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Part I

Natural history

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1 *Historiae Animalium*

> There is no evidence that any member of the present genus was known to the ancients. Such a spectacular animal as the mandrill would have impressed observers forcibly and called for comment.
>
> Hill, 1970

Sometimes, a picture truly can convey more than a thousand words. This is certainly the case where the discovery of the mandrill is concerned. For, although vague descriptions of monkeys that might possibly have been mandrills can be found in the ancient literature, there are no accurate accounts of the animal. The earliest unequivocal record of the mandrill's existence is a drawing, which appears in the published works of the sixteenth century Swiss naturalist and prolific encyclopaedist Conrad Gesner. Gesner died of the plague in 1565, when he was just 49 years of age. Yet, during his comparatively short life, he had produced intellectually diverse and monumental works. These included the *Bibliotheca Universalis*, which listed in Latin, Greek and Hebrew 1800 authors together with critiques of their various publications. Gesner's *Mithridates De Differentiis Linguarum* gave an account of all the 130 languages that were then known to scholars. However, it is his *Historiae Animalium* (1551–1558) for which he is best remembered. Four volumes of Gesner's great work on natural history were published in Zurich during his lifetime, and a later German edition, *Das Thierbuch* (1606), contained the drawing of a mandrill that is included here in Figure 1.1.

Gesner thought that this rather bristly and dog-like creature might be some type of hyaena! Yet, for all its limitations, the drawing is clearly an adult male mandrill, as evidenced by its stocky build, stumpy tail, and large rump. The hands and feet are plainly those of a monkey. However, the head is poorly rendered, for although the snout is quite prominent, it is foreshortened and lacks the longitudinal paranasal swellings that are so characteristic of mature male mandrills. Nor is there any indication of the bright bare areas of sexual skin, the beard, crest and thick pelage of this species. For comparative purposes, these features are shown in the modern drawing of a male mandrill included in Figure 1.1.

In fairness to Conrad Gesner, it is most unlikely that he ever had the opportunity to examine a living mandrill; it was only much later that accurate descriptions of it appeared, based upon observations of animals that had been brought back to Europe. The Danish anatomist and physician Thomas Bartholin dissected a male specimen and published an illustrated account of his findings (1671–1672). Pennant included illustrations of mandrills in his *Synopsis of Quadrupeds* (1771) and *History of Quadrupeds*

