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Osteological limb proportions in Australo-Papuan kingfishers (Alcedinidae)

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Abstract. A comparison of proportions of major skeletal elements of the fore- and hindlimbs shows considerable uniformity among the Sacred Kingfisher *Todiramphus sanctus* and other Australian species of *Todiramphus*, whereas species of paradise kingfishers *Tanysiptera* and yellow-billed kingfishers *Syma* have relatively longer distal leg elements. Kookaburra species *Dacelo* have proportionally shorter distal elements, a trend that is very marked in the Azure Kingfisher *Ceyx azureus* and other water kingfishers of genus *Ceyx*.

Introduction

Australia has ten breeding species of kingfishers (Alcedinidae), with a further three recorded as vagrants. Of the breeding species, eight are land or tree kingfishers in the subfamily Halcyoninae. The remaining two are water or river kingfishers (subfamily Alcedininae). A third subfamily, Cerylinae, also known as water kingfishers, is restricted to the New World.

The Halcyoninae contains around 70 species, distributed mainly through Africa, Asia, Australo-Papua and the Pacific. The nominate genus *Halcyon* was formerly considered to comprise about 45 species that occurred throughout this range. *Halcyon*, as then accepted, could be divided into several subgroups, including *Todiramphus* and *Syma*. Placement of all into a single genus was conventional practice for many years (e.g. Fry 1980; Forshaw 1983, 1985; Fry *et al.* 1992). Suggestions that these, and several other subgroups, were generically distinct from *Halcyon* were verified by Moyle (2006).

Todiramphus comprises around 30 species, ranging from Wallacea east to French Polynesia, south to New Zealand and north to the Philippine Islands and Micronesia, with a single outlier on the Red Sea. The greatest diversity occurs in Australo-Papua. The four that breed in Australia are the Sacred Kingfisher *T. sanctus*, Red-backed Kingfisher *T. pyrrhopygius*, Forest Kingfisher *T. macleayii* and Torresian Kingfisher *T. sordidus*. Traditionally, the Torresian Kingfisher has been included in the widespread Collared Kingfisher *T. chloris* complex; however, Andersen *et al.* (2015) found it to be polyphyletic, comprising several species. This separation is now accepted by AviList (AviList Core Team 2025), the Global Avian Checklist.

Syma (yellow-billed kingfishers) encompasses two species of northern Cape York Peninsula and New Guinea (Yellow-billed Kingfisher *S. torotoro* and Mountain Kingfisher *S. megarhyncha*). With the removal of these taxa, *Halcyon* is now restricted to 12 species in sub-Saharan Africa and southern and south-eastern Asia into Indonesia. Other halcyonine kingfishers breeding in Australia are two species of kookaburras (*Dacelo*) and a paradise kingfisher (*Tanysiptera*), with vagrant records of several additional species. New Guinea has several species of these genera, some shared with Australia, plus some monotypic endemics.

Water kingfishers occurring in Australia are the breeding species Azure Kingfisher *Ceyx azureus* and Little Kingfisher *C. pusillus*, with several vagrant records of Common Kingfisher *Alcedo atthis* from island territories.

Woodall (1991) investigated the relationship in kingfishers between morphometrics and diet. He divided these birds into four feeding categories: aquatic and the loosely circumscribed and somewhat overlapping terrestrial, fossorial and littoral. For these he compared mass and lengths of wing, culmen and tarsus. The aquatic foraging kingfishers had longer bills and shorter tarsi and tails, whereas the other categories differed less obviously.

The initial aim of this study was to examine proportional differences among Australian members of *Todiramphus.* These species appear externally to be quite similar, other than for overall size. Subsequently, the study was extended to other Australo-Papuan genera. Unlike Woodall (1991), comparisons here were made between the fore- and hindlimbs, specifically the relative lengths of the long bones in the wings (humerus, ulna, carpometacarpus) and legs (femur, tibiotarsus, tarsometatarsus). Scientific and English names follow AviList (AviList Core Team 2025).

