Links between the discovery of primates and anatomical comparisons with humans, the chain of being, our place in nature, and racism

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REVIEW

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Links between the discovery of primates and anatomical comparisons with humans, the chain of being, our place in nature, and racism

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Abstract

I focus on the crucial links between the discovery of nonhuman primates by Westerners, discussions on our place in nature, the chain of being, racism, and the history of primate comparative anatomy and of so-called "anatomical human racial studies." Strikingly, for more than a millennium humans knew more about the internal anatomy of a single monkey species than about that of their own bodies. This is because Galen used monkeys to infer human anatomy, in line with the human-animal continuity implied by the Greek notion of *scala naturae*. With the rise of Christianity, nonhuman primates were increasingly seen in a negative way. A more positive view emerged in the 14th century when nonhuman primates were directly studied/seen by Europeans, culminating in Tyson's 1699 work showing that chimps share more gross anatomical similarities with humans than with monkeys. However, the discomfort caused by this human-chimp similarity then led to a new idea of animal-human discontinuity, now related not to anatomy but to "civilization": between Europeans vs. non-Europeans + other primates. Moreover, Linnaeus' *Systema Naturae* and the emergence of "anatomical racial studies" influenced by Camper's craniology then led to even more extreme ideas, such as the notion that Europeans were both mentally and morphologically "ideal." Unfortunately the biased and often incorrect "results" of such studies, combined with ideas based on Darwin's "struggle for survival", became crucial in propaganda that lead to the rise of eugenics in the end of the 19th/first half of 20th centuries and that culminated in Nazism. Since the 1950s there has been an emphasis on the continuity/unity between all human groups and other primates, in great part influenced by what happened during World War 2. Reviews such as this one are, therefore, particularly necessary to illuminate and guard against attitudes against "the Other" and racist ideologies that are re-emerging in modern political discourse across the globe.

KEYWORDS

apes, colonialism, Galen, monkeys, morphology, primate evolution, race, scala naturae, struggle for survival, Tyson

1 | INTRODUCTION

Some works, including a few monographs, have discussed the links between the discovery of nonhuman primates by Westerners and discussions on our place in nature, and the notion of a chain of being or *scala naturae* ("ladder of nature" from "lower forms" to humans, which supposedly represent the culmination point of a "progression" toward perfection) (e.g., Barsanti, 2009; Bowler, 1987; Corbey, 2005; Corbey & Theunissen, 1995; Delisle, 2007; Engelmeier, 2016; Groves, 2008; Hoßfeld, 2016; Kuklick, 2008; Martin, 1984; Schmutz, 2000; Sommer, 2015). However, those publications do not focus specifically on the links between these subjects and the history of primate comparative anatomy. Most often, they instead mainly focus on a single anatomical work that is in fact key for discussions on these subjects—Tyson's

I believe our heavenly Father invented man because he was disappointed in the monkey

(Mark Twain)

TABLE 1 Historical background for the facts and ideas discussed in the present article

Aristotle (384–322 BC)	Published several works about the anatomy of several animals, and had a profound influence in biologists since then, including the Greek notion of a Scala Naturae ("ladder of nature").
Galen (130–210 AD)	Published several works that were then used for more than a thousand years as the basis of human anatomy, although in reality his descriptions were mainly based on dissections of nonhuman animals, particularly monkeys.
Andreas Vesalius (1514–1564 AD)	His most famous work, the *Fabrica*, was the first detailed anatomical report of humans based on actual human dissections, and done specifically to set the record straight (compared with Galen's descriptions of other animals as a base for human anatomy) and provide accurate information for humans.
Hiernonymus Fabricius (1537–1619 AD) and Julius Casserius (1552–1616)	Fabricius and his student Casserius (e.g., his famous work of 1600–1601) were a crucial component in and catalyzer for the numerous works published on the 17th century on comparative anatomy, which truly started as a discipline in about 1600 with works from these and other Renaissance scholars.
Edward Tyson (1651–1708 AD)	Published the first detailed anatomical description, including of internal soft tissues such as muscles, of an ape, specifically a chimpanzee, in 1699.
Carl Linnaeus (1707–1778 AD)	Linnaeus' 1735 *Systema Naturae* is an example of the impact of Tyson's 1699 monograph. He classified humans and apes in a the same (*Homo*) species, but at the same time he classified modern humans in different subgroups, thus suggesting an apparent discontinuity between humans themselves.
Petrus Camper (1722–1789 AD)	In 1778 and 1782 he provided the first detailed anatomical descriptions of orangutans (*Pongo*), and he is considered to be one of of the "fathers" of "anatomical racial studies" and of "craniology," which then led to extreme ideas such as those defending that Europeans were both mentally and morphologically "ideal."
Charles Darwin (1809–1882 AD)	Charles Darwin is mainly known by his 1859 book the *Origin of Species* (1859) as well as for other works, in particular the *Descent of Man* (1871), where he discusses extensively the origin of humans from apes.
Stephen Jay Gould (1941–2002 AD)	Gould was crucial for the exposure of the scientific flaws and biases of the "anatomical racial studies" published mainly in the 19th and first decades of the 20th centuries, and of the eugenic ideas that were so influential in the decades before World War 2, particularly in his 1981 book *The mismeasure of man*.
Dian Fossey (1932–1985 AD), Birute Galdikas (1946 AD-today) and Jane Goodall (1934 AD-today)	Fossey, Galdikas and Goodall, influenced themselves probably by the reflection of the changes that begun mainly after World War 2, were crucial for the strikingly fast changes that have occurred since then, in particular about the mental proximity between humans and apes. These changes have recently led some scholars to argue that humans and chimpanzees should be included in a same genus.