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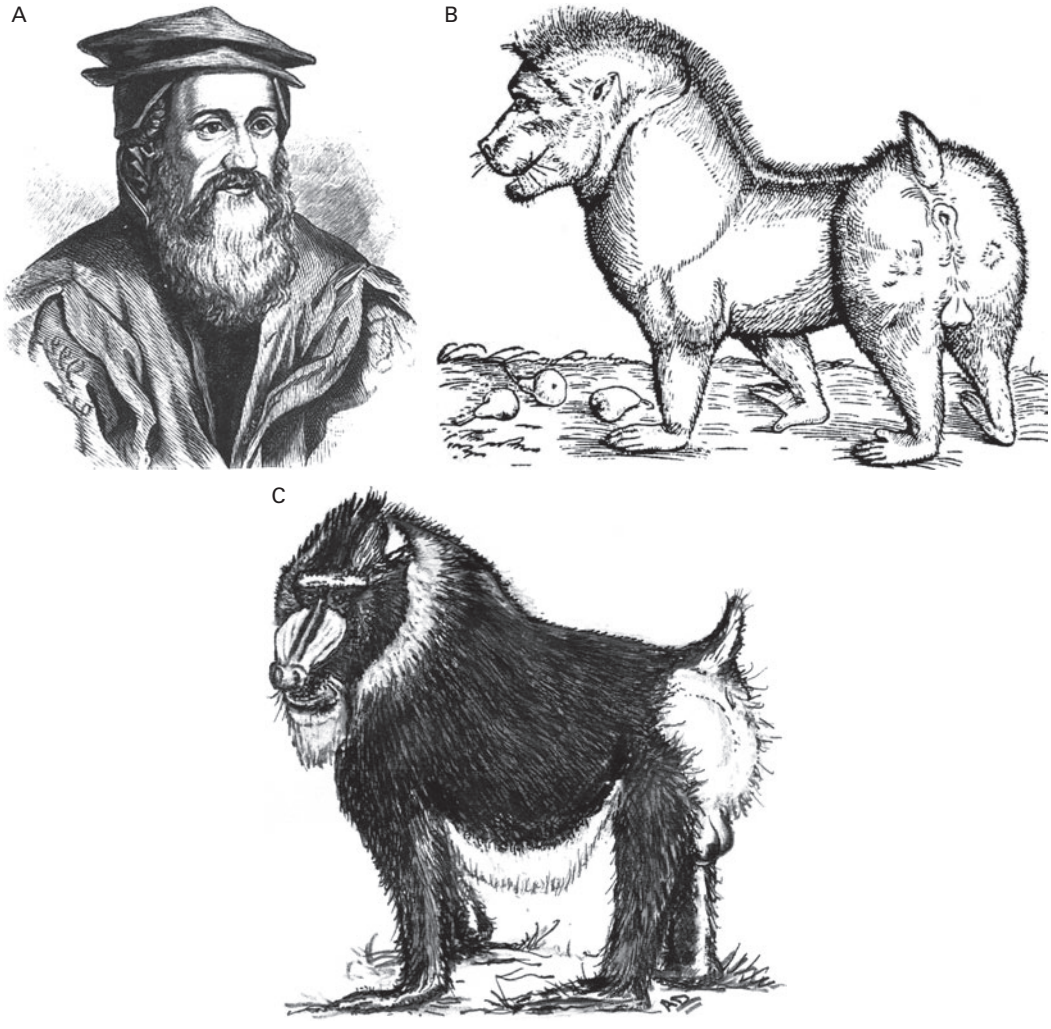

Figure 1.1. Conrad Gesner (1516–1565) (**A**) provided the first published illustration of the mandrill (**B**), as part of his *Historiae Animalium* (1551–1558). A modern drawing of an adult male mandrill (**C**) is included here for comparison with Gesner's illustration, which is taken from the German edition of his work (*Das Thierbuch*, 1606).

(1781), referring to them as 'tufted apes', 'great baboons' and (my particular favourite) 'ribbed-nose baboons'. Buffon (1766) took the opportunity to observe living mandrills in the Paris Menagerie, and so was able to make much more realistic illustrations of both sexes. He was also the first scholar to call this monkey 'the mandrill', perhaps because traders had heard this name applied to the specimens they had acquired in western Africa.

The genus *Mandrillus* (Ritgen, 1824) contains only two species, the mandrill (*M. sphinx*), and the drill (*M. leucophaeus*). Hill (1970) has pointed out that the drill remained unknown to science for much longer than the mandrill. Cuvier (1807, 1833)

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was the first to describe living specimens of the drill, again based upon animals held in the Paris Menagerie. Prior to Cuvier's account, there had been only conflicting reports that a second species of forest baboon might exist in west Africa. The drill resembles the mandrill in its overall proportions, although adult male drills are less massive than male mandrills. Females are much smaller than males in both species. Female drills and mandrills are also quite similar in appearance; a fact that has led and still leads to incorrect identifications and claims that the two species are sympatric in certain areas. The adult male drill is markedly different to the adult male mandrill, however, as its facial skin is predominantly black, in contrast to the red and blue colouration of the mandrill. Drills also have a lighter brown, or more olive-greenish hue to their pelage.

