

# 1 Systematics and Evolution of Kestrels

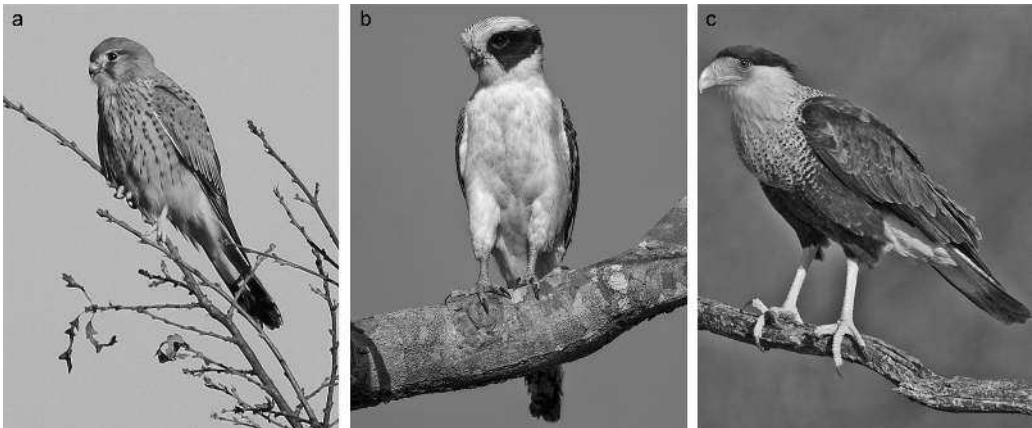
## 1.1 Chapter Summary

The family Falconidae constitutes a group of small to medium-sized diurnal raptors whose monophyly is strongly supported. Kestrels are included in the subfamily Falconinae. There are at least 13 species that belong to the kestrel group, but recent genetic studies suggest that the number of kestrel species might be larger, possibly 16. The paleontological and molecular evidence is congruent in suggesting an evolutionary radiation of kestrels from the Late Miocene (4.0–9.8 million years ago) through the Early Pleistocene. However, the geographic area where kestrels originated and dispersed from is unclear.

## 1.2 Diversification of Falcons

The Falconidae is a monophyletic family of diurnal birds of prey that occupy a wide variety of ecological niches and geographic regions (White et al., 1994). Three subfamilies are currently recognised and their validity is supported by both molecular and morphological data (Griffiths, 1999; Griffiths et al., 2004; Fuchs et al., 2012, 2015): (i) Falconinae (falcons, falconets and kestrels), (ii) Herpetherinae (forest falcons *Micrastur* sp. and laughing falcon *Herpetheres cachinnans*) and (iii) Polyborinae (caracaras) (Figure 1.1). Dickinson (2003) has recognised 11 genera and 64 species of Falconidae, but figures can vary slightly across authors.

Both the Herpetherinae and the Polyborinae occur only in the New World, while the Falconinae (the subfamily to which kestrels belong) are widespread across both the New and Old World with 46 species, 40 of which belong to the genus *Falco* (Fuchs et al., 2015). Molecular genetic estimates of diversification within Falconidae, based on fossil calibration using two *Falco* ancestors (*Pedohierax* and *Thegornis*) and on the analyses of DNA sequences from eight loci, indicated that the diversification started between 22.3 (95% confidence interval: 19.6–25.6) and 34.2 (95% confidence interval: 26.2–43.2) million years ago for the Falconidae; between 12.6 (95% confidence interval: 10.6–14.7) and 19.3 (95% confidence interval: 14.4–24.6) million years ago for the