(1699) description of a common chimp—but that is actually only part of a much more complex and less known story. For instance, in his highly influential book *Primate Functional Morphology and Evolution*, Tuttle (1975) stated that Tyson provided the first detailed anatomical description of a nonhuman primate. However, the first detailed gross anatomical studies of nonhuman primates date further back, to the Greeks, being in reality even older than the first detailed anatomical studies of humans. This is because the anatomical descriptions of Galen (129–200 AD) that were used for centuries as the "basis of human anatomy" were mainly based on dissection of the "Barbary ape," which is in reality an Old World monkey with a vestigial tail (*Macaca sylvanus*) (Persaud, 1984; Persaud, Loukas, & Tubbs, 2014). Moreover, previous publications do also not focus specifically on how detailed gross anatomical comparisons—and not merely external comparisons—were crucial for the invention of the concepts of race in humans, in the 18th, 19th, and 20th centuries. Racism—differential treatment or regard of people based on, for example, morphological criteria—is in fact profoundly related to our tendency to explain nature using teleological and often hierarchical narratives and in particular to the notion of a great chain of being (Gould, 1981). The aim of this work is, therefore, to provide a succinct but more accurate account on the links between the history of comparative anatomy—including of nonhuman primates, of different human groups, and comparisons between humans and other primates—and on the discussions about our place in nature, the notion of chain of being, and racism.

2 | FROM THE FIRST DETAILED ANATOMICAL DESCRIPTION OF NONHUMAN PRIMATES (GALEN) TO TYSON

Although this is not often acknowledged in the literature, for more than a millennium, humans actually knew more about the internal anatomy of a single monkey species than about that of their own bodies (see Table 1, which briefly summarizes the history of comparative primate anatomy as discussed in the present article). This is because the first detailed gross anatomical studies of nonhuman primates date back to the Greeks, who also developed the notion of *scala naturae*, or "ladder of nature," usually known as the "great chain of being," as will be explained below. The culture of human dissection developed mainly in the Christian West, in contrast to the Greco-Roman culture of the dead body, in which the human corpse was often considered as impure (Park, 2006). In fact, Galen based his descriptions of human anatomy on dissections of animals such as sheep, oxen, pigs, dogs, bears, and particularly the "Barbary ape" (*Macaca sylvanus*) as explained above (Cole, 1975; Singer, 1959). It is remarkable that, for a millennium (before Vesalius: see below), few authors recognized this fact. Whereas the anatomy of this monkey species is roughly similar to that of humans, there are still numerous specific anatomical differences between them, principally concerning soft tissues such as muscles (reviewed in Diogo & Wood, 2011, 2012, 2013, 2016).

My colleagues and I have recently published detailed tables comparing, for each muscle, the descriptions of Galen versus the current knowledge on human anatomy (Alghamdi, Ziermann, & Diogo, 2017). Therefore, I will only provide here a few emblematic examples illustrating these differences and also the very detailed way in which Galen described *Macaca sylvanus*. For instance, Galen carefully described each and every *M. sylvanus* flexor forelimb muscle, but because this species lacks a flexor pollicis longus and an extensor pollicis brevis he incorrectly extrapolated that humans did not have these muscles. These two muscles were particularly important for human evolutionary history (Diogo & Abdala, 2010; Diogo, Richmond, & Wood, 2012; Diogo et al., 2016). In addition, in a few instances Galen inaccurately described some of those features of macaques that are in fact present in humans, therefore contributing to further erroneous ideas about what then became to be accepted by most as the "standard human anatomy." For example, Galen did not recognize the extensor carpi radialis brevis and longus as separate muscles in the monkeys he dissected, despite the fact that these two muscles are present in monkeys and humans alike (Alghamdi et al., 2017).

More known to the general public are Galen's descriptions of skeletal elements that are also clearly based on observations of macaques and other animals and that do not apply at all to humans, for example his descriptions of separated left and right lower jaws and of premaxillae. As recently reviewed in Alghamdi et al. (2017), "these errors had crucial repercussions for anatomy in particular, and biology and science in general, because Galen so impressed the people of his time and of succeeding ages that for centuries his works were regarded as almost infallible." This reverence for Galen is "partially related to the fact that, although he remained a pagan, he believed in one God and developed the idea that every organ in the human body was created by a God in the best possible form and for its perfect use, an idea that fitted in well with that of Christianity" (Alghamdi et al., 2017; see also Cunningham, 1997; Mayr, 1976). In reality only very few pre-Vesalius authors—including some Muslim scholars (Alghamdi et al., 2017)—realized and/or were brave enough to state that Galen's descriptions did not match human anatomy. Vesalius later dissected monkeys and conclusively showed that the descriptions of Galen were mainly based on monkey anatomy (Cole, 1975; Lagerkvist, 2005). Still, the *Fabrica* of Vesalius (1543) is often seen by historians as a "corrected and expanded version" of the *Corpus Galenicum* (Cole, 1975, p. 42), a view that is only partially correct. This is because the *Corpus Galenicum* is the first detailed anatomical description of nonhuman primates while the *Fabrica* is the first detailed anatomical report of humans based on actual human dissections, and done specifically to set the record straight and provide accurate information concerning humans, despite the fact that Vesalius was a Galenist nonetheless and that he made some errors of his own (Cole, 1975; Persaud et al., 2014).

