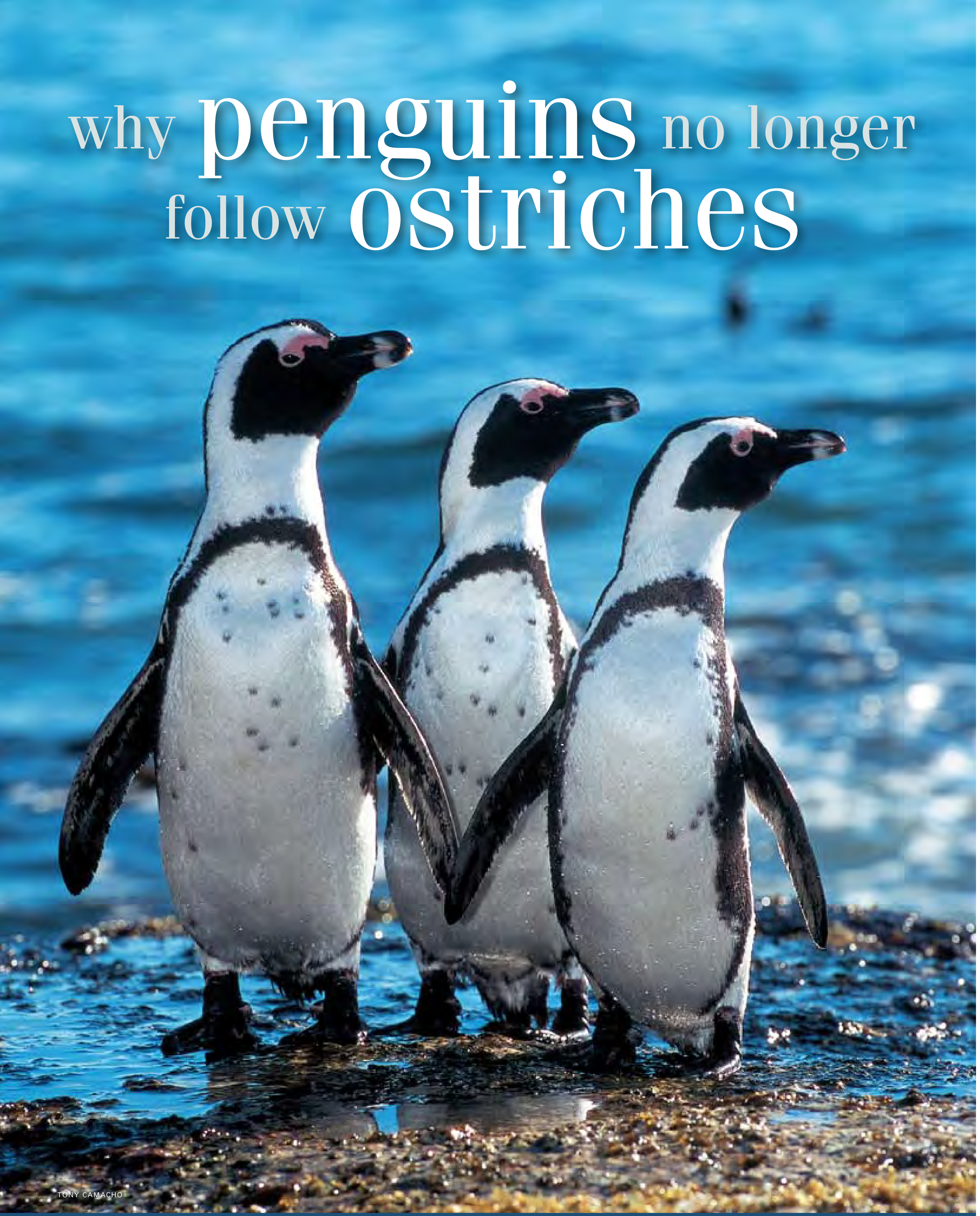
why penguins no longer follow ostriches



TONY CAMACHO

The unique structural adaptations for life as a flightless, wing-propelled diver resulted in penguins being placed at the start of the sequence of modern birds, but they don't reflect the penguins' true relationships.

