



Ape

John Sorenson



Animal series

Ape



Animal

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1 Natural History

Apes belong to the order of Primates, a collection of complex creatures ranging from smaller, little-known prosimians such as aye-ayes, angwantibos, galagos, lemurs and lorises to the engaging and charismatic chimpanzees, orangutans and gorillas, as well as humans. Although not all have all these features, primates are distinguished by relatively large brains, frontally placed eyes with binocular vision and protected by bony sockets, grasping hands and feet with opposable thumbs and large toes, nails rather than claws, small litters and slowly maturing young. Great variation exists in size and many species are sexually dimorphic. Primates are mainly vegetarian, relying on fruit or other plant material, but many also feed on insects; some occasionally prey on larger animals. They occupy various habitats but most are skilled climbers with specially developed locomotion. While smaller prosimians such as tarsiers and lemurs leap through trees and monkeys run along branches, gibbons and orangutans use brachiation, a specialized style of alternating arm swings, to move rapidly from branch to branch. Gorillas, bonobos and chimpanzees move quadrupedally on the palms, fists or knuckles of their hands, while humans habitually walk bipedally. Generally, features such as the anatomical structure of the shoulders that allows brachiation, shortened spine, absence of a tail, a y-5 cusp pattern on the molars and a more developed brain differentiate apes from monkeys, but in popular usage the terms are often interchangeable.

In *The History of Four-footed Beasts* (1607), a bestiary illustrating actual and mythical animals, Edward Topsell reported that apes are terrified of snails.



Like other primates apes communicate vocally, by gestures and by scent and have a variety of social systems and behaviours. Most are gregarious, and even species that tend toward more solitary behaviour are more social where food supplies are abundant. Seasonal distribution of food is a major factor in population densities and movement.

Outside captivity, apes are found in Africa and Asia. Gibbons exist throughout Asia, while orangutans, once distributed from China to Malaysia, now live only in lowland rainforests and swamps in Borneo and Sumatra. African apes, too, live in rain-forests but also occupy other habitats and elevations, including mountains, dry forests and savanna. In all cases their environments are threatened by commercial logging, plantations, mining and human settlement. Even low levels of human forest usage have a severe impact on ape populations and unrestrained exploitation will mean extinction for the apes, along with other animals.

Orangutans are the most solitary apes. Although females contact them when they are ovulating, males seem intolerant of each other's presence and, through their calls, space themselves out in overlapping ranges. But some community behaviour has been noted and these animals coordinate their movements in ways that observers do not fully understand. Gibbons live in monogamous pairs, raising offspring together, and negotiate relationships and territory through loud, prolonged calls and songs. African apes are more social. Gorillas live in groups of up to 50 individuals. These groups usually include one or two mature males, several related junior males and several females and their infants. Young females leave the group and join those of males with whom they mate. Bonobos may congregate in groups of up to 120 individuals and chimpanzees also gather in smaller numbers.



Gibbons, the smallest apes, are known for their agility and their vocal displays.

Unique patterns of learned behaviour – culture – have been noted among different groups of the same species in terms of food processing, production and use of tools and grooming. Tool use, once considered a defining human characteristic, has been

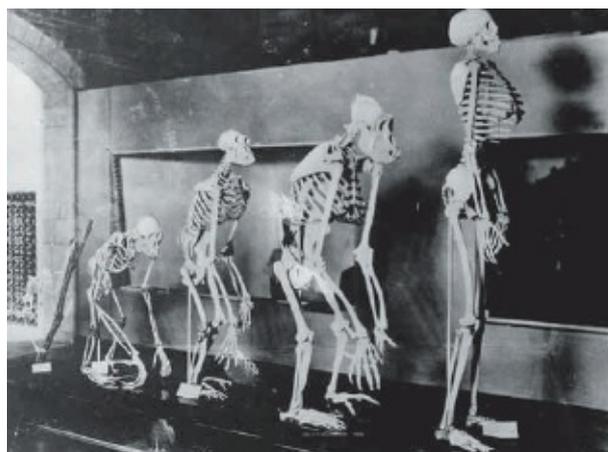
seen among birds and monkeys but is widespread among apes, who use different tools for different purposes and who pass on their knowledge through generations.