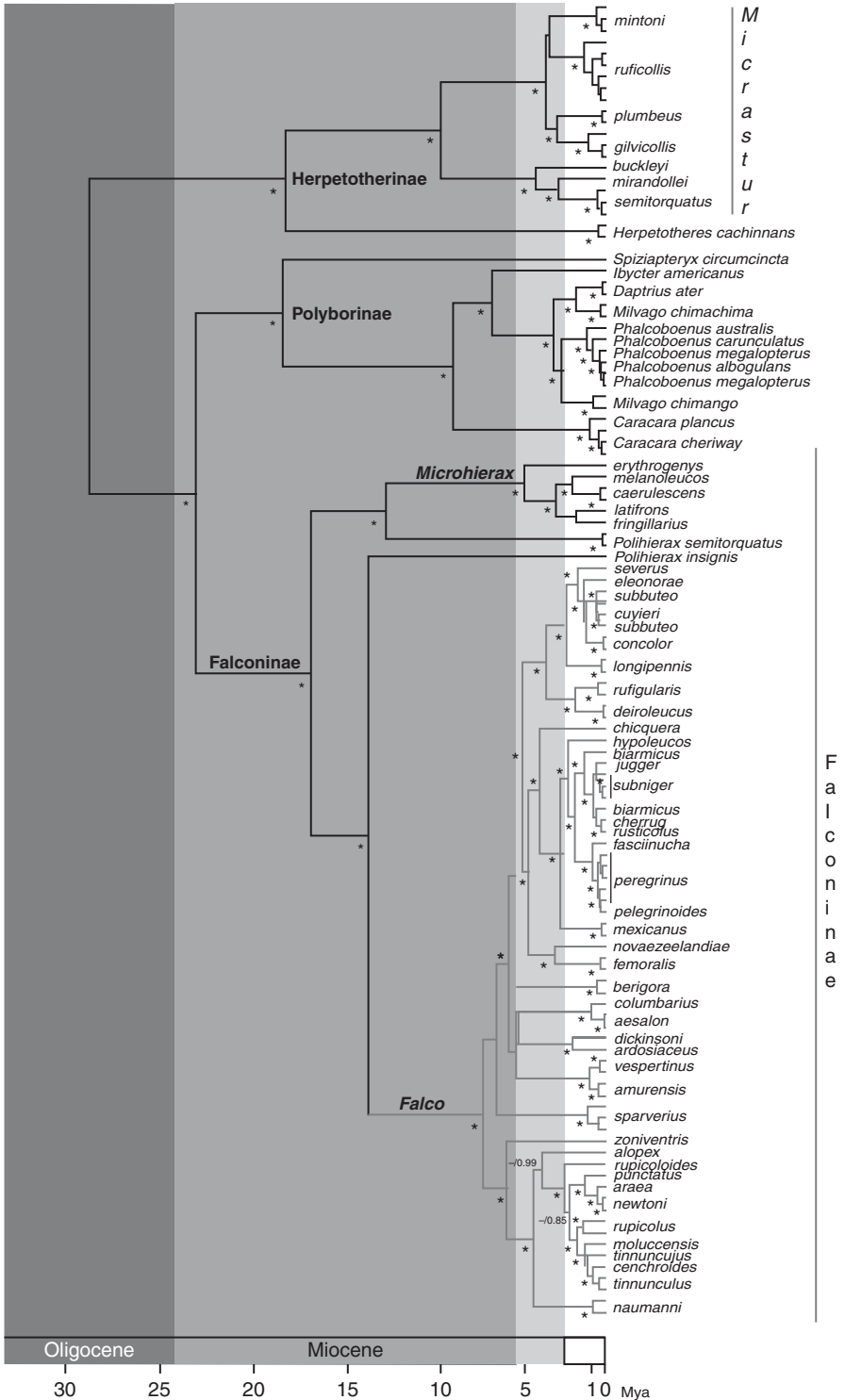
**Figure 1.1** The family *Falconidae* includes three subfamilies: (a) Falconinae (*Falco tinnunculus*, photograph by David Costantini); (b) Herpetotherinae (*Herpetotheres cachimans*, photograph by Andreas Trepte, via Wikimedia Commons); (c) Polyborinae (*Caracara cheriway*, photography by www.naturespicsonline.com, via Wikimedia Commons).

Falconinae; and between 5.0 (95% confidence interval: 4.0–6.1) and 7.7 (95% confidence interval: 5.6–9.8) million years ago for the genus *Falco* (Figure 1.2; Fuchs et al., 2015).

