of naturalists having sound judgment and wide experience" (Darwin 1859: 62). It led to the biological species concept being used for taxonomic manipulation, by conveniently downgrading species where hybridisation was encountered, even though "No one has been able to point out what kind or what amount of difference, in any recognisable character, is sufficient to prevent two species crossing" (Darwin 1859: 307).

Mayr (1963: 112) suggested that "the mere possibility of hybridisation in captivity proves nothing as far as species status is concerned". What it did prove was a fundamental flaw in the biological species concept. Wherever mate selection is inhibited, either in the wilds or in captivity, hybridisation is almost habitual. The vast extent of hybridisation among birds has been catalogued by McCarthy (2006). This indicates that speciation is effected on other grounds, mainly changes in behaviour, habitat and/or vocalisation, long before breeding exclusivity is achieved. Although pheromones have not yet been implicated in avian speciation (Caro & Balthazart 2010), the uropygial gland may play a role (Salibián & Moltalti 2009).

Arnaiz-Villena *et al.* (1999: 9) found that in captivity "male hybrids obtained by crossing *S. canaria* with *S. sulphuratus*, *S. atrogularis*, and *S. mozambicus* are sterile (Baseggio 1995, pp. 116-198). However, male hybrid sterility may not be a sign of unrelatedness since F1 males from *S. canaria* and some South American siskins (i.e., *C. cucullata* and *C. xanthogaster*) are fertile (Baseggio 1995, pp. 116-198). This suggests that geographically closer species may develop hybridization barriers in the speciation process at meiotic, gamete, maturation, or other levels".

Among passerids bigeneric hybridisation occurs up to and including members of the same subtribe and taxonomically interbreeding is not indicative of conspecificity, for it can "be clearly shown that mere external dissimilarity between two species does not determine their greater or lesser degree of sterility when crossed" (Darwin 1859: 241). Since "good species" can and do interbreed, and phenotypically there is no difference between a subspecies and a species, genealogically a species comprises all the subspecies down to the last significant evolutionary dichotomy (Wiley 1981).

Species
Lamarck (1802) was the first to attempt the definition of a species, into which perspicaciously he introduced time and habitat as key factors. He defined a species (translated from the French by Mayr 1963) as comprising "individuals all resembling each other, and reproducing their like by generation, so long as the surrounding conditions do not undergo changes sufficient to cause their habits, characters, and forms to vary". By contrast Darwin (1859: 69) considered "the term species as one arbitrarily given, for the sake of convenience, to a set of individuals closely resembling each other".

Since then the avian species concept has filled countless tomes (Simpson 1951; Cracraft 1983; Paterson 1985; Iwatsuki *et al.* 1986; Bock 1992; Haffer 1992; Zink 1996, 1997; Zink & McKitrick 1995; Mayr 1996; Aldhebiani 2018) but a definition that suits all has proven elusive; "Scientists have named more than a million different species, but they still argue over how any given species evolves into another and do not even agree on what, exactly, a "species" is … It is really laughable to see what different ideas are prominent in various naturalists' minds" (Crair 2021: 2). Thus, just as when first penned, "No one definition has as yet satisfied all naturalists; yet every naturalist knows vaguely what he means when he speaks of a species" (Darwin 1859: 58), and it still remains that "no definite distinction is made between geographical

races [= subspecies], ecophenotypes, sibling species, and host races" (Mayr 1963: 209).

Summers-Smith (2010) outlined the problem of *Passer domesticus*, the subspecies of which fall into two distinct groups (clades), for which a number of authors favoured specific separation. However Summers-Smith (2010) refuted the latter proposal with the dismissive judgment that "I do not consider the differences justify specific separation". Such capricious synonymy, based on a preconceived species concept, is phylogenetically indefensible.

While scientists debate the species concept one thing is clear - species recognise their own kind. Thus the problem of species identification lies not with the organisms, but with the humans studying them, leading to "the cynical definition of a species as a group of individuals sufficiently distinct from other groups to be considered by taxonomist to worth specific rank" (Aldhebiani 2018: 440).

It is crucial to survival that all individuals know the species to which they belong, and where their limits lie. Consequently self recognition, of which mate recognition (Paterson 1985) is but a part, is an essential component of the genetic code of all organisms. Every species has a set of characters that serve as a unique fingerprint to identity, that immediately distinguish it from its closest relatives. They aid recognition and social cohesion and, importantly, serve to expose aliens. Thus in the animal world differences in one or more of appearance (morphology), behaviour, habitat, vocalisation (call) or odour (scent) are sufficient to distinguish (create) different species; disparity in all guarantees it. Some reproductively isolated species however remain morphologically indistinguishable. In these sibling species recognition relies on differences in behaviour, habitat, scent or call.