Debates continue about the relationship of living apes to fossil discoveries. Many extinct forms are missing from the fossil record. The earliest primate fossils may date to the Paleocene about 65 million years ago (MYA) and recognizably at least from the early Eocene epoch, about 55 MYA. These are small animals, resembling living prosimians. In the past primate evolution was explained as adaptation to arboreal life, suggesting that this encouraged selection of the above-mentioned features, but the absence of these features in other arboreal animals has led to explanations based on diet. Many primates subsist on fruit and flowers and primates may have evolved to pluck these foods from slender terminal branches.

During the Miocene epoch (26–25 MYA), apes emerged as a distinct lineage, and it is assumed that a much greater variety of forms existed than those reflected in the fossil remains. Living forms therefore represent only a fraction of previous diversity. Found in African deposits, the best-known early fossil apes are those categorized as the genus *Proconsul*, arboreal, frugivorous animals lacking tails (as noted, one common characteristic of all living apes). Later in the Miocene, apes dispersed through Eurasia and it is debated whether the last common ancestor of the great apes lived in Africa or Eurasia.

Around 15 MYA gibbons diverged first from the line that has led to the other living apes, followed by orangutans at 11 MYA, then around 6.5 MYA gorillas split from the branch, leading to bonobos, chimpanzees and humans. A 13 million-year-old partial skeleton discovered in Spain in 2004 may represent a primate who lived after the lesser apes diverged but before the great apes began to diversify into the forms we know today. Named *Pierolapithecus catalaunicus*, this animal may have been one of the last common ancestors of all the great apes, including humans. But others question if *Pierolapithecus* was in fact ancestral to orangutans or a creature in the evolutionary line of African apes and humans. Another fossil species, *Nakalipithecus nakayama*, discovered in northern Kenya in 2007, has been suggested as a candidate for the last common ancestor of bonobos, chimpanzees, gorillas and humans. Another 2007 discovery, in Ethiopia, of some 10 million-year-old teeth belonging to *Chororapithecus abyssinicus*, possibly an early form of gorilla, raised new questions about timelines of ape evolution. Some thought the 6–7 million-year-old Toumai skull discovered in Chad in 2001 represented the oldest fossil of a member of the human family, but others maintained it was one of many species of human-like beings that existed at the same time, or an ancestral form of contemporary gorillas. Until very recently research suggested that bonobos, chimpanzees and humans diverged around 5 MYA in Africa, with bonobos and chimpanzees splitting between 1 and 2 MYA. However, new genetic evidence suggests that chimpanzee and human lineages diverged more recently than previously believed and that interbreeding could have occurred between these lines for thousands or even millions of years after the original divergence, producing multiple hybrid forms.

Comparisons of the skeletons of gibbon,
orangutan, chimpanzee and man.



Contemporary humans are distinguished from our nearest ape relatives by a larger brain, habitual bipedalism and differences in dentition. Despite much determined effort to deny it, our proximity to other apes is readily apparent in shared morphological features and is supported by evidence from molecular biology and genetics. Of all living animals, the great apes are closest to us. We possess a shared evolutionary history, a close biochemical and genetic composition, as well as similar anatomy, appearance, cognition and behaviour. These similarities are so evident that many scientists have concluded it is an error, based on our own vanity, to classify humans separately: either we should include apes as members of our own classification or consider ourselves a type of chimpanzee. Geneticists have estimated that our similarity with chimpanzees and bonobos is over 98 per cent,¹ meaning that we are closer to these animals than either is to gorillas or orangutans. However, Roy Britten at the California Institute of Technology challenges this, arguing that measurements of indels (insertions or deletions of DNA sections) result in similarities of only about 95 per cent.² Based on 2003 studies, Morris Goodman of Wayne State University found humans and chimpanzees were 99.4 per cent identical in functionally important DNA, which codes for proteins.³ Goodman argued that both humans and chimpanzees should occupy the genus *Homo*.

Insisting that we should be classified separately from other closely related species, some taxonomists limit the family *Hominidae* to humans and their now-extinct fossil relatives and place other great apes into a separate family, *Pongidae*. However, most taxonomists now divide all living apes into two families. *Hominidae* includes seven living species: eastern lowland gorillas (*Gorilla berengi*), western lowland gorillas (*G. gorilla*), orangutans of Sumatra (*Pongo abelii*) and Borneo (*P. pygmaeus*), chimpanzees (*Pan troglodytes*), bonobos (*P. paniscus*) and humans (*Homo sapiens*). The other family, *Hylobatidae*, includes twelve species of gibbons. Many think bonobos, chimpanzees, gorillas and human beings should be classed in a single genus, *Homo*.