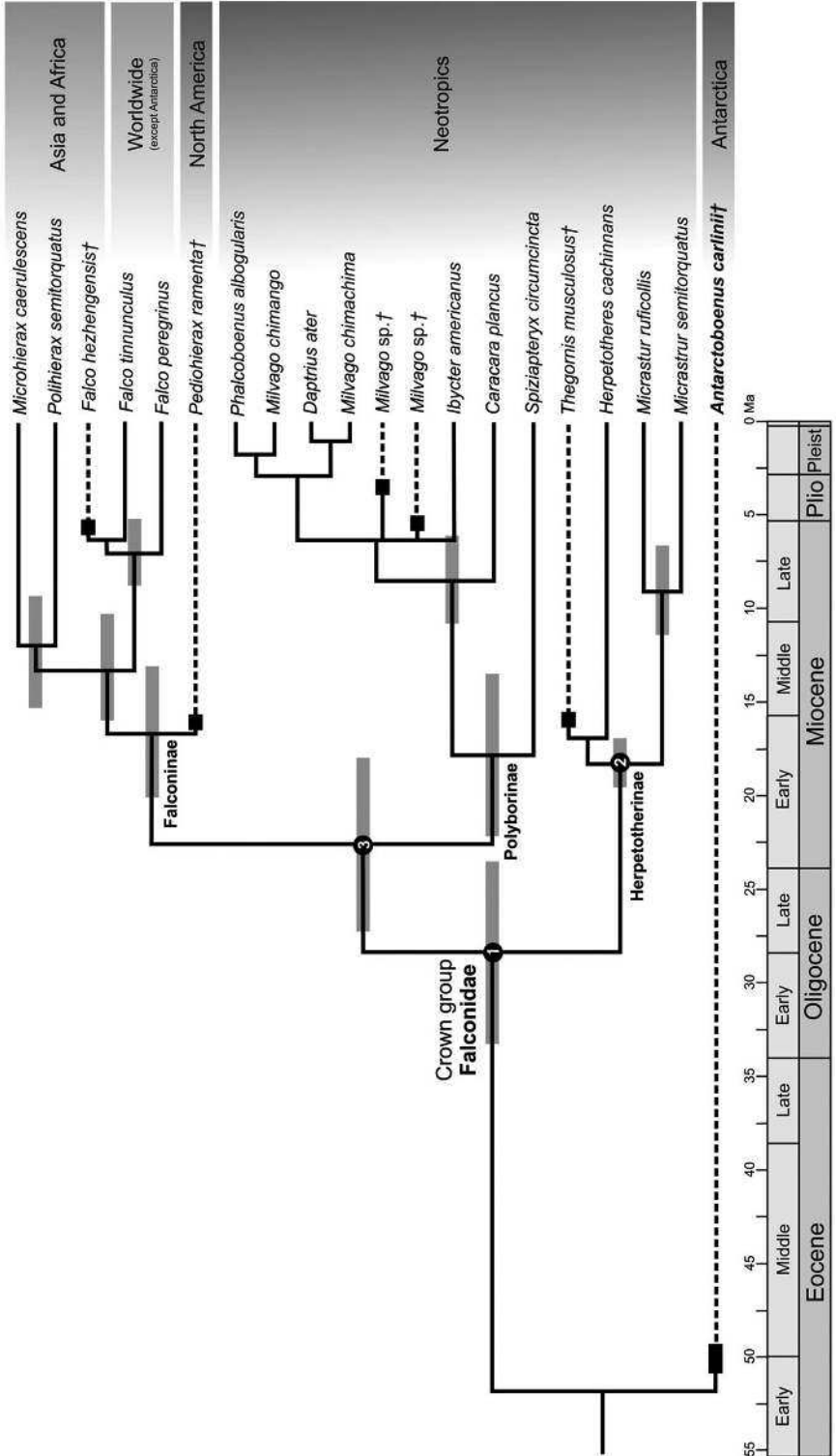
Genizo et al. (2016) proposed that the Lower Eocene *Antarctoboenus carlinii*, a fossil species found on Seymour island (west Antarctica), could represent the most ancient falconiform described so far (Figure 1.3); this discovery would give support to a Neotropical or Austral origin of Falconidae (Ericson et al., 2006; Ericson, 2012; Fuchs et al., 2015).