For the purpose of the present work, an important question is: why did Galen extrapolate that the anatomical features he saw in his dissections of *Macaca sylvanus* would apply to humans, when faced with the problems concerning actually undertaking human dissections that were typical of his epoch? The answer is that he considered that some monkeys are essentially similar, in the inside, to us (e.g., Lagerkvist, 2005), a view in line with the human-animal continuity implied by the notion of the "great chain of being," or *scala naturae* ("ladder of being"). In his treatise *On Anatomical Procedure*, Galen wrote: "of all other animals, monkeys are most like humans in viscera, muscles, arteries, veins, and nerves . . . because of this they walk on two legs and use their forelimbs as hands . . . the more human sort have a nearly erect posture" (Groves, 2008, pp. 16–17). As explained in detail by Lovejoy (1936), the notion of *scala naturae* dates back to Plato (*c.*428–348 BC), and was then further developed by Aristotle (385–323BC) and other Greek naturalists and philosophers, being a crucial aspect of the Greco-Roman way of seeing our place in nature by Galen's time (*c.*129–210AD).

Aristotle did not hold that all organisms can be arranged in one ascending sequence of forms, but he introduced the idea of continuity that was destined to fuse with the Platonic doctrine of the necessary "fullness" of the world. He stated, for instance that "nature passes so gradually from the inanimate to the animate that their continuity renders the boundary between them indistinguishable . . . and the transition from plants to animals is continuous" (Lovejoy, 1936, pp. 55–56). Specifically about primates, Aristotle noted that it cannot be said that mammals are either quadrupeds or bipeds, the latter being solely represented by humans, for "participating in the nature of both man and quadrupeds is the ape" belonging to neither group or both (Lovejoy, 1936, p. 57) (N.B., until the 17th–18th centuries the name "ape" mainly referred to monkeys). In particular, the hierarchical arrangement of all organisms in Aristotle's *De Anima* paved the way for later naturalists and philosophers to arrange them in a single graded scala naturae leading to "perfection." This is because Aristotle referred to "powers of soul" from the nutritive, typical of plants, to the rational, characteristic of "man, and possibly another kind superior to his," each higher order possessing all the powers of those below it in the scale, and an additional differentiating one of its own (Lovejoy, 1936, p. 59).

The notion of scala naturae has been extremely influential in the history of religion, philosophy, and sciences since then, being applied in many different ways during the last two millennia (e.g., Leroi, 2014; Reiss, 2009). For instance, in the middle ages and the centuries that followed there were various philosophical conflicts about this notion. Although originally implying animal-human continuity, as clearly emphasized in the terms "chain or ladder of being," many medieval authors defended that humans were essentially different from animals. They argued that humans were made "in the image of God," and could, therefore, use all nonhuman organisms—including primates—as they pleased. An example is Francis Bacon's 1609 *De Sapientia Veterum*, which stated: "man . . . may be regarded as the centre of the world; insomuch that if man were taken away from the world, the rest would seem to be all astray, without aim or purpose . . . and leading to nothing . . . for the whole world works together in the service of man" (Lovejoy, 1936, p. 187).

This view was beautifully illustrated in a monograph edited by Perrault in 1676, that is, 67 years after the publication of Bacon's *Sapientia*—that was one of the first works illustrating in detail the internal anatomy, including the internal organs and brain, of both New Word and Old World monkeys. This monograph is one of the numerous works published on the 17th century on comparative anatomy, which truly