CHIMPANZEES

Chimpanzees are generally categorized into four sub-species: *Pan troglodytes*

troglodytes, *P.t. verus*, *P.t. schweinfurthii*, *P.t. vellerosus*. Chimpanzees are the most abundant and adaptable apes, occupying various habitats from lowland rainforests and swamps to dry forests and savannas. Their diet is also varied. They mainly consume fruit and plant material and were once thought to be vegetarian but are now understood to be omnivores who eat insects and small animals, as well as larger ones such as pigs and monkeys. While hunting provides protein, it is also energy-consuming and sometimes dangerous. Some believe hunting and sharing meat were important processes in human evolution, linked with development of bigger brains and social behaviour.

Chimpanzees are intelligent social animals who use tools and manipulate objects.



Chimpanzees sometimes form hunting parties and share the flesh of animals they kill. Most researchers assumed that adult males most often engaged in hunting and that hunting and sharing meat provided males, in particular, with a means to maintain social bonds and status. However, recent observations suggest that adolescent females and young chimpanzees in general are actually the most frequent hunters. In Senegal anthropologists Jill Pruetz and Paco Bertolani observed chimpanzees fashioning spears by breaking, stripping and sharpening branches and then using them to hunt; they suggest that adult males were the last to adopt innovations in tool manufacture and use.⁴

Chimpanzees live in groups, usually numbering around 30 individuals, although much larger bands have been seen. They occupy home ranges that are patrolled by males. These societies are philopatric, meaning that males stay in their natal group while females join those of their mates. Relationships between males are significant and intense, developed by grooming and formation of political alliances, while female social interactions seem more limited. Dominance and aggression characterize chimpanzee societies. In 1974, during fieldwork at Gombe in Tanzania, Jane Goodall observed chimpanzees not only hunting and killing other animals but also sometimes conducting murderous attacks on other groups of their own species. Lethal assaults within groups are less common but infanticide has been observed. Behaviour and group size are affected by ecological conditions: chimpanzees are characterized by a fission–fusion pattern in which groups temporarily split or merge within their territories, practices usually assumed to be related to distribution of food resources or

threats from predators.



Although closely related to both humans and chimpanzees, bonobos are known for their peaceful, egalitarian, matriarchal societies.

BONOBOS

Only recently recognized as a distinct species, bonobos are closely related to chimpanzees and were formerly called ‘pygmy chimpanzees’. Although the exact population is unknown, they are fewer in number and limited geographically to the Democratic Republic of Congo, where their range of forests and grasslands is limited by river systems. They have become well known only recently: although mentioned in nineteenth-century reports, bonobos were first described scientifically in 1929 and the first field studies were undertaken in the 1970s, most extensively by Japanese primatologist Takayoshi Kano. However, fieldwork was disrupted by war throughout the 1990s up to a peace agreement in 2002, followed by outbursts of violence that have prevented serious study.

Bonobos eat a variety of plant material but are mainly frugivorous. Although they have been seen eating small animals, such as flying squirrels and duikers, hunting does not appear to play as significant a role for them as for chimpanzees. Whereas chimpanzees have been seen to hunt monkeys, bonobos more often interact with them; bonobos have killed monkeys accidentally through rough play but seem less inclined to eat them.

Bonobos form larger groups than chimpanzees, although they maintain the same shifting fission–fusion behaviour. However, bonobo societies seem far more relaxed. Bonobos get along better within their own groups and with neighbouring groups so they spend more time in larger units. Despite their close genetic relationship with chimpanzees, their behaviour is strikingly different. Bonobos are more cooperative and peaceful, showing less aggression and less territorial defence; when food resources are abundant, neighbouring groups forage in proximity. Whereas chimpanzees react violently to such contact and engage in primitive forms of warfare, bonobos often appear excited to meet neighbours and do not engage in inter-communal raids. Unlike chimpanzee societies, both captive and free, in which much lethal intra-species aggression has been observed, such attacks seem rare among bonobos.