The diversification of the genus *Falco* started during a period characterised by increasing aridity and the spread of open savannahs (Cerling et al., 1997), which might have favoured the diversification of these open-land birds of prey (Cade & Digby, 1982). Molecular estimates of the diversification of species belonging to the genus *Falco* provided by Fuchs et al. (2015) are in agreement with the paleontological evidence, as fossils of several *Falco* paleospecies date from the Late Miocene to the Early Pliocene period (e.g. Umanskajaa, 1981; Becker, 1987; Boev, 1999, 2011a, 2011b, 2011c; Li et al., 2014). However, most *Falco* paleospecies are known only from fragmentary remains, which make phylogenetic inferences problematic. In conclusion, the recent molecular and paleontological data have supported the statement made by Cade and Digby (1982):

The Late Miocene or Early Pliocene would seem to have been about the right time, just when things were starting to go well for another group of open-country inhabitants, the early hominids. It is amusing and somehow prophetic to think that falcons and men both derive from the same evolutionary stimulus – the creation of open grasslands and savannahs with new and unexploited opportunities for both winged and bipedal hunters ... Thus it appears that the association between men and falcons is deep rooted indeed. What did ‘Lucy’ and her kin (*Australopithecus afarensis*) experience when they looked up into the azure sky over the Afar Plains and saw hunting falcons?



**Figure 1.2** Chronogram calculated using eight genetic markers and two fossil taxa (*Pedohierax* and *Thegornis*) as calibration points. Asterisks indicate posterior probabilities and maximum likelihood bootstrap support values higher than 0.95 and 70%, respectively. The different shades of grey indicate different geological epochs. The different branch colours indicate the two parts of the tree with different diversification rates. Reprinted from Fuchs et al. (2015) with permission from Elsevier.



**Figure 1.3** Geographical range, temporal distribution, and phylogenetic affinities of extant and fossil falconid birds. The temporal distribution of fossil taxa (dagger) is indicated by black squares. Grey bars indicate divergence times estimates for the primary lineages within the extant Falconids according to Fuchs et al. (2015). Reprinted from Cenizo et al. (2016) with permission from Springer Nature.

## 1.3 Systematics and Diversification of Kestrels

### 1.3.1 Morphological and Behavioural Evidences

Kestrels belong to the subfamily Falconinae. It is traditionally recognised that at least 13 species belong to the kestrel group, but recent molecular analyses have suggested that this number of species might be larger (Table 1.1).

Boyce and White (1987) suggested that there are 14 or 15 species of *Falco* that might be considered as kestrels. The classic kestrel group includes a single New World species (the American kestrel, *F. sparverius*) and 12 Old World species. The majority of kestrels (10 of 13 species) have been classified within the subgenus *Tinnunculus* (Brown & Amadon, 1968; Cade & Digby, 1982). This subgenus includes those species characterised by a classic kestrel form and brown-rufous plumage colouration. The three species characterised by grey plumage colouration – the grey kestrel (*F. ardosiaceus*), Madagascar banded kestrel (*F. zoniventris*) and Dickinson's kestrel (*F. dickinsoni*) – are all from Africa and have been placed within the subgenus *Dissodectes* (Snow, 1978). This distinction between *Tinnunculus* and *Dissodectes* kestrels has also been supported by the electrophoretic patterns of feather proteins (Olsen et al., 1989).

**Table 1.1** List of species that belong or have been suggested to belong to the kestrel group. 1 = Fuchs et al. (2015) have proposed that the subspecies *rupicolus* may warrant species status based on molecular genetic analyses. 2 = Brown and Amadon (1968) and Fuchs et al. (2015) suggested that *F. amurensis* and *F. vespertinus* might be part of the kestrel group.

Common name	Scientific name	Authority
Common kestrel	<i>Falco tinnunculus</i>	Linnaeus, 1758
Lesser kestrel	<i>Falco naumanni</i>	Fleischer, 1818
Fox kestrel	<i>Falco alopex</i>	Heuglin, 1861
Seychelles kestrel	<i>Falco araea</i>	Oberholser, 1917
Grey kestrel	<i>Falco ardosiaceus</i>	Vieillot, 1823
Dickinson's kestrel	<i>Falco dickinsoni</i>	Sclater, 1864
Moluccan or spotted kestrel	<i>Falco moluccensis</i>	Bonaparte, 1850
Madagascar kestrel	<i>Falco newtoni</i>	Gurney, 1863
Mauritius kestrel	<i>Falco punctatus</i>	Temminck, 1821
Greater kestrel	<i>Falco rupicoloides</i>	Smith, 1829
Madagascar banded kestrel	<i>Falco zoniventris</i>	Peters, 1854
Australian nankeen kestrel	<i>Falco cenchroides</i>	Vigors & Horsfield, 1827
American kestrel	<i>Falco sparverius</i>	Linnaeus, 1758
Rock kestrel	<i>Falco rupicolus</i> <sup>1</sup>	Daudin, 1800
Red-footed falcon	<i>Falco vespertinus</i> <sup>2</sup>	Linnaeus, 1766
Amur falcon	<i>Falco amurensis</i> <sup>2</sup>	Radde, 1863