Ever since their discovery, mandrills and drills have been exhibited in menageries and zoos, and their skins and skeletons have accumulated in museum collections around the world. Yet, as we shall see, only in the last 30 years or so has their ecology, behaviour and reproductive biology been subjected to detailed scientific scrutiny. In what follows, I shall deal firstly with the natural history of the mandrill, including its classification and distribution, as well as basic information concerning its anatomy, behaviour and ecology. Then, Part II focuses on reproductive biology, including the results of long-term studies conducted on semi-free ranging mandrills, as well as fieldwork on supergroups in Gabon. Finally, in Part III, the mandrill's evolutionary biology is reviewed and the role played by sexual selection is discussed in detail. The final chapter considers the conservation status of the mandrill and drill, as both these species now face an increasingly uncertain future.

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2 The genus *Mandrillus*: classification and distribution

Mandrills are not baboons

Like all the Old World monkeys, mandrills and drills belong to the Superfamily Cercopithecoidea, which is divisible into two Families; the Colobinae (comprising the African colobus monkeys, Asiatic langurs, leaf monkeys and proboscis monkeys), and the Cercopithecinae (including the guenons, patas monkey, talapoins, macaques, baboons and mangabeys, as well as *Mandrillus* and several other genera). One tribe of the cercopithecine monkeys, the Papionini, comprises the baboons (*Papio*), macaques (*Macaca*), arboreal mangabeys (*Lophocebus*), semi-terrestrial mangabeys (*Cercocebus*), the 'kipunji' (*Rungwecebus*) and the gelada (*Theropithecus*), as well as the genus *Mandrillus* (Table 2.1 and Figure 2.1).

The adaptive radiation of papionin monkeys in Africa and Asia has resulted in the convergent evolution of a number of primarily terrestrial, large and highly sexually dimorphic monkeys, with impressive canine teeth. Because both species of *Mandrillus* are large and superficially baboon-like monkeys, they have traditionally been considered as forest baboons and, as such, they were included in the genus *Papio* (e.g. Stammbach, 1987; Szalay and Delson, 1979). It is only quite recently that these ideas have been challenged and overturned. Similarities between mandrills and baboons are outweighed by many anatomical and genetic differences between the two genera. Comparative studies of mitochondrial DNA (Disotell, 2000; Disotell *et al*., 1992), as well as of skeletal and other traits (Fleagle and McGraw, 1999, 2002; Groves, 2000) have shown that the genus *Mandrillus* is more closely related to the semi-terrestrial mangabeys (*Cercocebus*) than it is to the true baboons.

The arboreal mangabeys (genus *Lophocebus*) are more closely aligned with members of the genus *Papio* (e.g. see Guevara and Steiper, 2014) rather than with *Cercocebus* or *Mandrillus*. These relationships are made clearer by referring to Figure 2.2.

The phylogenetic position of the 'kipunji' (*Rungwecebus kipunji*) is not shown in Figure 2.2, but this rare and little known species was originally assigned to the arboreal mangabeys (genus *Lophocebus*), based upon studies of a single specimen (Jones *et al*., 2005). However, subsequent molecular phylogenetic analyses indicate that the kipunji is probably intermediate between *Lophocebus* and *Papio* (Davenport *et al*., 2006; see also Roberts *et al*., 2009). As such, it is currently placed in its own genus, *Rungwecebus*, which was named in honour of Mt. Rungwe in Southern Tanzania, where the kipunji was discovered.

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Table 2.1. Genera belonging to the Tribe Papionini: numbers of extant species, and sex differences in body weight for selected examples

		Adult body weight (kg)		Body weight ratio
Genus	No. Species	Male	Female	Male/Female
Macaca	21			
M. mulatta		11.0	8.8	1.25
M. nigra		9.89	5.47	1.8
Cercocebus	7			
C. torquatus		8.0	5.5	1.45
C. atys	10.2		5.5	1.85
Mandrillus	2			
M. sphinx		32.21	9.34	3.44
Lophocebus	3			
L. albigena		8.25	6.02	1.37
L. aterrimus		7.84	5.76	1.36
Theropithecus	1			
T. gelada		19.0	11.7	1.6
Papio	5			
P. ursinus		29.8	14.8	2.01
P. hamadryas		16.9	9.9	1.7

The genus *Rungwecebus* is not included in this Table. (Data are from: Dixson, 2012; Smith and Jungers, 1997, and sources cited therein.)