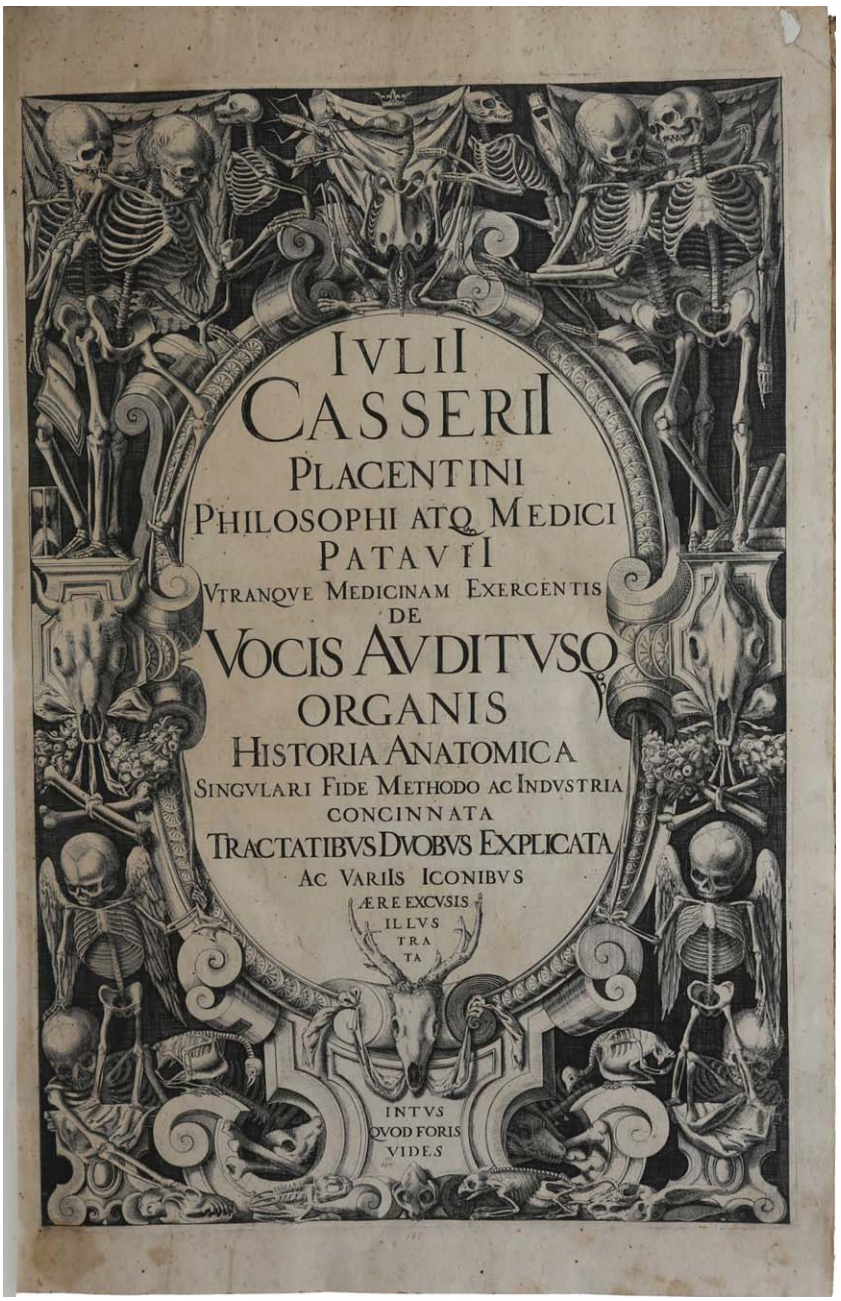

FIGURE 1 Ligozzi's title-page of Casserius 1600−1601 work is one of the most dramatic of the baroque period, depicting whole or partial skeletons of several animals discussed in this comparative anatomy book, including skulls of oxes, birds, dogs, and deers and tailless monkeys. As an aside, but notable for their peculiarity, are the skeletons at the lower right and left of two putti with wings, and at the upper left and right of humans embracing; for more details see text (copyright expired; freely available and adapted from Casserius, 1600−1601)

started as a discipline in about 1600 (Cole, 1975; Riva, Orrù, Pirino, & Riva, 2001). Notable examples of this are the works by Fabricius (e.g., his famous 1600s volume *De formato foetu*) and his student Casserius (e.g., his famous work of 1600–1601), which included textual and visual descriptions of the skull and laryngeal region of several animals including monkeys (Figure 1). These authors were influenced by Vesalius' 1543 study of human anatomy and Belon's previous comparisons of humans and birds (Cole, 1975). Casserius in particular is renowned for his detailed anatomical studies of animals as diverse as fish, insects, and mammals, and for giving private courses in his house in which he dissected humans, dogs and monkeys. He is also renowned for describing in detail not only their larynx but also the auditory ossicles, including their minuscule muscles, although strangely he did not find them in monkeys (Cole, 1975).

French scholars followed and further developed this tradition of comparative anatomy, and the 1676 volume *Memoires pour servir a l'histoire naturelle des animaux* edited by Perrault is an emblematic example of this (Guerrini, 2015). As explained by Guerrini, the beautiful figure that shows the "sapajou," or capuchin monkey from South America, and the "guenon," or *Cercopithecus* from Africa, and their internal