Materials

Measurements of the greatest length of the long bones were made from museum specimens using vernier calipers accurate to 0.05 mm and rounded to the nearest 0.1 mm.

Ratio-diagrams of the log differences were constructed following the method of Simpson (1941). The length measurements of the bones are converted to logarithms. One taxon, in this instance Sacred Kingfisher, is arbitrarily chosen as the standard, and the difference between its converted measurements and the corresponding ones for each taxon are calculated (the logarithms of the ratios). The standard taxon thus has all ratios of 1.00 (zero difference in logarithms), which when plotted along a horizontal axis form a straight line. The logarithmic ratios for each taxon are plotted such that the points on a single vertical line represent different values of the same variable.

Table 1. Mean element lengths (mm) of Australo-Papuan kingfisher species used in analyses, with sample sizes (*n*). HUM = humerus, ULN = ulna, CMC = carpometacarpus, FEM = femur, TIB = tibiotarsus, TAR = tarsometatarsus. Scientific and English names follow AviList (AviList Core Team 2025).

Kingfisher species		*n*	*HUM*	*ULN*	*CMC*	*FEM*	*TIB*	*TAR*
Halcyoninae								
Rufous-bellied Kookaburra	*Dacelo gaudichaud*	2	39.4	50.3	20.7	25.6	37.4	16.1
Blue-winged Kookaburra	*Dacelo leachii*	4	65.4	85.3	33.5	38.3	57.8	25.5
Laughing Kookaburra	*Dacelo novaeguineae*	2	69.1	86.6	34.9	38.6	58.5	26.4
Hook-billed Kingfisher	*Melidora macrorrhina*	1	39.4	49.2	18.9	25.6	40.2	19.3
Mountain Kingfisher	*Syma megarhyncha*	2	29.1	35.5	14.2	19.3	32.5	15.0
Yellow-billed Kingfisher	*Syma torotoro*	3	27.0	34.0	13.5	17.9	29.2	14.3
Common Paradise Kingfisher	*Tanysiptera galatea*	2	30.4	38.4	15.9	19.7	31.7	16.1
Buff-breasted Paradise Kingfisher	*Tanysiptera sylvia*	3	30.1	37.8	15.3	18.9	31.9	15.3
Forest Kingfisher	*Todiramphus macleayii*	9	29.2	37.3	15.0	17.7	27.7	12.8
Red-backed Kingfisher	*Todiramphus pyrrhopygius*	3	31.6	40.6	16.1	19.4	29.9	14.0
Sacred Kingfisher	*Todiramphus sanctus*	9	30.1	38.9	15.2	18.4	28.5	13.4
Torresian Kingfisher	*Todiramphus sordidus*	2	34.7	43.4	17.2	21.4	32.7	15.5
Alcedininae								
Common Kingfisher	*Alcedo atthis*	1	26.1	32.0	13.8	16.1	25.8	10.3
Azure Kingfisher	*Ceyx azureus*	5	25.9	31.5	12.9	16.5	26.3	10.2
Little Kingfisher	*Ceyx pusillus*	1	18.0	23.2	8.9	12.1	19.8	7.8
Cerylinae								
Belted Kingfisher	*Megaceryle alcyon*	5	46.6	57.7	26.5	26.5	36.0	10.8

Values greater than the standard fall above the standard line, the smaller ones below it. The points of each taxon are connected with a line. Taxa with proportions identical to the standard taxon will have lines parallel to its line. Variations from a parallel line are indicative of variations in the proportions from that of the standard taxon. All of the values used in constructing the diagrams are given in Table 1.

On the scale of the *y*-axis, 0.1 is roughly 1.26 times the value of the standard. Other approximate values are, respectively, 0.2 (1.59 times), 0.3 (2 times), 0.4 (2.5 times), – 0.1 (0.8 times), – 0.2 (0.63 times) and – 0.3 (0.5 times).

Institutional prefixes to registration numbers of specimens used in this study are AM (Australian Museum), ANWC (Australian National Wildlife Collection), MV (Museums Victoria) and QM (Queensland Museum).