In recognition of the close relationship between *Mandrillus* and the semi-terrestrial mangabeys, Goodman *et al*. (1998) sought to place the mandrill and drill in the same genus as the mangabeys (*Cercocebus*). They did so on the basis that molecular evidence suggests that forms ancestral to *Mandrillus* split from a common ancestor with *Cercocebus* about four million years ago. Goodman *et al*. regarded a time depth of at least seven to eleven million years as being necessary for the recognition of two separate genera, and the *Mandrillus–Cercocebus* split thus fell well outside this time criterion. Yet, it is difficult to understand why it should be necessary for taxa to share a last common ancestor seven to eleven million years ago, rather than four or five million years ago, before a generic separation is justified. Colin Groves (2000) expressed similar concerns, and he also doubted 'whether the world is quite ready for *Cercocebus sphinx* and *Cercocebus leucophaeus*'. In this book, I adopt the position that it is more constructive to avoid causing unnecessary confusion by combining these two genera and radically changing the Latin names of the mandrill and drill.

Recognition of the phylogenetic relationship between *Cercocebus* and *Mandrillus* is important because it helps us to better appreciate the evolutionary affinities of the mandrill and drill, as the descendants of a smaller-bodied and more arboreal ancestor. They share this ancestor with extant mangabeys, and especially those West African species belonging to the *torquatus* species group (*Cercocebus torquatus, C. atys* and *C. lunulatus*). Comparative studies of craniodental morphology indicate that

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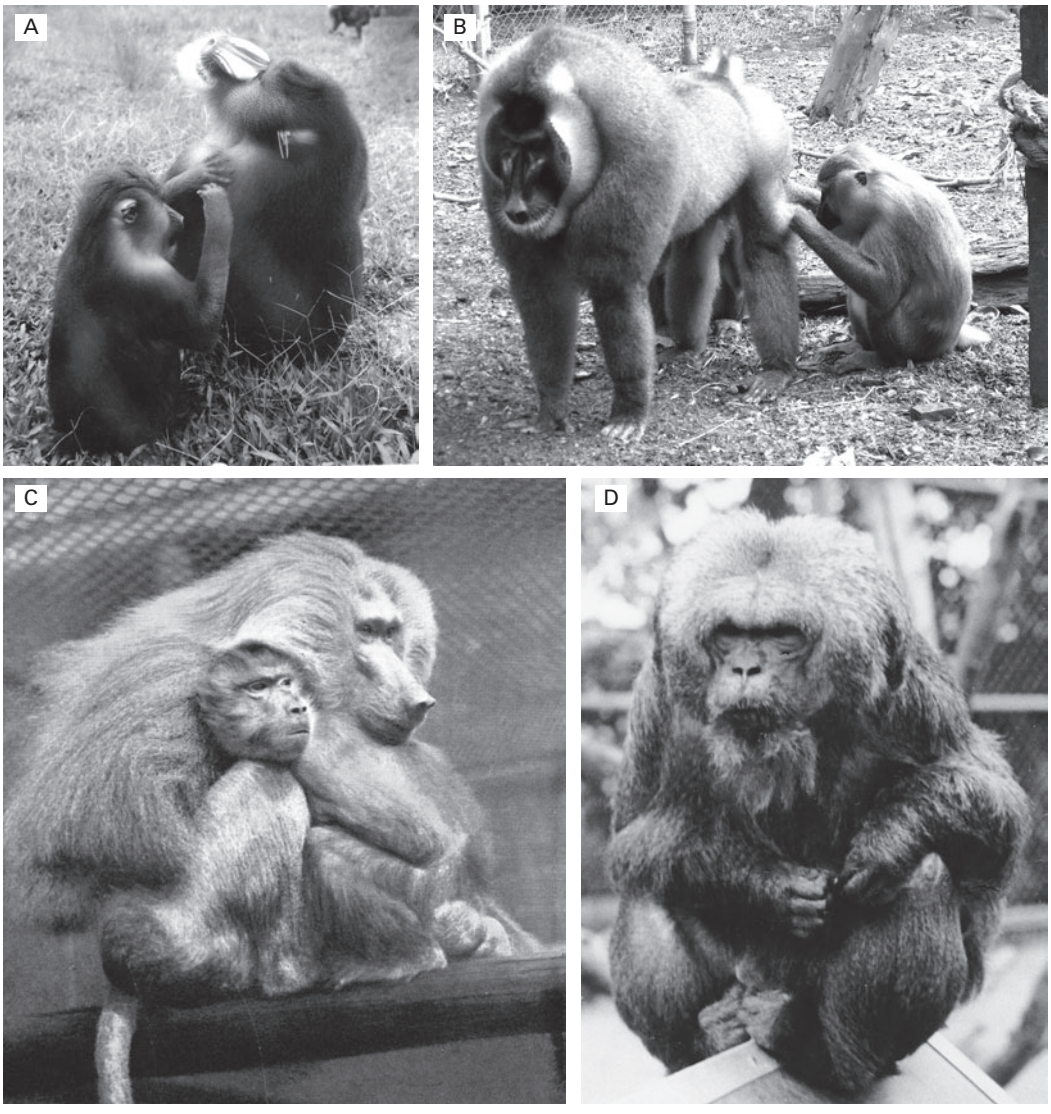