As defined here a species, largely in accord with Lamarck, is a naturally occurring population with a unique recognition system, specific habitat requirements, and a preference to breed among itself. Generally species look different from their closest relatives but, if not, they behave, call or smell differently.

What is important to emphasise is the small phenotypic difference involved in speciation. This is exemplified by countless "superspecies" and "species complexes" among African passerids, epitomised by grey-headed sparrows (*Xanthodira* spp.), African sparrows (*Megapasser* spp.), masked weavers (*Microploceus* spp.), paradise whydahs (*Steganura* spp.), indigobirds (*Hypochera* spp.), forest canaries (*Dendrospiza* spp.), pytilias (*Pytilia* spp.), cordon-bleus (*Uraeginthus* spp.) and mannikins (*Pseudospermestes* spp.).

Superspecies

The superspecies concept is so widely used in ornithology that Fry *et al.* (2004) considered it "invaluable in treating continental avifaunas". It was introduced for "A group of entirely or essentially allopatric taxa that were once races of a single species but which now have achieved specific status" (Amadon 1966: 245). Hence, as conceptualised, superspecies record the most recent speciation event within a lineage and typically come in pairs (allospecies). The term allospecies was introduced "to denote a boundary situation when the species or subspecies dilemma cannot be unambiguously resolved (Amadon, 1966). This is a terminal "prespecies" stage in allopatric speciation, when there is no way to determine objectively whether speciation has been completed" (Vinarski 2015: 407). The assumption is that, in the case of a subsequent contact, allospecies remain reproductively viable and free to hybridize.

Taxonomically however superspecies have been used mainly as a method of maintaining the number of admitted genera to a minimum (*cf.* Hall & Moreau 1970). Actually all this does is create a cumbersome terminology - it is far easier to talk and write about *Poliospiza* than "seedeaters of the *tristriata* superspecies". Moreover the superspecies concept has been broadened unacceptably (*cf.* Fry *et al.* 2004) to incorporate members of more distant speciation events so that many "superspecies" include substantially more than two allospecies. In all too many cases this informal taxon has become no more than a subjective hotchpotch of species, allospecies and isospecies. Although Vinarski (2015) considered the superspecies of value, taxonomically it is, at the very least, synonymous with genus.

Subgenera

A subgenus comprises a group of related species and cannot stand alone; it has to be part of a genus. Its usage however is wholly subjective and arbitrary, and the requirement to attach it to the nominate genus, irrespective of ancestry, makes it a dubious taxon since many subgenera are closer to one other than they are to the nominate subgenus. In the writer's opinion, once inferred relationships are depicted on a cladogram/dendrogram/phenogram, most subgenera become unnecessary, more so since they merely create a clumsy and tedious nomenclature of trinomens and quadrinomens, e.g. *Bufo (Bufo) bufo bufo* (Linnaeus).

Genus

Traditionally species are grouped on the basis of similarity into genera, "but naturalists differ widely in determining what characters are of generic value; all such valuation being at present empirical" (Darwin 1859: 15) and, as a result, had to concede "that genera are merely artificial combinations made for convenience" (p.437). A lack of definition continues to plague taxonomy to this day and, as a result, because "generic limits are not defined by any rules .... for practical reasons, the lumping of several distinct species-groups into a single genus is currently in vogue" (Fry *et al.* 2004: 456). Such subjectivity is the fickle grounds on which Linnaean genera are constructed and dismissed, what Cooper (2015: 159) termed "the tyranny of taxonomy." It is the failure to satisfactorily recognise and define a genus that has been the downfall of molecular classifications, more so since only 63% of animal genera based on morphology have been verified genetically (Jablonski & Finarelli 2009).

It is important to appreciate that every extant genus represents merely the end member of an evolutionary lineage that goes back millions of years and includes far more extinct species than living. Hence, by definition, every genus is separated from its nearest living relatives (congeners) by a phenotypic discontinuity that is generally minor but may be more.

As a case study many workers have chosen not to recognize the waxbill genus *Granatina*, preferring to admit only five species of *Uraeginthus* (Olsson & Alström 2020). Within this group however the three cordon-bleus (*Uraeginthus* spp.) form a compact monophyletic clade, as do the two extant grenadiers (*Granatina* spp.). The slight differences between the species of *Uraeginthus* emphasize the very small phenotypic change involved in speciation, as found also by Westwood "in regard to insects, that in large genera the amount of difference between the species is often exceedingly small" (Darwin 1859: 73). Hence the phenotypic discontinuity separating the two clades points to the substantial number of extinct species required to connect

Granatina to *Uraeginthus*. It is this prominent twig of the evolutionary tree (Fig. 1) that validates the two genera.

Fig. 1. Evolutionary relationships within the *Uraeginthus/Granatina* lineages. Note the significant phenotypic discontinuity between *Uraeginthus* and *Granatina*, and the small phenotypic differences between species of *Uraeginthus*.