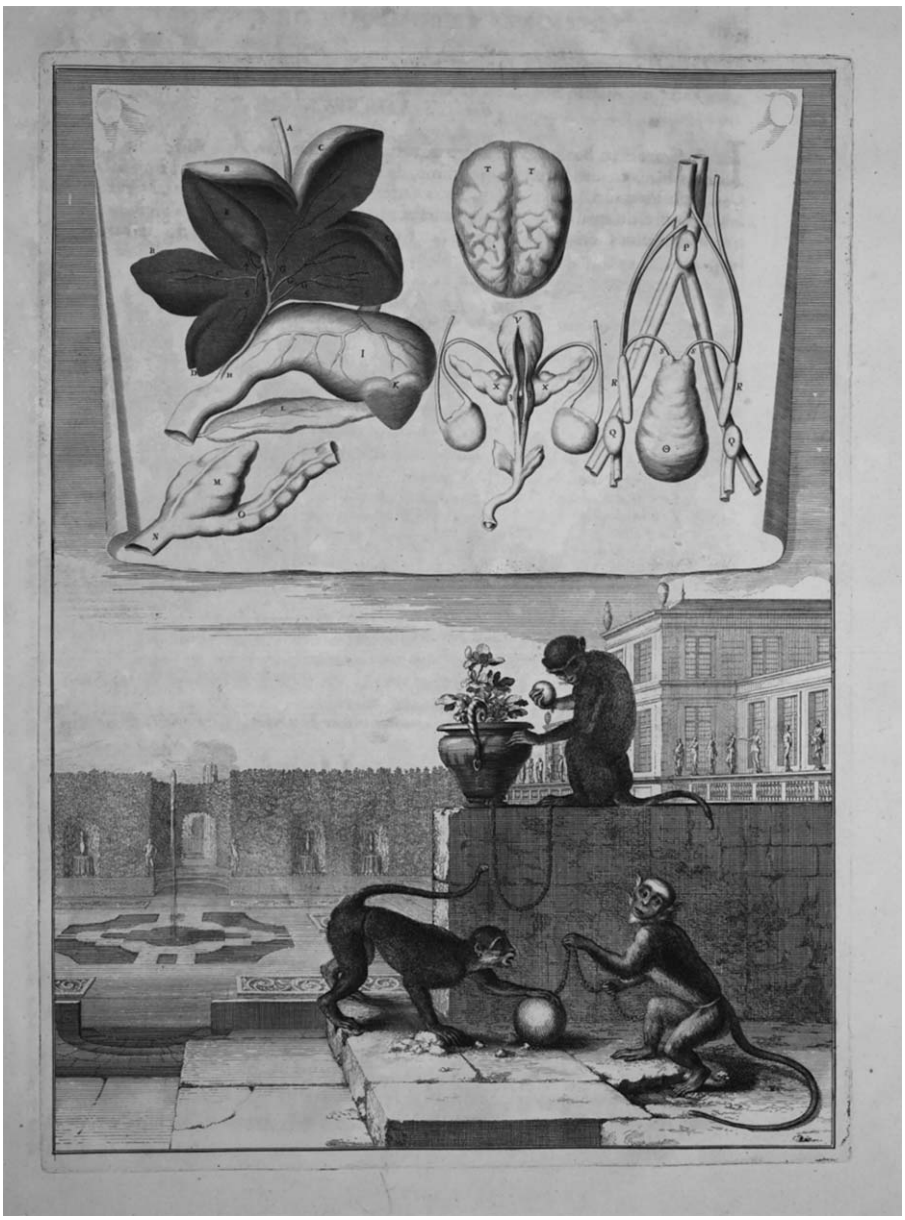

FIGURE 2 "Sapajou et Guenon," showing the internal organs of these monkeys on top and the monkeys on a domesticated background on the bottom to reinforce the idea of human hegemony that was shared by many scholars and painters in the 17th century; for more details see text (copyright expired; freely available and adapted from Perrault, 1676)

anatomy (Figure 2) is a powerful example of the "man-the-master" view defended by authors such as Francis Bacon for several reasons. For instance, at the time it was usual for painters, including the court painter Lebrun, to show human buildings in the background, even if humans were not present, to reinforce that what was seen was not the natural habitat of the animals displayed, but instead their human ownership. That is, although the monkeys were depicted outside the buildings where they spent their last days, "these animals nonetheless were shown in domesticated landscapes for denatured animals, human settings rather than animal settings" (Guerrini, 2015, p. 160). The inclusion of dissected animal parts and of the potted plant and the monkey chains further asserted "human hegemony" and a "nature completely subsumed to human desires" (Guerrini, 2015, p. 160). Such a view of "humans as the masters of nature," which was strongly criticized by authors such as Descartes, was related to another conflict regarding the exact place of humans in the "ladder of being." Those scholars that considered that all organisms were made by God to be merely used by humans usually emphasized the very prominent position of humans in the ladder, while their opponents typically highlighted instead the "infinite" distance between humans and God in that ladder (Lovejoy, 1936). For instance, in the 17th century John Locke, who defended the idea of human-animal continuity, stated that "there are far more species of creatures above us (e.g. angels), than there are beneath; we being in degrees of perfection much more remote from the infinite Being of God, than we are from the lowest state of being" (Lovejoy, 1936, p. 190).

Interestingly, despite these highly different and conflicting ideas about the place of humans in nature, the popular views about nonhuman primates in Europe during the rise of Christianity until the last centuries of the middle ages were more constant in the sense that they were generally more negative than they had been before, or for that matter than they were at any time in most other regions of the globe (e.g., Corbey, 2005; Groves, 2008; Morris, 2013; Sorenson, 2009; Veracini & Teixeira, 2016). As it happens in many cases, including in cases of racism against other human groups (e.g., Bancel, David, & Thomas, 2014; Gould, 1981), these negative views were in great part related to the lack of physical proximity between the people defending them and the subjects of their negative comments. That is, they were due to the fact that with the exception of *Macaca sylvanus* from the small island of Gibraltar (in the Mediterranean sea between the West regions of Europe and Africa), during those times there were no nonhuman primates in Europe (Groves, 2008, explains in detail how Greeks such as Galen obtained monkeys for anatomical dissections). Consequently, there was no knowledge at all about nonhuman primate biology, and the authors of those negative ideas, who were in great part theologians, mainly referred to exaggerations of some old, mainly fantasized, stories about monkeys written by the Greeks, or even to completely made-up stories about mythological human-like creatures (see below). In many cases, these stories had clear strategic purposes for Christianity, such as directly criticizing the previous nonmonotheistic religions. As noted by Morris (2013, p. 46), "from the fall of the Roman empire until the late Middle Ages the official view of the Christian Church was that the monkey was a diabolical beast." For instance, "in the 4th century, when early Christian zealots were eagerly setting about the destruction of Egyptian idols in Alexandria, their leader ordered that one statue should be preserved as a monument to heathen depravity . . . needless to say, that statue was one of a sacred baboon." That is, "the monkey-god of ancient Egyptians had, in one powerful gesture, become the monkey-devil of Christianity . . . the Devil himself became known as Simia Dei or God's Monkey" (Morris, 2013, p. 46).