Results

Intra-specific variation – Sacred Kingfisher Todiramphus sanctus

As a test of proportional variation within a species, ratio-diagrams of log differences of the long bones were plotted for nine specimens of Sacred Kingfisher (Figure 1). Only minor differences were observed, all values falling within 0.93 and 1.08 of the log values of the standard, with 78% falling within 0.97–1.03 of the standard. This general uniformity among specimens permits the mean of each bone length to be used as a suitable representative for the standard values for subsequent, inter-taxon comparisons. Values for other species, based on smaller samples sizes, are assumed to be also representative for their respective taxa.

Intra-generic variation – Australian Todiramphus *species*

Within *Todiramphus*, the species compared varied in size but little in proportions (Figure 2). Two species, Sacred Kingfisher and Forest Kingfisher, exhibited considerable overlap in their plots, indicating similar sizes and proportions. Red-backed Kingfisher and Collared Kingfisher had plots parallel to those of Sacred Kingfisher, showing that despite their larger sizes, they had the same long bone proportions.

Inter-generic variation – Syma *and* Tanysiptera

Members of the genera *Syma* (yellow-billed kingfishers) and *Tanysiptera* (paradise kingfishers) are sympatric with *Todiramphus* and most are of similar body size. In *Tanysiptera* and in *Syma* the species examined within each are almost the same size and show little variation in proportions (Figure 3). Members of both genera are similar in proportions. Their wing proportions and those of *Todiramphus* are much alike, but the legs are proportionally longer in *Tanysiptera* and particularly *Syma*.

Inter-generic variation – Dacelo *and* Melidora

The largest members of the Halcyoninae include the kookaburras (*Dacelo*) and Hook-billed Kingfisher *Melidora macrorrhina* of New Guinea. The Laughing

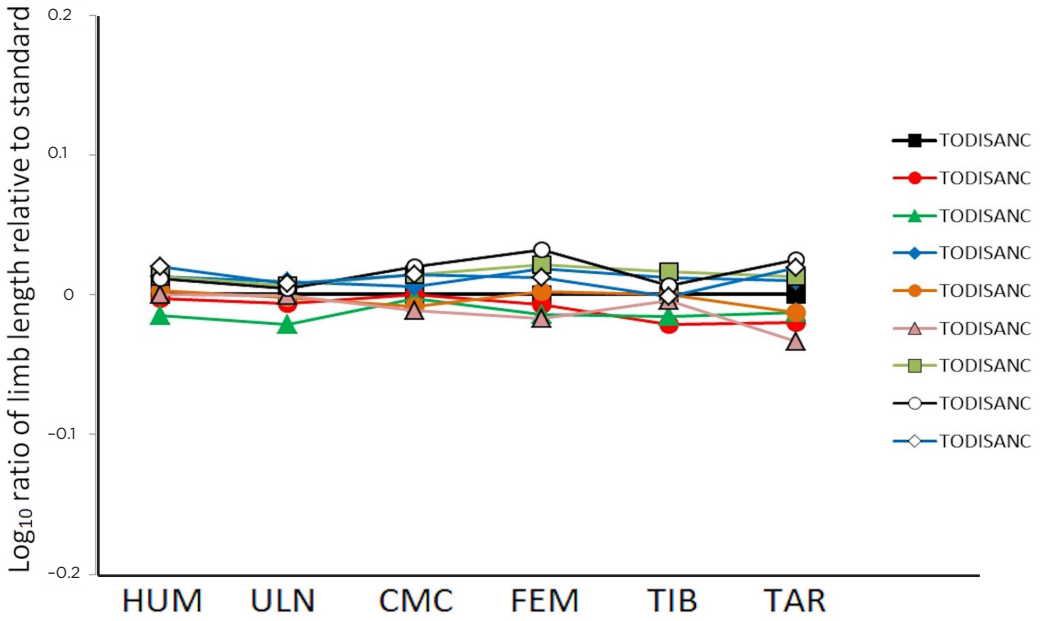

Figure 1. Relative lengths of limb elements of nine individuals of Sacred Kingfisher *Todiramphus sanctus* (TODISANC) showing strong uniformity among specimens. See Materials for further details.