Figure 2.1. **A:** Male and female mandrills (*Mandrillus sphinx*). **B:** Male and female drills (*M.leucophaeus*), as compared to two other large-bodied terrestrial representatives of the Papionini. **C:** Male and female hamadryas baboons (*Papio hamadryas*). **D:** A male stump-tail macaque (*Macaca arctoides*). (Photographs: A and D: Author's collection; B: Dr Kathy Wood; C: F. Bond.)

C. torquatus is likely to represent the basal member of the *Cercocebus* 'clade' (Devreese and Gilbert, 2013).

These advances in our understanding of the classification and origins of the genus *Mandrillus* lead to a discussion of the current distribution of the mandrill and drill, and to a consideration of how changes in climate, and associated contractions and expansions of the African rainforest, may have affected their evolution during the last four to five million years.

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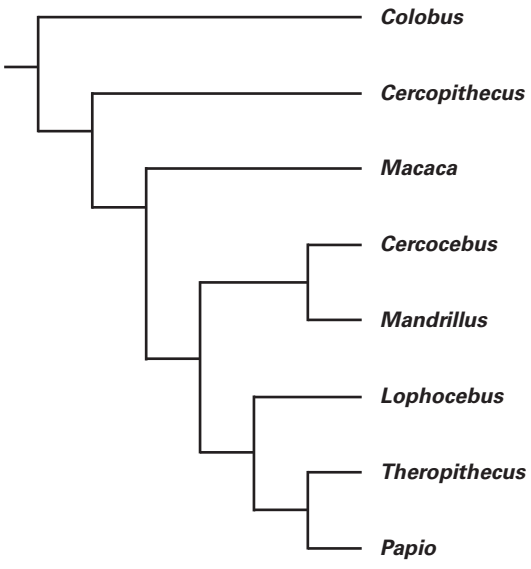

Figure 2.2. Phylogenetic relationships among the Papionini and some other Old World monkey genera. A maximum parsimony tree of mitochondrial cytochrome oxidase subunit II sequences. (Redrawn from Disotell, 2000.)

Historic distribution range and speciation

The distribution ranges of the mandrill and drill in Western Central Africa are shown in Figure 2.3. The term 'historic distribution range' is used advisedly here because rainforest destruction, hunting and other human activities have greatly reduced the ranges of both species, especially so in the case of the drill. This topic will be addressed in the final section of this book, in relation to the conservation status of the mandrill and drill. The distribution map shown in Figure 2.3 is based primarily upon the classic work of Peter Grubb (1973), who assembled compelling evidence that the two *Mandrillus* species are allopatric; the drill occurs in forests to the north of the Sanaga River in Cameroon, whereas the mandrill occurs to the south of this river. In addition to Grubb's data, I have added information derived from more recent reports (as listed in the caption to Figure 2.3); each point on the map refers to well-documented evidence of mandrill or drill presence at a given site. This is, I believe, preferable to showing these species' distributions as shaded areas on the map, as if the animals were uniformly present across the landscape.