As also noted by Morris (2013, p. 45), one needs to recognize that contrary to Aristotle and Galen and most other Greek scholars, some Greeks did have a negative view of monkeys. For instance, in the 7th century BC the Greek poet Simonides identified, based on external anatomical comparisons, "the very worst kind of woman" as descending from monkeys: "she is short, in the neck, hardly moves, has no buttocks, is withered of limb . . . . . and she knows all the intrigues and tricks like a monkey." But the rare negative views of Greeks were often not related directly to monkeys, as happens in this example, but instead with "half human-half animal" features that were fantasized or at least based on exaggerations of what was reported from monkeys and possibly, in at least some cases, from true apes.

In fact, it is possible that Greeks had reports about true apes (i.e., nonhuman hominoids according to current terminology). This is because some authors consider that the first written accounts on the existence of true apes seemingly occurred in the 5th century BC, when the Greek Herodotus described African apes in *The Histories*, following the description of the Phoenician Hanno's Periplus or circumnavigation of Africa: a strange creature inhabiting a fabulous land (far-) west of Cyrenaica (probably coinciding with the extant Cameroon: M. Masseti, personal communication). This might explain the common references, in the Greco-Roman literature, to, for example, "pygmies" and other semi-human creatures, known for instance for their lasciviousness. An example is given in Pliny's 77 AD *Natural History*, which was a "beautiful mixture of accurate information, acute observation, and credulity" (Groves, 2008, p. 30). Groves agrees with Tyson's 1699 work (see below) in that many of these "semi-human creatures" do not seem to refer to true apes, for example Pliny's "satyrs" generally had hooves and tails while true apes are tailless. But in some cases they probably did refer to chimpanzees—for example, the 6th century BC "onocentaura" quoted by Aelian reported by Pythagoras—and possibly, but less likely, even gorillas—for example, 6th century BC quote by Hanno.

As noted above and as explained in detail by authors such as Janson (1952), Sorenson (2009), Groves (2008), Morris (2013), and Corbey (2005), there were some negative views of a few Greek scholars about monkeys and/or "semi-human creatures" that might in fact refer to true apes in some cases. However, no other culture and/or region of the globe displayed the consistent highly negative views of monkeys typical of the European Christian Middle Ages. There are a few exceptions, such as in Sub-Saharan African regions where there is actual competition for crops with large-sized monkeys such as baboons, where the views are negative or at least ambiguous. This is the case of, for instance, the Dogon tribe (Morris, 2013). However, most non-European cultures have in general a positive view of monkeys, in particular those in which people have a closer physical proximity with, and, thus, more knowledge about the biology of, other primates (Morris, 2013). One illustrative example is the God-monkey of Egyptians, who commonly used monkeys as pets and knew several aspects of their biology, including the reactions of baboons to the sun-rise and their relatively lengthy penis and the fact that they spent a great deal of time sitting in the squatting posture. In fact, in one more interesting link between comparative anatomy and the human views on other primates and their relations and value to us, Morris (2013, p. 13) notes that "compared with the human penis, that of the hamadryas (baboons) appears to lack a foreskin and the animal was therefore thought to be born circumcised." He added that "it has been suggested that the Egyptian priests who attended the sacred baboons honored them by imitating this condition . . . in this way the ritual of human circumcision is thought to have arisen, spreading later to nearby tribes who wished to emulate the advanced Egyptians" (Figure 3). Other examples include the Indian monkey God Hanuman, the sacred forest monkey of Bali, the monkey King Sun Wukong of China, the three wise monkeys of Japan, the Aztec monkey God Ozmatli, and the Mayan monkey deity Batz, among many others (e.g., Corbey, 2005; Groves, 2008; Morris, 2013; Sorenson, 2009).