Although both chimpanzees and bonobos are philopatric, gender relations are very

different. In contrast to patterns of male dominance noted among primates, bonobo social systems are structured around coalitions of females who control and share food and influence males. Whereas chimpanzee society is structured by male hierarchies, female bonobos have equal status with males and form alliances to dominate them. Mother–son bonds are strong and a male’s status is linked with that of his mother, whose own status is largely age-determined. Primatologist Frans de Waal suggests that primatologists’ own cultural sensibilities led them to deny the reality of female dominance in bonobo societies and acknowledges that he initially dismissed his own observations of this behaviour.⁵

Bonobos differ from chimpanzees physically and behaviourally. They exhibit less sexual dimorphism, are less aggressive and negotiate relationships by sexual contact rather than through direct forms of dominance. Sexual activity is extensive and most sexual activity is not directed towards reproduction. Intercourse and mutual genital rubbing, along with a wide variety of other sexual contact, are frequent, often initiated by females, and these sexual contacts are believed to build alliances, reduce tension, negotiate food sharing, achieve reconciliations and contribute to a more egalitarian society. Although high-status males may be more successful in mating, they do not monopolize females and there is no aggressive male competition over females; instead, relations between the sexes are friendly. Infanticide, common among some other primates, has not been reported among bonobos. Some suggest that this is because of the ambiguity of paternity in their societies.

GORILLAS

Gorillas are classified into two species, eastern (*Gorilla berengei*) and western (*G. gorilla*). These are further divided into two sub-species: eastern lowland (*G.b. graueri*) and mountain gorilla (*G.b. berengei*) and western lowland (*G.g. gorilla*) and Cross River (*G.g. diehli*). The two species are quite similar and were formerly considered sub-species but DNA analysis suggests a divergence about 2 MYA. Genetically, they are very close to humans.

Gorillas are extremely impressive, very large, with hairless black faces and a sagittal crest along the skull; mature males have silver hair on their backs. They are sexually dimorphic, with adult males weighing 200 kg, about twice the size of females. Gorillas are vegetarian, subsisting on leaves, shoots and fruit, as well as bark and twigs. Because of this diet, gorillas must eat a great deal and rest while digesting. Rather than maintaining a limited range, gorillas fully exploit an area and then travel on, returning only after it has recovered. Movement is linked to availability of food, as well as avoidance of humans and other predators. Gorillas typically move on all fours, using a distinctive knuckle-walking motion. During bursts of display, they may run bipedally for short distances and beat their chests with their hands.

Gorillas form smaller groups than chimpanzees or bonobos, usually of fewer than fifteen, but occasionally twice as many individuals, consisting of a dominant silverback male, several females, their offspring and some junior males. Young males may form groups but it is more common for a male to leave his natal group, taking some females with him, and start his own unit. A female sometimes transfers from one

group to another but if she has offspring with her they may be killed by another male who wants to mate with her.

Gorillas communicate by a variety of vocalizations, such as alarm calls and barks to warn of specific dangers but also employ frequent humming or rumbling that is answered by others. These sounds may be used to negotiate space, avoid confrontations or offer appeasements but also may indicate intentions about travel. Gorillas are intelligent animals and tool use has been seen recently. In 2005 Thomas Breuer of the Wildlife Conservation Society reported what he claimed to be the first observation of 'wild' gorillas using tools.⁶ He observed a gorilla using a stick to determine the depth of a stream she was crossing and another gorilla using a rock to break open palm nuts. Similar use of stones to crack nuts has been observed in captive gorillas. Although gorillas had been previously observed, captured for zoos or killed as museum specimens, few scientific field studies have been done until recently.



Mugaruka, one-handed silverback in ParcNational Kahuzi-Biega, DRC.

ORANGUTANS

Orangutans diverged from the line of African apes and humans about 11 MYA and their ancestral forms spread throughout Asia. The only great ape existing outside Africa, they are found now only in Borneo and Sumatra, in lineages that diverged 1–2 MYA. There are three sub-species of the Borneo orangutan, *Pongo pygmaeus*: *P.p. pygmaeus*, found in western Kalimantan and Sarawak; *P.p. wurmbii*, the largest of the orangutans, found in western and central Kalimantan; and the smallest, found in Sabah and eastern Kalimantan, *P.p. morio*. There are no sub-species of the Sumatra orangutan. Orangutans live about 45 years in nature, inhabiting overlapping ranges. They are

mainly arboreal but occasionally walk bipedally on the ground. Their diet consists of leaves, bark, seeds, shoots, honey and insects and they use a variety of tools to get their food. Unlike other great apes, orangutans live in loose communities of genetically related females and adult males with whom they mate. However, they sometimes travel together for short periods and cluster where fruit is plentiful. Females reach puberty at ten years of age, give birth at fifteen and have pregnancies lasting eight and a half months. Bonds between mothers and infants are especially strong. Mothers suckle their infants for three years but carry them beyond that age and children remain with their mothers until they are about seven. Females bear infants only once every seven to nine years, so they can produce at most four offspring over their lifetime; this means any disruption in reproduction can have significant effects.