There are no clear diagnostic features that define what a kestrel is and clarify the evolutionary relationships among kestrel species. For example, while many kestrel species perform hovering for hunting small mammals, this hunting technique appears to be very uncommon in the grey kestrel, Madagascar kestrel (*F. newtoni*) or fox kestrel (*F. alopex*) (Gaymer, 1967; Boyce & White, 1987; Londei, 2002). However, we know very little about the behaviour and the ecology of kestrels in Africa and Asia, which limits the reliability of any conclusions. Sexual dimorphism in plumage is also not common across all kestrel species. For example, sexual dimorphism is apparent in the common kestrel (*F. tinnunculus*), the lesser kestrel (*F. naumanni*) and the Australian nankeen kestrel (*F. cenchroides*), while it is barely evident in other species. As for the plumage colouration in nestlings, while they usually resemble adult females, male and female American kestrel nestlings differ in plumage colouration (Village, 1990).

Phylogenetic analyses carried out using data sets of morphological (e.g. plumage colouration, wing size) and behavioural (e.g. hovering) traits led Boyce and White (1987) to conclude that the fox kestrel might be the ancestor species of the current red and grey kestrel species, mainly because it does not hover and has negligible age or colour dimorphism between sexes. This conclusion was also based on the assumption that both the lack of hovering and the negligible colour dimorphism are primitive characters, i.e. closer to the most ancestral kestrel species. This might be plausible if the ancestor species were a raptor living in forests, where hovering would not have been an efficient hunting strategy. However, the fox kestrel can hover (Londei, 2002) and the phylogenetic value of hovering is unclear. Boyce and White (1987) also concluded that the American kestrel might be the most recently evolved species of kestrel because (i) it has strong adult sexual dimorphism; (ii) male and female nestlings differ in colouration, with each sex resembling their respective adult sex rather than the female; and (iii) the species occupies an extensive geographic area with 17 subspecies (14 in Boyce & White, 1987) that have not diverged enough to be considered distinct species. Finally, the analyses further suggested that the lesser kestrel might share a direct ancestor species with the Amur falcon (*F. amurensis*) and the red-footed falcon (*F. vespertinus*).

Reconstruction of phylogenetic trees based on morphological characters may be questioned because two species might be similar to each other because of convergent evolution; this occurs when species share a trait that is different from the trait inferred to have been present in their common ancestor. Thus, the same trait has evolved independently in the two species in order to perform a similar function. Other problems in using morphological traits may arise with insular species. For example, the negligible sexual dimorphism of the Mauritius kestrel (*F. punctatus*) might (i) represent the ancestral condition, (ii) indicate the loss of dimorphism due to the insular isolation or (iii) suggest that barely dimorphic individuals were those that colonised the islands. Also, compared to other kestrel species, the Mauritius kestrel has more rounded wings (like those of forest-dwelling raptors), probably because of its adaptations to hunt in forested habitats. Thus, molecular data (e.g. DNA sequences of marker genes) are needed to elucidate evolutionary relationships because they are less biased by convergent evolution than are morphological traits.

### 1.3.2 Molecular Evidence

Finer subdivisions within the *Tinnunculus* kestrels have been contentious for years. Groombridge et al. (2002) constructed a molecular phylogeny of *Tinnunculus* kestrels using the mitochondrial cytochrome *b* DNA sequence. All analytical approaches used by Groombridge et al. (2002) produced phylogenetic trees of broadly similar topology, but with inconsistent positions for the Mauritius kestrel and the greater kestrel (*F. rupicoloides*). The molecular analyses provided strong support for a common ancestor shared between the Madagascar kestrel and the Seychelles kestrel (*F. araea*). The molecular data indicated that the kestrels that colonised the Seychelles likely came from Madagascar between 0.3 and 1.0 million years ago, probably favoured by the lower sea level due to glaciation (Groombridge et al., 2002). Given this scenario, it has been suggested that the Aldabran kestrel (*F. newtoni aldabranus*), a subspecies of the Madagascar kestrel (Benson, 1967; Benson & Penny, 1971), might be a possible relict of such dispersal (Groombridge et al., 2002). It has also been hypothesised that the colonisation of Mauritius occurred via Madagascar less than 3 million years ago (Groombridge et al., 2002). The combination of molecular and geological data led to the hypothesis that the colonisation of Mauritius by kestrels occurred about 1.9–2.6 million years ago, a period characterised by an interruption in the volcanic activity on Mauritius (Groombridge et al., 2002). As compared to the Madagascar kestrel, both the Seychelles kestrel and the Mauritius kestrel show morphological adaptations for forest-dwelling. Such adaptations might have evolved on the islands after the dispersion from Madagascar ended (Groombridge et al., 2002). Alternatively, it might be that individual Madagascar kestrels with a more forest-kestrel form might have been the pioneers of such colonisation.