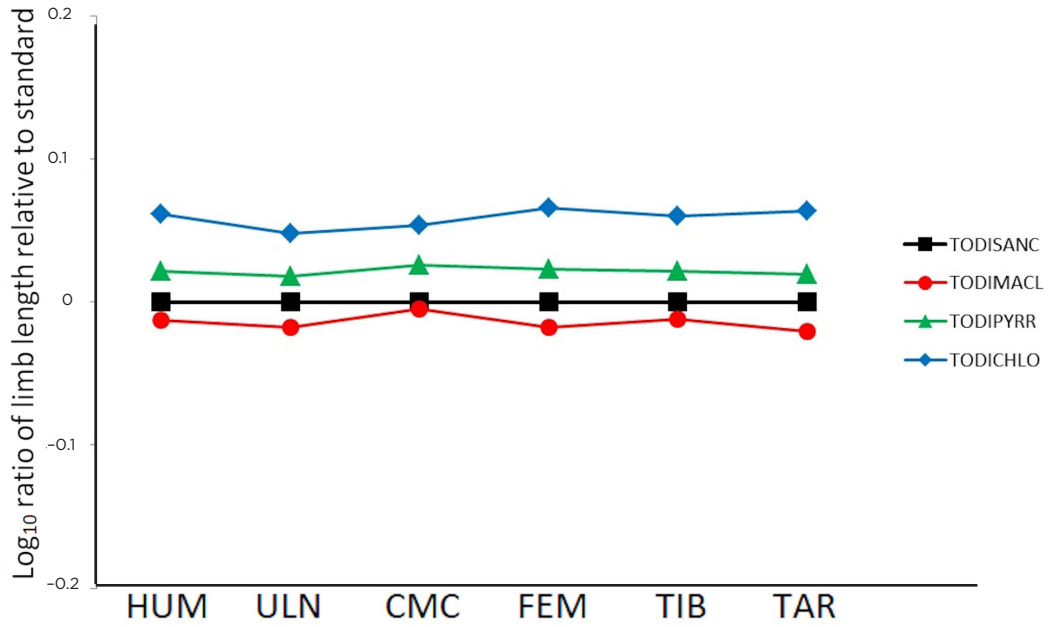

Figure 2. Relative lengths of limb elements for species of *Todiramphus* that breed in Australia: Torresian Kingfisher *T. sordidus* (TODISORD), Forest Kingfisher *T. macleayii* (TODIMACL) and Red-backed Kingfisher *T. pyrrhopyius* (TODIPYRR). Standard species Sacred Kingfisher *T. sanctus* (TODISANC). See Materials for further details.

D. novaeguineae and Blue-winged Kookaburras *D. leachii* are substantially larger than any other species examined. They are identical in proportions, with the hindlimbs shorter relative to the wing elements (Figure 4). The smaller Rufous-bellied Kookaburra *D. gaudichaud* of New Guinea exhibits a similar, although less pronounced, pattern. The single species of *Melidora* differs by having hindlimb elements that are substantially longer relative to the wing elements.

Water kingfishers – Alcedininae and Cerylinae

There are two other subfamilies of kingfishers: Alcedininae of the Old World with two breeding species in Australia, and Cerylinae, which is restricted to the New World. In members of both groups, prey capture is much more reliant on diving onto prey from a perch, with little or no time spent standing on the ground while foraging. Although both