THE NEW WORLD ORDER

THE PAST FEW DECADES have seen a revolution in bird systematics – the study of bird relationships. Molecular techniques assessing genetic differences between species have forced some radical changes in the way we think birds evolved – and hence the way we classify them. This process is ongoing, but sufficient consensus has emerged for several field guides and bird books to take the plunge and adopt the new order. **Peter Ryan** explains some of the major changes.

Biologists attempt to classify birds and other organisms in a hierarchy that reflects their evolutionary relationships. This is termed natural classification, and implies that species in the same genus are more closely related to each other than those in other genera, and that families in the same order are more closely related to each other than to other families, etc. There are other ways to group birds – by colour, size or even alphabetically – but these are artificial classifications which, albeit useful for some purposes, are imposed rather than inherent. The advantage of using a natural classification system is that it tells us about the fundamental relationships among birds. The main disadvantage is that as our knowledge improves, so the classification is likely to change. Such changes have even taken place at the highest levels of classification. Whereas there used to be two kingdoms of organisms, animals and plants, we now recognise six kingdoms, divided into two domains.

Orders and families take their names from one of their typical genera, but are distinguished by specific suffixes: -iformes for orders and -idae for families. Other levels in the hierarchy may be recognised, such as Superfamily (-oidea), Subfamily (-inae) and Tribe (-ini, between subfamily and genus). Sometimes the level at which a group is pegged is debatable. For example, the avocets and stilts are often treated as a subfamily Recurvirostrinae of a more inclusive Charadriidae, the plovers and lapwings.

Evolutionary relationships can be inferred from the pattern of shared derived characters – features common to a group that are not shared with more distantly-related species. The trick is to identify which sets of characters convey a meaningful evolutionary signal. Many birds share the same characteristics simply because they live in the same environment or feed on the same type of food. This is termed convergent evolution. Relationships are also confounded by reversals in character states, whereby some of a related group of organisms have reverted to the ancestral condition.

Initial attempts to infer the relationships among birds were based largely on their shape and structure, but it soon became apparent that characters subject to selection for immediate survival, such as bill, wing and leg shape, carry little deep evolutionary signal. Focus then switched to more conserved characters, such as bones, muscles and other internal structures. These formed the basis for the classification of birds into orders and families, whereas external appearance and structure were used to group similar species into genera.

Bird taxonomy was hotly debated during the late 19th and early 20th centuries, but a fairly stable order was established by the 1950s, reflecting at best a consensus based on the available evidence, or at worst a compromise between opposing factions. This resulted in the familiar sequence in which birds were listed in bird books.

The past few decades have seen a revolution in taxonomy thanks to the development of techniques that detect and analyse differences among organisms in the most fundamental building blocks of life – their genes. Because most genes mutate at random, they provide powerful tools for inferring evolutionary relationships. Different genes evolve at different rates, providing biologists with a toolkit they can use to assess the relationships among all levels of life. For the most part, the new genetic evidence has supported the relationships among birds, at least at the level of orders, but there have been some major changes in the relationships among and within orders.

CLASSIFYING BIRDS

Every species is placed in a hierarchical structure that should reflect its evolutionary history. For example, the Black-winged Stilt is classified as follows:

Domain: Eukarya (as distinct from Prokarya, the bacteria and archaebacteria)

Kingdom: Animalia (as distinct from Plantae, Fungi and Protista)

Phylum: Chordata (as distinct from all the invertebrate phyla)

Class: Aves (all birds, although strictly birds are a subset of dinosaurian reptiles)

Order (-iformes): Charadriiformes (waders, gulls, terns, auks and sandgrouse)

Family (-idae): Recurvirostridae (avocets and stilts)

Genus: *Himantopus* (the stilts)