Molecular data produced by Groombridge et al. (2002) suggest a close affinity between the common kestrel and the Australian nankeen kestrel, supporting a recent divergence, probably due to Pleistocene glacial events that pushed the common kestrel stock southwards from Asia, as previously hypothesised by Boyce and White (1987) on the basis of morphological traits. Further work based on the mitochondrial cytochrome *b* gene clustered the red-footed falcon, the Amur falcon, Dickinson's kestrel and the American kestrel separately from the kestrel group (Wink & Sauer-Gürth, 2004).

More recent molecular analyses made by Fuchs et al. (2015) did not provide support for the traditional hypothesis proposing (i) the American kestrel as closely related to the Old World kestrels and (ii) the Madagascar banded kestrel as closely related to the grey kestrel and Dickinson's kestrel. Rather, Fuchs et al. (2015) hypothesised (i) the existence of a group including the Old World kestrels together with the Madagascar banded kestrel and (ii) that the American kestrel would be more closely related to other falcons (e.g. red-footed falcon) than to the Old World kestrels, as previously suggested by DNA/DNA hybridisation studies (Sibley & Ahlquist, 1990) and by analyses of mitochondrial cytochrome *b* DNA sequence (Groombridge et al., 2002). These results might indicate that either the kestrel group should include more than the 13 species classically recognised or that the position of the American kestrel within the kestrel

group might need to be reconsidered. Analyses of molecular genetic markers made by Fuchs et al. (2015) also suggested that the Amur falcon and the red-footed falcon might be part of the kestrel group, as previously proposed by Brown and Amadon (1968). Finally, Fuchs et al. (2015) found that the fox kestrel might not be the sister species of the greater kestrel as traditionally thought. Rather, both the fox kestrel and the greater kestrel would form a paraphyletic group (i.e. a group which does not include all descendants of the same ancestor), with the greater kestrel being sister to all other kestrels included in the *F. tinnunculus* group.

### 1.3.3 Paleontological Evidence

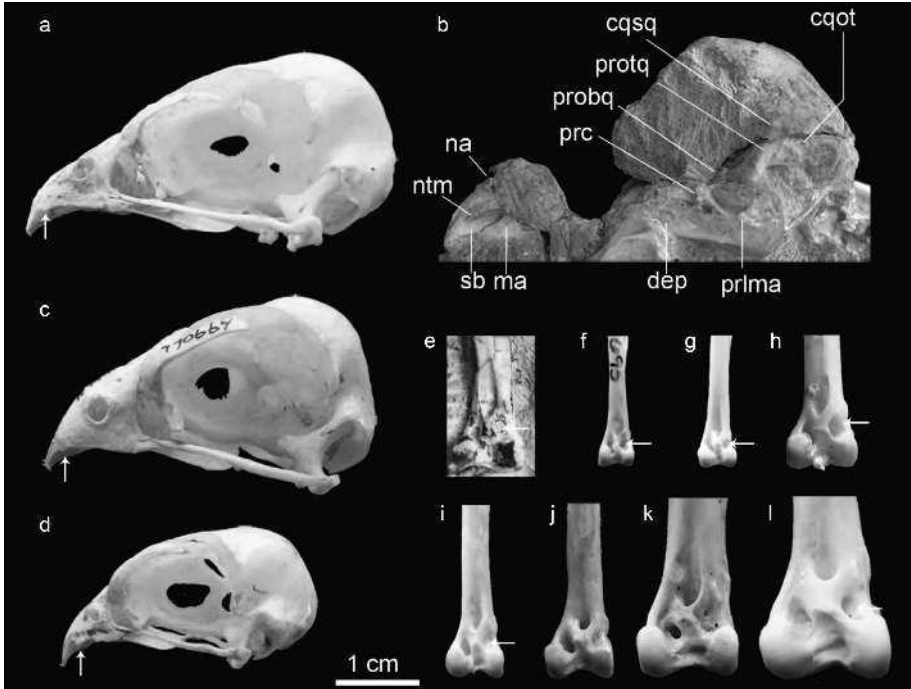
There is scarce information about the fossil history of raptors belonging to the genus *Falco*, particularly because of poor preservation of bone remains. Two close relative species of the common kestrel are the Late Pliocene *F. bakalovi*, whose remains were found near the town of Varshets in northwest Bulgaria (Boev, 1999, 2011a, 2011b), and the Late Miocene *F. bulgaricus*, whose remains were found near the town of Hadzhidimovo in southwest Bulgaria (Boev, 2011c). As with other *Falco* fossils, both *F. bakalovi* and *F. bulgaricus* have been described on the basis of a limited number of isolated bones, which makes their description and systematic classification problematic. One of the best-preserved specimens of a fossil falconid so far recovered has been classified as *F. hezhengensis* (Figure 1.4) by Li et al. (2014).