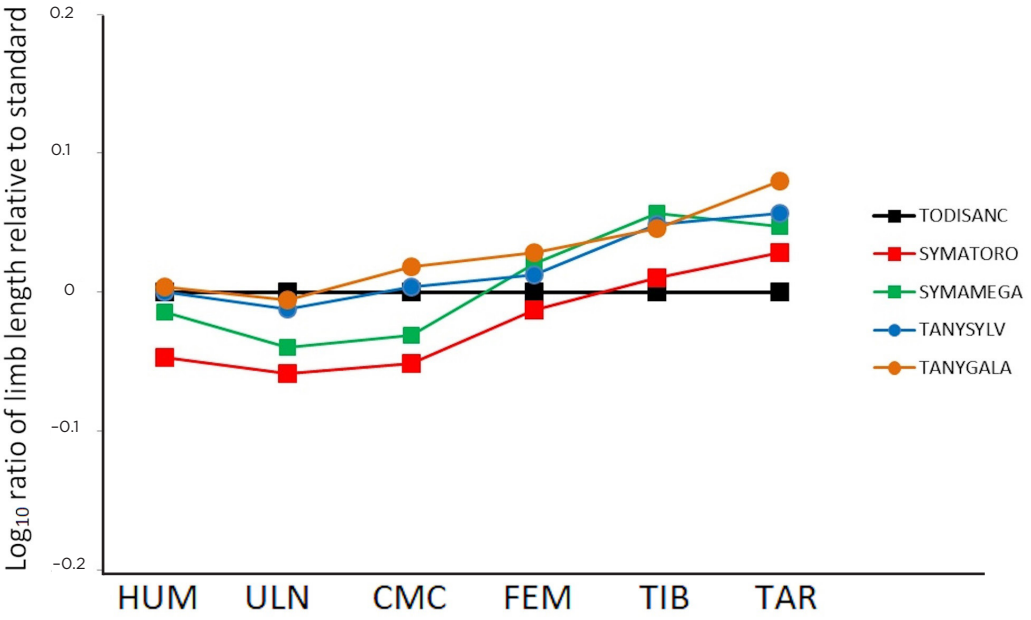

Figure 3. Relative lengths of limb elements for representatives of *Syma* and *Tanysiptera*: Mountain Kingfisher *S. megarhyncha* (SYMAMEGA), Yellow-billed Kingfisher *S. torotoro* (SYMATORO), Buff-breasted Paradise Kingfisher *T. sylvia* (TANYSYLV), Common Paradise Kingfisher *T. galatea* (TANYGALA). Standard species Sacred Kingfisher *Todiramphus sanctus* (TODISANC). See Materials for further details.