Head of an orangutan, 1895.

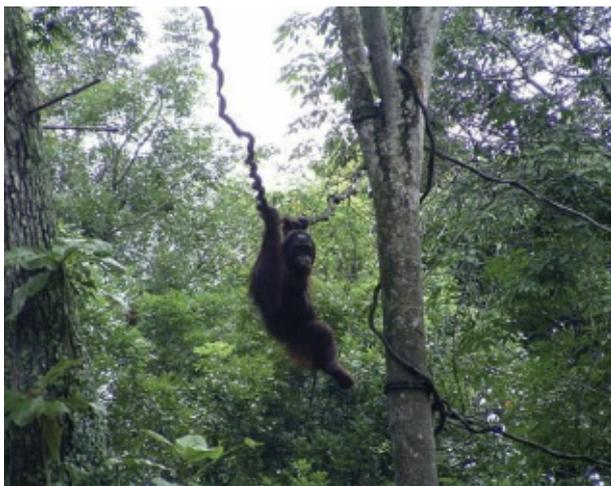
Orangutans are among the most solitary and sexually dimorphic of the apes. Only a few live in captivity and their essentially arboreal lifestyle and relatively solitary nature means that orangutans have been studied less than other apes who are more gregarious and ground-dwelling and thus more accessible.

Like gorillas, orangutans have a striking appearance: large animals with expressive faces, covered in reddish hair, with elongated arms that allow them to swing rapidly through the trees, where they spend most of their time. Borneo orangutans are darker and heavier, with a large, hanging throat sac. Males are larger than females and are subject to a curious process known as bimaturation: some develop large cheekpads (flanges), while in others this process is delayed for many years. This may be related to testosterone levels and status but the process is not fully understood. Flanged males may have reproductive advantages because of their dominant status, linked to access to food and receptive females, but flanged males are much more aggressive, meaning that they also face higher risks of injury and individuals cannot sustain this condition for more than a few years. Afterwards they pass into another stage in which their flanges shrivel and they become less aggressive. Flanged males make loud calls to

alert others of their presence and these calls may affect levels of testosterone production in other males. Females prefer mating with flanged males and typically initiate this after being attracted by the male's calls but they are sometimes forced by unflanged males. Generally, male and female adult orangutans lead separate lives, with no lasting relationships or paternal bonds with offspring. There are long intervals between births, with reproduction about every eight years, perhaps the lowest reproduction rate among mammals. Mothers carry their infants for years, providing them with much attention and care.



Samuel Howitt, drawing of a young orangutan, around 1817; watercolour over pencil.



Orangutan on rope at Singapore Zoo. Zoos face difficulties in providing adequate space for such large arboreal creatures.



Orangutans demonstrate close bonds between mothers and infants.

Females stay close to where they were born and maintain relationships with other females in that area, while males are more solitary and occupy wider ranges. Although orangutans do not defend their territory, they have stable, overlapping ranges in which males do not tolerate each other but seek to spread themselves out. Mothers and infants maintain a close bond but this weakens over time as offspring mature. These behaviours result in a loose community with subtle processes of coordination.

Mainly vegetarian, orangutans eat various plant materials but prefer fruit, and food supplies affect social behaviour. Fruit is more abundant in Sumatra, allowing for more social interaction among animals. In Borneo fruit supplies are less regular and orangutans tend to gorge on fruit when it is available and range in search of other foods when fruit is scarce. Orangutans maintain mental maps of food sources and remember routes through the forest to reach them. When fruit is unavailable they exploit other less-nutritious plant resources. Although they consume insects, orangutans have not been seen to eat other animals regularly. Reproduction and development seem directly linked with their environment. To cope with insects, trees have evolved a pattern known as mast fruiting, in which all bear fruit simultaneously, every four years. Female orangutan hormone levels are elevated in accord with fruit cycles and male development also may be affected. This means that orangutans conceive during periods of plentiful nutritious food, providing them with energy during pregnancy and ensuring good physical condition for birth and lactation.