This falconid species was found in the Late Miocene deposits of Linxia Basin in north-western China. The analysis of 66 osteological characters led the authors to place this new *Falco* paleospecies as the sister group of the common kestrel and the greater kestrel (Li et al., 2014). This new paleospecies has also provided paleontological evidence in favour of an earlier divergence of kestrels from the peregrine falcon (*F. peregrinus*) in the Late Miocene. Although the paleontological evidence is congruent with the molecular data in suggesting a radiation of kestrels from the Late Miocene through the Early Pleistocene, the timing and location of the radiation are still ambiguous because of the paucity of well-preserved fossils over a wide geographic area. It has been suggested that the presence of the majority of kestrel taxa on the African continent could be evidence for an African origin of the kestrel group. However, the absence of a Pre-Pleistocene kestrel fossil record from Africa has meant that assumptions of kestrel divergence within and from the African continent have not been easy to confirm. Li et al. (2014) suggested that *F. hezhengensis* might represent an early dispersal event after the origin of kestrels occurred or, alternatively, it might be interpreted as evidence in favour of an Eurasian origin of kestrels.

## 1.4 Diversification and Geographic Distribution of Kestrels

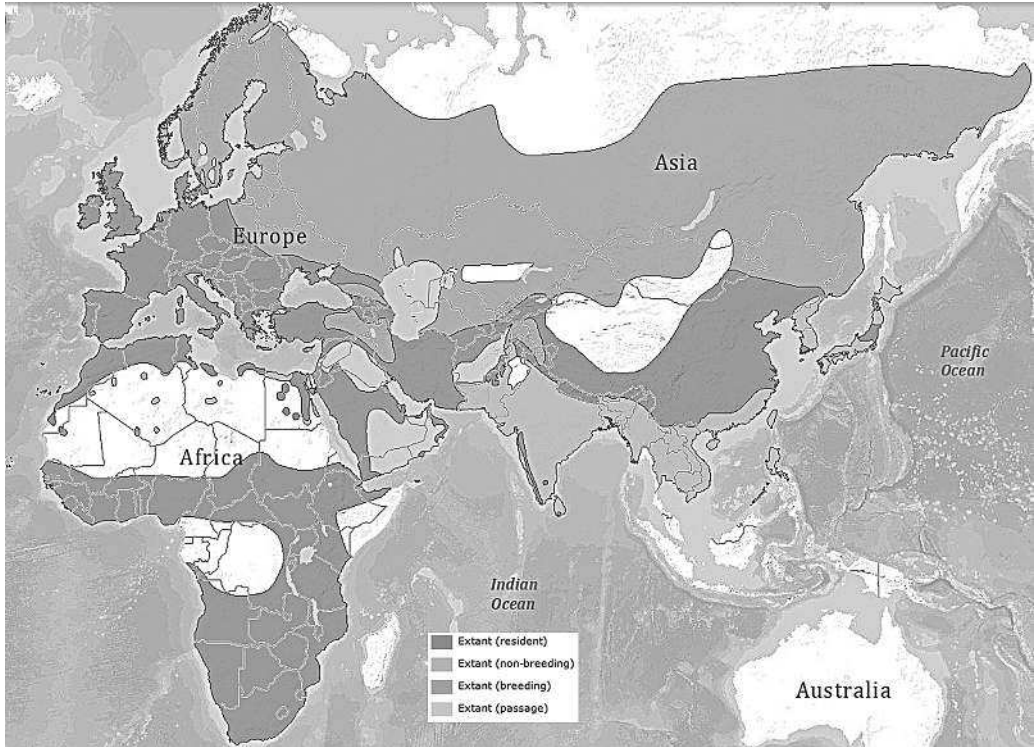
The kestrel group is truly cosmopolitan, occupying wide geographical areas and different environments. Most kestrels are open-land predators, and avoid deserts,