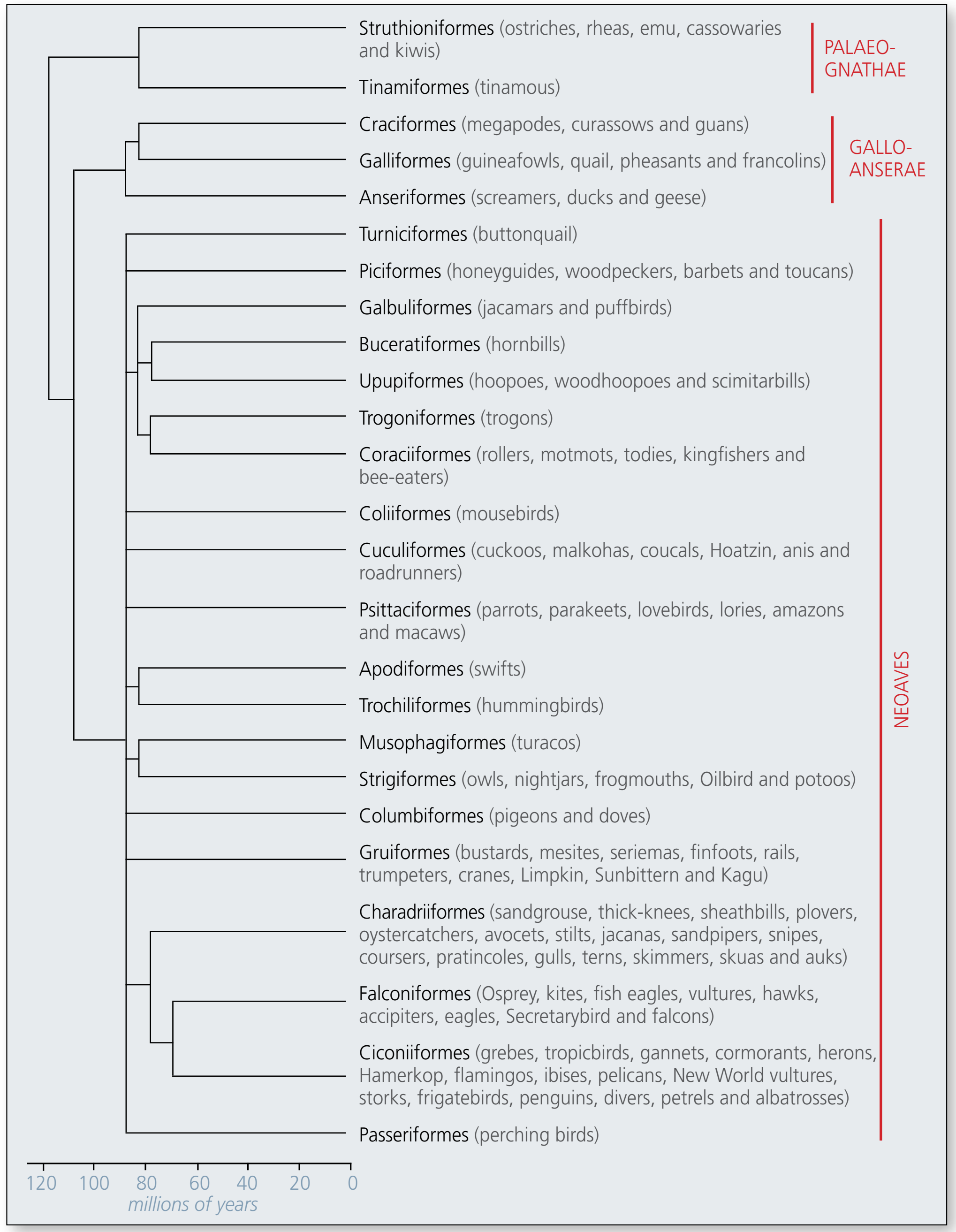
Species: *himantopus* (the Black-winged Stilt)

SIBLEY'S 'TAPESTRY'

Charles Sibley devoted much of his career to using molecular markers to infer evolutionary relationships. During the 1980s he used a relatively crude technique called DNA-DNA hybridisation to conduct pair-wise comparisons between the DNA of birds from virtually all major groups. Together with Jon ▷

Ahlquist, he amassed enough information to propose an entirely new view on avian relationships.