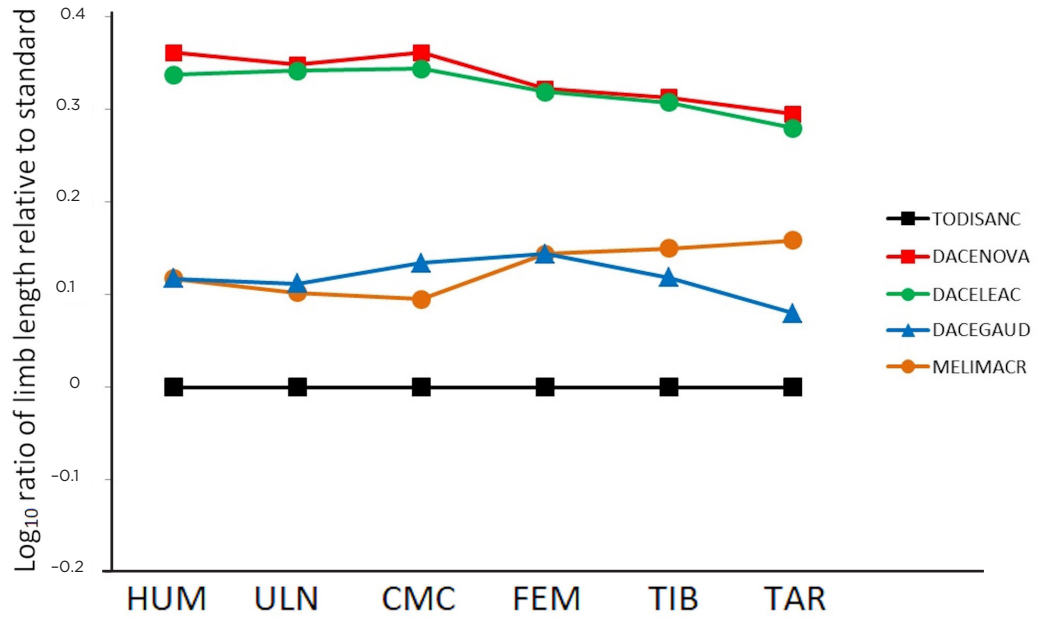

Figure 4. Relative lengths of limb elements for representatives of *Dacelo* and *Melidora*: Laughing Kookaburra *D. novaeguineae* (DACENOVA), Blue-winged Kookaburra *D. leachii* (DACELEAC), Rufous-bellied Kookaburra *D. gaudichaud* (DACEGAUD), Hook-billed Kingfisher *M. macrorrhina* (MELIMACR). Standard species Sacred Kingfisher *Todiramphus sanctus* (TODISANC). See Materials for further details.

groups are called water kingfishers, there are differences between their respective foraging methods. Species of *Ceyx* and *Alcedo* include both piscivores and terrestrial insectivores (Fry *et al*. 1992). In contrast, members of the Cerylinae are exclusively piscivorous. The Australian species of Alcedininae and the widespread Common Kingfisher *Alcedo atthis* are smaller-bodied birds with leg elements that are smaller relative to those of the wing than in members of Halcyoninae (Figure 5). This comparative shortness of the hindlimb is highly pronounced in a member of the Cerylinae, with the leg elements being markedly shorter in their proportions.

Discussion

Halcyonine kingfishers exhibit considerable overall uniformity in shape and external proportions. This exercise