When Europeans started to see, interact and directly study nonhuman primates more regularly, particularly from the 14th century on when they travelled more often to and traded with other regions of the globe, the popular views about these primates started to be more positive. This change of view was also deeply related with the Renaissance, the period of European history from the 14th to the 17th century that was the cultural bridge between the Middle Ages and the so-

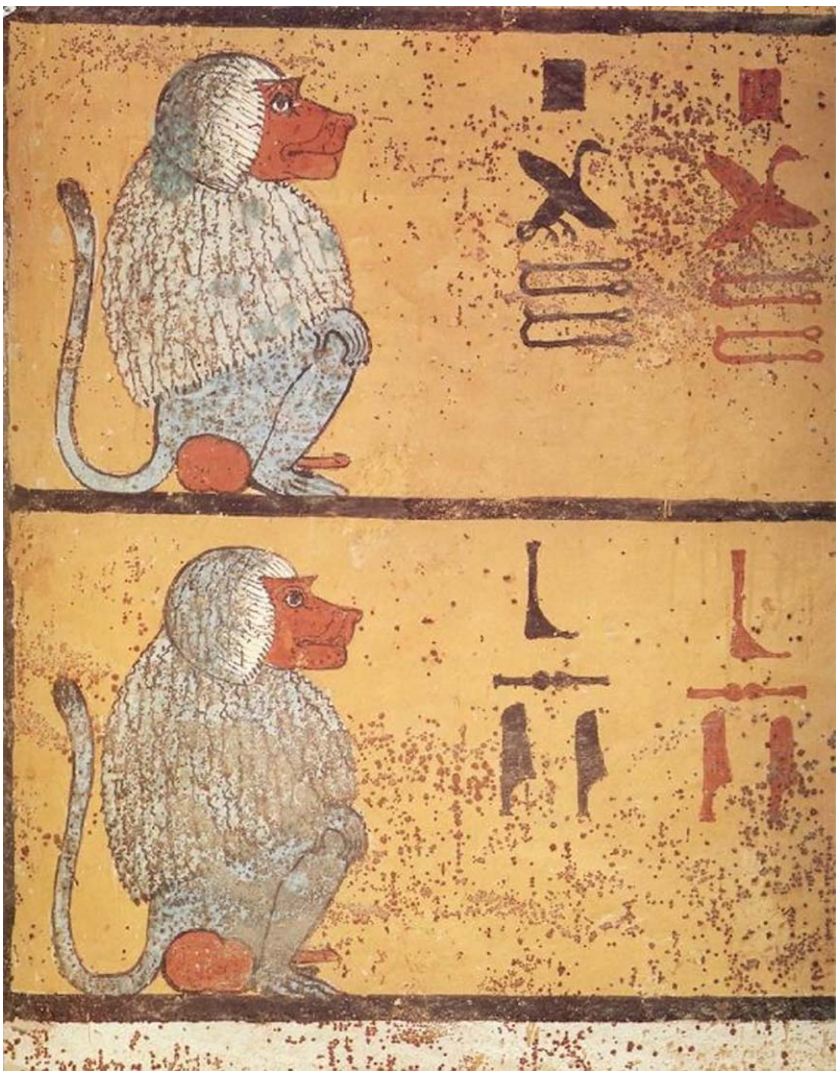

FIGURE 3 Wall painting of sacred baboons from the tomb of Tutankhamun. Although seemingly the Egyptians did not provide detailed reports on the internal anatomy of baboons, they had a relatively good knowledge on their external anatomy. Some authors argue that it was their detailed anatomical comparisons with humans that actually lead to the origin and spread of the ritual of human circumcision in at least some African regions (for more details, see text) (copyright expired; freely available and adapted from https://www.pinterest.com/pin/371617406729501758/)

called modern history, in which observation and direct study of Nature was largely promoted (Groves, 2008). Groves explains in some detail how Europeans started to get monkeys from Sub-Saharan Africa well before the first European navigators—the Portuguese—reached even Cape Bojador in 1434. He refers for instance to the Trans-Saharan caravan routes that passed through Mali. Figure 4 is an illustrative examples of how, before that year, Renaissance artists were already painting monkeys more realistically, for instance showing their true proportions, postures and gestures, rather than in the unrealistic and mainly religiously symbolic manner in which they were almost always depicted during the Middle Ages. These points, together with the fact that monkeys started to be commonly used as pets, led to a mindset where monkeys started to be more and more seen not as terrifying evil creatures but as funny (e.g., as clumsy human imitators), as they are still often portrayed nowadays (Corbey, 2005; Morris, 2013). This trend was also paralleled in the 17th century when the first direct contacts between Europeans and true apes started to occur, culminating in Tyson's description and depiction of the common chimp dissected by him, as will be seen in the next section.

3 | FROM THE FIRST DETAILED ANATOMICAL REPORT OF AN APE (TYSON) TO DARWIN

In the first confirmed written report of a direct close contact between an ape and an European, Purchas' 1625 *Purchas His Pilgrimes* tells a story of a sailor that Samuel met in 1610 and that was previously captive by the Portuguese in Angola, and that referred to an ape that was "very tall . . . his face and ears are without hair, and his hands also . . . his body is full of hair, but not very thick . . . they feed on fruit they find in the woods" (Groves, 2008. pp. 63–64). This story, which still retains some old habits of exaggerating or even making up certain