Sibley confirmed that the most basic division among birds is between the Palaeognathae ('ancient jaws') and Neognathae ('new jaws'), which have fundamentally different palate structures. The former group, comprising the ratites (ostriches, emus, cassowaries and kiwis, as well as the extinct moas and Elephant Bird) and the South American tinamous, are represented in Africa only by the ostriches. The striking similarity of the large, flightless ratites in all the southern continents suggests that they evolved on the ancient southern super-continent Gondwanaland, which broke up during the Cretaceous, about 120–85 million years ago, to form Africa, Australia, South America, Antarctica, Madagascar and the Indian subcontinent.



Relationships among bird orders, showing the approximate time that lineages diverged. Many of the relationships among Neoaves orders remain unresolved.

Until recently, it was assumed that the break-up of Gondwanaland took place too long ago to have influenced the radiation of the more modern neognaths, despite intriguing similarities between some widely scattered birds. For example, the flightless Kagu of New Caledonia is surprisingly similar to the Sunbittern from Central and South America. The problem was that fossils, mainly from the northern hemisphere, suggest that modern birds only appeared approximately 65 million years ago, immediately after the Cretaceous–Tertiary extinction which saw the demise of the dinosaurs. However, differences in gene sequences suggest that the neognath orders diverged at least 80–90 million years ago, when the southern continents were still close together. The appearance of modern bird fossils in the northern hemisphere coincides with the collision between the Indian plate and Asia some 65 million years ago.

Within the neognaths, there are two major groupings: a basal radiation of gamebirds and waterfowl, the Galloanserae, with all remaining birds in the Neoaves ('new birds'). Among the Galloanserae, only the Craciformes (megapodes, guans and currassows) are not found in Africa. Both the Galliformes and Anseriformes are well represented here, including an endemic family, the guineafowls, Numididae. Previously, penguins were placed at the start of the neognaths, but their peculiar morphology is merely an extreme adaptation to their diving lifestyle. In fact, they are quite closely related to albatrosses and petrels, and more distantly to a suite of other waterbirds, including grebes, herons, storks and cormorants.

The sequence of orders within the Neoaves remains poorly resolved, possibly because their initial radiation was quite rapid. DNA-DNA hybridisation suggests that buttonquails are the basal group, followed by woodpeckers, barbets and a slew of other 'near-passerine' orders. Of the orders in Neoaves, only the Galbuliformes (jacamars and puffbirds) and Trochiliformes (hummingbirds) are not represented in Africa, with one order, the Musophagiformes (turacos), being confined to the continent. Despite their diverse morphology, most waterbirds, shorebirds and diurnal raptors are more closely related than previously thought, leading to the lumping of several orders of birds. Indeed, Sibley and Ahlquist advocate lumping them all into a single enlarged order, Ciconiiformes.

Some orders proved not to be natural groups. Among the former Pelecaniformes, characterised by four webbed toes, cormorants, darters, gannets and boobies are closely related, but pelicans, tropicbirds and frigatebirds are not. Similar errors were detected at other taxonomic levels. Families such as the cuckoos and barbets were split because they are not natural groups, and new light was shed on the long-debated positions of several enigmatic taxa. For example, the Shoebill *Balaeniceps rex* is a derived pelican, and the New World vultures and condors are related to storks, and are merely convergent with Old World vultures.

Perhaps the most exciting result was the development of a framework for the largest avian order, the Passeriformes. With more than 5 700 species, passerines make up some 60 per cent of the world's birds. Traditionally, differences in syrinx musculature and other structural differences have been used to divide them into two groups: the suboscines (pittas, broadbills, asities and a host of Neotropical groups including woodcreepers, antbirds, tapaculos, cotingas, manakins and tyrant-flycatchers) and the oscines. Among the oscines or songbirds there has been no convincing structure, with convergence clearly confounding relationships among groups such as warblers and flycatchers.

Sibley and Ahlquist found that a diverse array of enigmatic passerines from Australasia are not the last gasp of boreal radiations, but rather are basal forms of the original radiation of oscine passerines. They recognised two major groups, one of which, the Corvida, comprises Australo-Papuan endemics, plus several more widespread lineages. Families found in Africa include crows, shrikes, drongos, crested-flycatchers, orioles and cuckooshrikes, with bush-shrikes, batises and wattle-eyes endemic to the continent. All remaining species (some 35 per cent of all birds) were placed in the Passerida, with three superfamilies: the Muscicapoidea (thrushes, flycatchers, starlings and allies), the Sylvioidea (tits, larks, warblers, babblers, bulbuls, white-eyes and allies) and the Passeroidea (sunbirds, weavers, sparrows, pipits, canaries, buntings and allies).