**Figure 1.4** Comparison of the skull and distal tibiotarsus of the holotype *Falco hezhengensis* with other Falconidae species: (a) *F. tinmuculus* (USNM 610371); (b, e) *F. hezhengensis* (IVPP V14586); (c) *Polihierax insignis* (USNM 490664); (d, f) *Microhierax erythrogegens* (USNM 613695); (g) *P. semitorquatus* (USNM 621024); (h) *F. rupicoloides* (USNM 430626); (i) *Spiziapteryx circumcincta* (USNM 319445); (j) *Micrastur ruficollis* (USNM 621387); (k) *Herpetheres cachinnans* (USNM 346714); and (l) *Caracara plancus* (USNM 614583). The vertical arrows indicate the tomial notch on the premaxilla that is present in Falconinae; the horizontal arrows indicate a third opening into the extensor groove located medial to the supratendinal bridge that is present in Falconinae and Polyborinae but not in Herpetherinae. Anatomical abbreviations: cqot, cotyla quadrati otici; cqsq, cotyla quadrati squamosa; dep, depression; ma, mandible; na, naris; ntm, notched tomial margin; prc, processus coronoideus; prlma, processus lateralis mandibulae; probq, processus orbitalis quadrati; protq, processus oticus quadrati; sb, septal bar. Reprinted from Li et al. (2014) with permission from the American Ornithological Society.

dense forests and the Arctic–Antarctic poles. Some kestrel species show large geographic variation in both morphology and genetics, which led to the recognition of several subspecies. The higher number of species and subspecies near the equator might be due to greater speciation favoured by a more sedentary style of local birds as compared to kestrels at higher latitudes, whose migratory habits limit isolation among populations. There are, however, a number of factors that have likely contributed to the diversification of kestrels, such as physical barriers and geographic isolation (Village, 1990). We currently lack studies that elucidate the roles that different barriers had in driving the diversification of kestrels.



**Figure 1.5** Distribution map of the common kestrel (*Falco tinnunculus*). From BirdLife International and Handbook of the Birds of the World (2017). Reproduced with permission from BirdLife International. A black and white version of this figure will appear in some formats. For the colour version, refer to the plate section.

The common (also known as Eurasian) kestrel is widespread across Europe, Africa and Asia (Figure 1.5), but sporadic observations of free-ranging kestrels have been recorded in the New World (Campbell, 1985; Pranty et al., 2004).

It is classically recognised that there are 11 subspecies of common kestrel (Village, 1990). However, recent molecular analyses led Fuchs et al. (2015) to propose that the subspecies *rupicolus* (Table 1.1) may warrant species status (IOC World Bird List: Gill & Donsker, 2018). The species or subspecies *rupicolus* (illustrated in Figure 1.6b) occurs from north-western Angola and southern Democratic Republic of Congo to southern Tanzania and South Africa. The subspecies belonging to the *tinnunculus* group differ in colouration, body size and distribution (Figures 1.6a,b). The nominal subspecies *tinnunculus* breeds from Europe and north Africa east to Siberia, Bhutan and western China. It is partially migratory, wintering in the regions from south to central Africa, India and south-eastern Asia (Figure 1.6a; Village, 1990; BirdLife International and Handbook of the Birds of the World, 2017). Four subspecies are endemic to the Atlantic islands of Macaronesia. The subspecies *neglectus* inhabits the north Cape Verde islands and the subspecies *alexandri* inhabits the south-east Cape