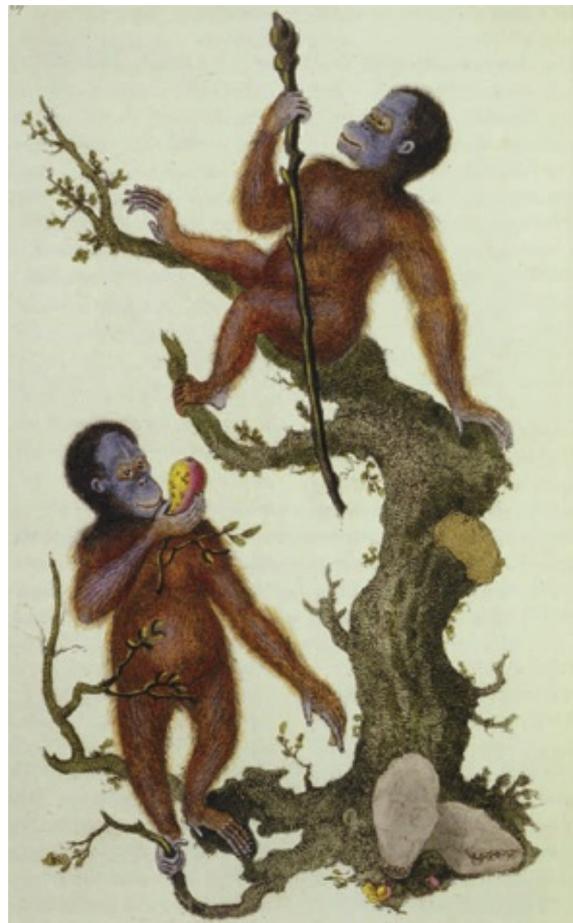
Tool use is seen among orangutans, such as the use of large leaves for umbrellas or as protection when eating fruit from thorny plants. Particularly in Sumatra, orangutans are seen employing tools to obtain food, such as using sticks to probe and extract food from holes in trees, to dig out seeds or scrape thorns from fruit. Orangutans are renowned for using medicinal plants.

Thomas Landseer, etching of orangutan for Edward Griffith's *The Animal Kingdom* . . . (1827), translated from George Cuvier's *Le Règne animal distribué d'après son organisation* (1817). From his



observations of a young female orangutan, Cuvier concluded her senses were comparable to humans' and that she had a sense of the future.

Anonymous hand-coloured etching of an orangutan, from Edward Donovan, *The Naturalist's Repository* (1824).



In addition to using natural objects, orangutans sometimes adopt human tools for their own use. Primatologist Birute Gal dikas reports orangutans using dugout canoes from her camp in Borneo and describes one female using a tube of ointment to treat her son's blind eye while refusing to let others touch the tube.⁷ Captive orangutans quickly adopt human-type tool use and pass this learned behaviour on to others, so it is assumed they have the capacity to use tools but that limited social interaction in their natural habitat restricts development of these activities. Reviewing decades of data, primatologists identified various behaviours, many involving tool use, that seem to

have been culturally transmitted; they concluded that culture was established among the great apes 14 MYA, when the ancestor of the orangutans and the African apes lived. More cultural variation exists where orangutans have more social contacts and opportunities to learn from each other. Again, evidence demonstrates that culture is not a uniquely human trait as formerly supposed. Primatologist Carel van Schaik theorizes that greater sociability not only allowed more efficient food acquisition but that cooperation conferred evolutionary advantages and influenced the success of early humans. He thinks orangutans' arboreal lifestyle, with less risk from predators, allowed them to develop far greater intelligence and culture than many believe.⁸ James Lee at Harvard University suggests that of all non-human great apes, orangutans have developed the greatest problem-solving abilities.⁹ However, their arguments are not widely accepted among primatologists.



'Simia', from H.G.L. Reichenbach, *Die vollständigste Naturgeschichte der Affen . . .* (1862–3).

GIBBONS

Gibbons constitute the lesser apes, meaning that they are generally smaller, but they could also be considered the lesser-known apes, since vastly more attention is given to their larger relatives. The gibbon lineage diverged from other apes about 15 MYA. Gibbons are found throughout south-east Asia as well as in Borneo, Java, Sumatra and other islands. They are classified into four genera and twelve species, with several