PETER RYAN

Rheas, such as this Greater Rhea, bear a striking resemblance to ostriches, even though South America broke away from Africa some 110 million years ago.

A TREE OF LIFE FOR BIRDS

Subsequent work using conserved nuclear gene sequences has refined some of Sibley and Ahlquist's original conclusions, and a coherent picture of how the passerines evolved is slowly emerging. The New Zealand wrens (Acanthisittidae) are basal to all other passerines, again emphasising the importance of the southern hemisphere in avian evolution (at least as a refuge for relictual species). The fundamental split into suboscines and oscines is supported, but all the oscines appear to have arisen from the Australasian radiation, with the Passerida nested within the Corvida. And within this radiation, some enigmatic African species have assumed prominent positions. The rockjumpers of southern African and the picathartes of West and Central Africa are sister groups, basal to all other passeridan birds. This suggests that Africa played an important role in the early radiation of the Passerida.

There is still lots to learn about the Passerida. Sibley's view of three major groups has been challenged, with several families falling outside the neat tripartite structure. From an African perspective, several unexpected relationships have emerged. The elminias, a group of small, fan-tailed 'flycatchers', are merely convergent with the crested-flycatchers and paradise-flycatchers of the Corvoidea, and fall within the Passerida. Together with the Asian *Culicicapa* flycatchers and the Fairy Flycatcher, they form a separate radiation allied to the tits. Livingstone's Flycatcher and the other *Erythrocercus* flycatchers apparently form a separate flycatcher-like radiation within the Sylvioidea. The nicators, which have been bounced back and forth between the bulbuls and bush-shrikes, belong to neither group, apparently forming a basal lineage within the Sylvioidea. And one of the most bizarre results is that the sugarbirds, endemic to southern Africa, appear to be basal to the Passeroidea, together with Spot-throat and Dapple-throat, enigmatic forest understorey 'babblers' confined to the Eastern Arc mountains of East–Central Africa.

One of the least well understood groups has been the Old World warbler-babbler complex. The warblers were traditionally placed in a single family, Sylviidae. Sibley recognised the distinctiveness of the largely African Cisticolidae (prinias, cisticolas, apalises, camaropteras, tailorbirds, etc), but failed to appreciate the full extent of the problem within the remaining warblers. The predominantly Palearctic *Sylvia* ▷

PETER RYAN

The taxonomy of the Old World Warblers, such as this Lesser Swamp Warbler, remain in a state of flux. It is likely that they will be split into several new families.

warblers are more closely related to babblers, white-eyes and laughing-thrushes than to other warblers. Preliminary evidence suggests that the remaining warblers also are deeply divided and probably should be split into several new families, including another largely African group that would embrace the crombecs, eremomelas, longbills, Grassbird, Rockrunner and Victorin's Warbler. True *Bradypterus* warblers form part of a diverse array of African, Asian and Australasian warblers that groups with the Madagascan radiation of 'babblers' and 'bulbuls'.

Much work remains to be done, but the rate of progress is astounding. Molecular techniques have improved to the point where what once seemed impossible, such as sequencing the entire human genome, is merely tedious. Earlier this year the entire genome for the chicken was published with surprisingly little fanfare. Within systematics, there is a concerted push to discover the 'tree of life', the history of the evolution of all life on earth. This requires sequencing a suite of conserved genes from literally thousands of organisms, including hundreds of birds. Such initiatives will result in a stable family-level structure within the next few years, but new surprises will doubtless emerge as more and more genera are sequenced.

Some birders may consider these discoveries irrelevant, and grumble about changes to the old, familiar bird sequence. But you cannot understand an organism and how it fits into its environment without also knowing its evolutionary history, and the constraints imposed by that history. Knowing the relationships among the birds we watch can only enhance our birding experience.

Relationships within the Passeriformes, the largest order of birds.