Phylogenetically a genus can comprise only a limited number of living species, especially when it is appreciated that most of its congeners are extinct. Sibley & Munroe (1990) recognized 17 species of *Euplectes*, 19 species of *Estrilda*, 23 species of *Passer*, 37 species of *Lonchura*, 47 species of *Serinus* and 62 species of *Ploceus*. Phylogenetically implicit to such taxonomic lumping is that every species of every genus evolved from the same ancestral species which, obviously, is false. Their "genera" are artificial and unnatural constructs, and phylogenetically there are far more genera of passerines than admitted by current avian taxonomy.

As a practicing palaeontologist the writer has searched the fossil record for nearly 50 years for the maximum number of species deemed to have evolved from a single ancestral species so as to constitute an evolutionary fan - the most is 6. This suggests, pragmatically, that "evolutionary fans" comprising more than ten species have been constructed by ignoring taxonomically meaningful evolutionary dichotomies in favour of "categories of convenience".

Lone divergent species conveniently lumped as congeneric led to the unnecessary concept of isospecies (Amadon & Short 1992), i.e. species that do not form part of a superspecies but represent the sole survivor of a discrete evolutionary lineage. Isospecies are monotypic genera, their "isolation" due to a long line of extinct antecedents. Without doubt there are far more monotypic genera than currently admitted by prevailing (Linnaean) taxonomy, and the current systematics of African (and World) birds is far from natural. In fact Olson (1981: 193) suggested that "the present classification of birds amounts to little more than superstition and bears about as much relationship to a true phylogeny of the Class Aves as Greek mythology does to the theory of relativity." Little has changed over the last 40 years except now ornithologists allow computers to make their errors.

Subtribes
Subtribes have not been used in African ornithology (*cf.* Fry *et al.* 2004). As the smallest formally recognised suprageneric taxonomic unit, phylogenetically they are a group of genera that define a discrete twig on the evolutionary tree and share the most recent common ancestor. Hence a subtribe comprises all the genera down to the last significant evolutionary dichotomy, the majority of which will be extinct. The number of extinct genera is to be inferred by the magnitude of the phenotypic discontinuity separating it from its closest relatives. The frequent occurrence of bigeneric hybrids indicates that breeding viability persists at least to this level, as it does in botany.

Tribes
Phylogenetically a tribe is a group of genera that define a discrete branchlet on the evolutionary tree and share the most recent common ancestor. Hybridisation among passerids is not reported at this level or above, and reproductive isolation seems to be established at this level.

CONCLUSION

Passerins (infraorder Passerini) are a predominantly African radiation of birds whose origin dates back to the Early Tertiary. While the most primitive representatives are likely to have been insectivores and frugivores, their proliferation and diversification accompanied the Miocene rise and spread of savanna grassland and adaptation to granivory. However this remarkable radiation has not been reflected in the systematics of the group due to a widespread failure to recognise the true purpose of taxonomy, viz. the accurate replication of genealogy. Since evolution is a complex process a natural classification must be complex also, and simple classifications are utilitarian. Far more taxa are required than currently admitted to accurately portray the genealogy of passerines. Although most of these names are available in the literature, they have been obfuscated by subjective synonymy in favour of "categories of convenience". Phylogenetic (= Darwinian) taxonomy requires identification of primitive and derived characters since weighting of these two character-sets greatly influences taxonomic placement. It demands recognition of the phenotypic discontinuities created by extinct/unknown taxa that are paramount in assigning taxonomic rank. Since the internodal gaps of cladograms represent phenotypic discontinuity of variable magnitude, that is different for every branch of every cladogram, their equalization results in cladograms placing taxa far closer phylogenetically than they are biologically. Hence their use as an accurate replication of phylogeny is a grave error that leads to incongruous taxonomic associations; PAUP analysis has the same failing. Linnaean and Darwinian taxonomy are not different

methodologies but simply draw the cut-off line at different levels in the evolutionary tree; Linnaean taxonomy trims the leaves and outer twigs to expose plesiomorphic branchlets that are indicative of affiliation, whereas Darwinian taxonomy insists on their retention as a record of the most recent genealogy. Since evolution is a continuum, it is suggested that quantum evolution and punctuated equilibrium are not different evolutionary processes, but have been created factitiously by phenotypic discontinuities, taxonomic lumping and alternating episodes of cladogenesis and anagenesis. Molecular classification has introduced some of the most incongruous taxonomic associations ever to have afflicted avian systematics and, to date, has failed to produce a classification that is even remotely natural. It is maintained that phenotypic analysis remains the only method capable of tracking close relationships and, with due deference to "trifling characters", accurately replicating the finest intricacies of the evolutionary process necessary to achieve a natural classification.

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