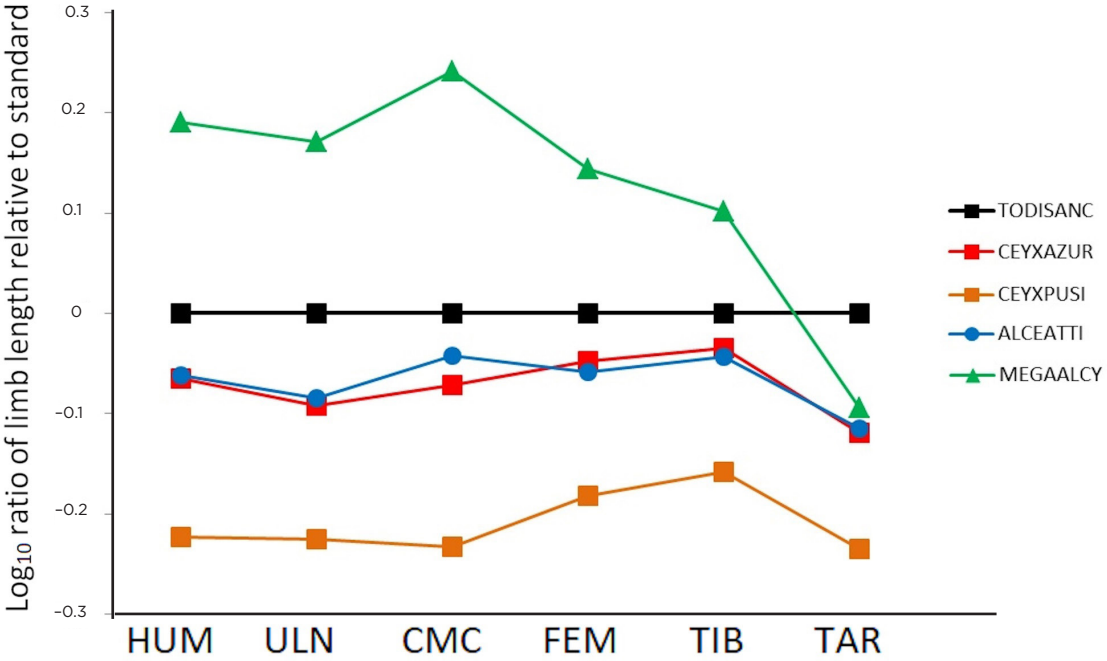

Figure 5. Relative lengths of limb elements for representatives of the subfamilies Alcedininae and Cerylinae. Alcedininae: Azure Kingfisher *Ceyx azureus* (CEYXAZUR), Little Kingfisher *C. pusillus* (CEYXPUSI) (both Australia), Common Kingfisher *Alcedo atthis* (ALCEATTH). Cerylinae: Belted Kingfisher *Megaceryle alcyon* (MEGAALCY). Standard species Sacred Kingfisher *Todiramphus sanctus* (TODISANC). See Materials for further details.

examined variation between fore- and hindlimb elements among species of *Todiramphus* and other members of this subfamily. Australian *Todiramphus* species exhibit little variation in their proportions of the limb elements. Proportionally much longer tibiotarsi and tarsometatarsi are pronounced in species of *Tanysiptera* and *Syma*. In contrast, a noticeable comparative reduction in relative leg length occurs in species of *Dacelo*.

Compared with the hindlimbs of *Todiramphus*, the shortening or lengthening of the hindlimb elements increases distally. Among halcyonines examined, the reduction is most pronounced in the large-bodied species. This trend could also be related to habitat differences: the shorter-legged kingfishers are usually birds of more open habitats, whereas *Syma*, *Tanysiptera* and *Melidora* are primarily birds of the rainforest. These habitat assignments are only generalisations, and there are numerous counter-examples.

Water kingfishers of both subfamilies exhibit reduction of the hindlimb elements and, as in halcyonines, this reduction increases distally. This reduction is not unexpected since, unlike halcyonines, these birds spend little time moving on the ground, using the legs primarily for perching. They forage by diving from an elevated site or while hovering, and then returning to the perch after prey capture. On occasion, species of Alcedininae will spend short periods on the ground when capturing terrestrial invertebrates. They show moderate relative reduction of the hindlimb elements, particularly the tarsometatarsus. The pronounced reduction of the distal leg elements in the Cerylinae reflects the exclusively piscivorous foraging from a perch.

Wing length in the live bird is a factor of both the lengths of the osteological elements and of primary feathers. Migratory birds often have longer wings than conspecifics that do not migrate, this difference caused by an increase in the length of the outer primary feathers (Winkler & Leisler 1992). Among Australian species of *Todiramphus*, only the Sacred Kingfisher is migratory. A comparison of wing lengths between this species and the similar-sized Forest Kingfisher might be predicted to show a relatively long wing in the Sacred Kingfisher. A plot of wing length (values from Higgins 1999) versus the sum of the lengths of the forelimb elements (not shown) revealed no differences among these species.

The previously equivocal position of *Syma* relative to *Todiramphus* has been clarified by genetic studies (Moyle 2006). The separation of these taxa generically is corroborated by the findings here. *Syma* has distinctively different hindlimb proportions from *Todiramphus*.

Some variation identified here reflects true differences among taxa. In other instances, the observed variation is small, and is likely to be affected by differences between individual birds. It would undoubtedly be modified by incorporating additional specimens. Whether such apparent variation persists in such cases warrants further investigation.

The four Australian species of *Todiramphus* are nearly identical in proportions of the limb long bones, differing primarily in size. It would be interesting to see if this relationship extends to extra-limital members of the genus, particularly some Pacific taxa that capture a significant proportion of their prey in flight. Also meriting attention is the variation among populations traditionally included in the Collared Kingfisher *T. chloris* (*sensu lato*), distributed across Wallacea, New Guinea, Australia, Melanesia, Polynesia, Micronesia, south-eastern Asia, India and the Red Sea (Woodall 2001), but recently divided into at least six species, including Torresian Kingfisher *T. sordidus* (AviList Core Team 2025). Species of *Halcyon* are much

more variable in plumage pattern and coloration than those of *Todiramphus*. Whether this variation between genera is also present in the osteological elements invites examination.

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