The drill is found in S. E. Nigeria (in Cross River State), in Cameroon in forests from the north bank of the Sanaga to the Cross River, and on Bioko Island (Equatorial Guinea). The mandrill's range extends from southern Cameroon (south of the Sanaga River), the mainland of Equatorial Guinea (formerly Rio Muni), throughout Gabon (to the west of the upper reaches of the Ivindo and Ogooué Rivers, which constitute barriers to the eastward dispersal of the species) and in some areas of Congo Brazzaville, in forests to the north of the Congo river.

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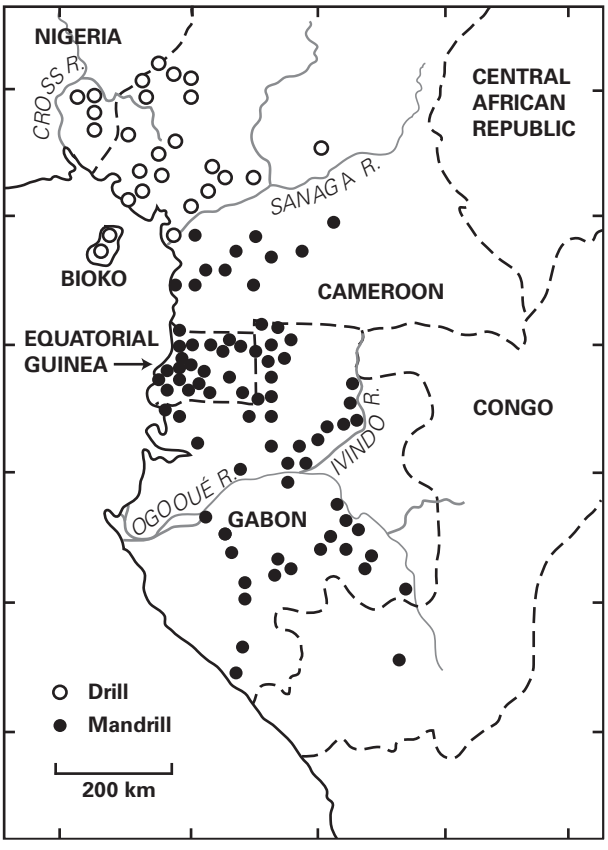

Figure 2.3. The historical distribution range of the mandrill and drill, based upon Grubb's (1973) distribution map, and incorporating additional records from Bossi, 1991; Harrison, 1988; Jouventin, 1975a; Morgan *et al*., 2013; Telfer, 2006, and Wild *et al*., 2005.

Prior to the publication of Grubb's (1973) paper in *Folia Primatologica*, mandrills and drills were considered to be partially sympatric in their distribution, as both species were thought to inhabit forests on each side of the Sanaga River. For example, in Volume 8 of his monograph *Primates: Comparative Anatomy and Taxonomy*, Hill (1970) followed Dobroruka (1966) in recognizing three subspecies of *M. sphinx* and three subspecies of *M. leucophaeus*, as follows:

Mandrillus sphinx sphinx* and *M. leucophaeus mundamensis: north of the Sanaga River.

M. sphinx madarogaster* and *M. leucophaeus leucophaeus: south of the Sanaga River.

M. sphinx insularis* and *M. leucophaeus poensis: on Bioko Island.

It is now clear that mandrills are definitely not found on Bioko Island (which was formerly known as Fernando Po). Specimens collected on the African mainland, but shipped via Bioko, probably gave rise to the mistaken impression that the Island was their point of origin. Only a small population of drills currently survives on Bioko, a

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