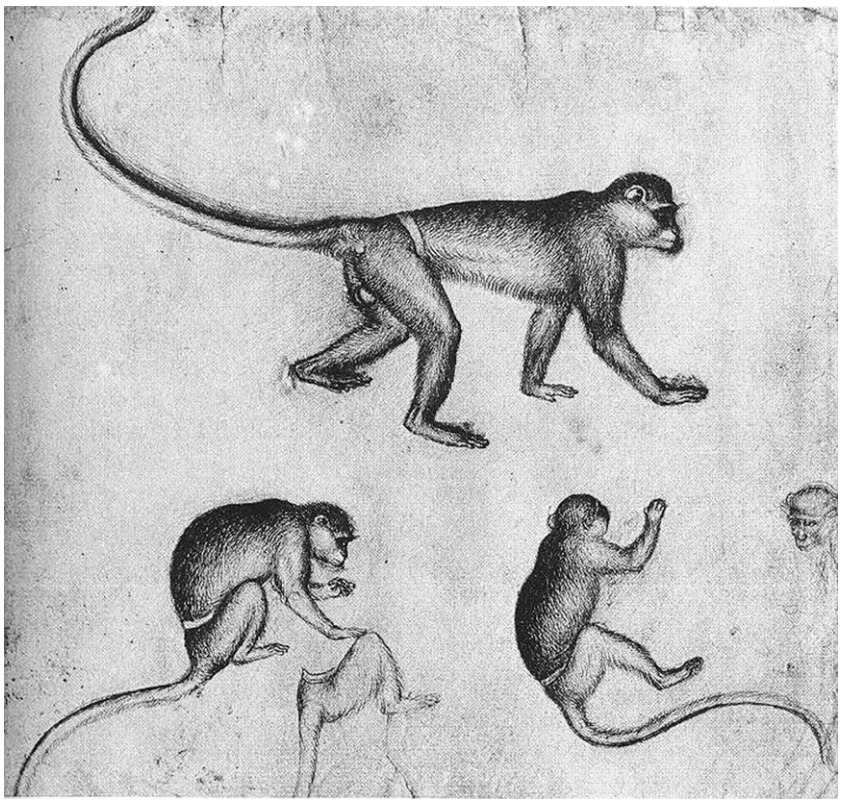

FIGURE 4 From *Six Monkeys and a Sturgeon*, 1430s Pisanello sketchbook—note that Groves (2008) stated that the monkey species is Campbell's mona, but in reality there are doubts about its true identity, with some scholars considering that it is very like a *Chlorocebus* species, possibly *Chlorocebus aethiops* (C. Veracini, personal communication) (copyright expired; freely available and adapted from https://uk.pinterest.com/pin/29273466299986614/)

features but also incorporates the more sober type of naturalistic facts that were more and more typical in his epoch, clearly seems to refer to a Gorilla: "and so the last of the Great Apes to be described scientifically was the first to be described popularly" (Groves, 2008, p. 65).

Just 16 years later, Tulpius, a physician and anatomist immortalized in Rembrandt's painting *The Anatomical Lesson* that showed him as the central figure, published the first relatively realistic external anatomical depiction of a great ape (Figure 5). Because Tulpius referred only to the external morphology and did not dissect the ape, there is still a lot of controversy on whether it was a common chimp, a bonobo, or even an orangutan (see e.g., Corbey, 2005; Groves, 2008; Sorenson, 2009). Be that as it may, what is important for the purpose of the present work is instead to note how this illustration is an emblematic example of the more realistic type of details provided in such artistic works. Note, for example, the anatomically correct details about the size of the big toe and its distance to the other toes—and how even great apes were effectively generally depicted in a rather positive, even docile, way in the 17th century (Figure 5).

The first comprehensive description of the internal anatomy of an ape was that of Tyson (1699), which is in a sense a climax of the trend that begun in the 14th century to depict nonhuman primates in a more naturalistic, realistic, and also positive way. Tyson's 1699 work is considered to be one of the most outstanding landmarks not only in the history of comparative anatomy, but also of biology and even of science as a whole (Montagu, 1943). In the preface of his book Montagu (1943, page xx in Preface) noted that Tyson "did not discover the theory of evolution. But he accomplished in a modest and honest way a goodly share of the (anatomical) analytical work without which the scientific formulation of that theory would have remained impossible," being in this sense "a forerunner . . . of (Darwin's) the *Origin of Species* (1859) and the *Descent of Man* (1871)." However, as also noted by Montagu (1943, pp. 240–242), most authors "entirely overlooked . . . Tyson's (transitional) gradational view of the relation of animals in general, and of the special kind of relationship of . . . the chimpanzee to man in particular." For instance, Tyson stated "we may better observe Nature's Gradation in the Formation of Animal Bodies, and the Transitions made from one to another . . . the animal of which I have given the anatomy, coming nearest to Mankind, seems the nexus of the Animal and Rational . . . in the Chain of the Creation, as an intermediate link between an ape (monkey) and a man, I would place our pygmie." One of the many beautiful depictions of the common chimp (*Pan troglodytes*) dissected by Tyson that clearly reflects his idea of gradation and special kind of relationship with humans is shown in Figure 6.

That common chimp came from Angola and died a few months after its arrival in London before Tyson dissected it, being probably a juvenile "a little over two years old," since it "had only its milk dentition, and since none of its permanent teeth had erupted" (Montagu, 1943, p. 300). Therefore, the name "pygmie" used by Tyson probably

FIGURE 5 Depiction of a great ape in Tulpius' 1641 *Observationes medicae* (copyright expired; freely available and adapted from https://commons.wikimedia.org/wiki/File: Nicolaes_Tulp_1641_3de_capvt_lvi_satyr.JPG)

FIGURE 6 One of the depictions of the muscles of the immature common chimp (*Pan troglodytes*) dissected in Tyson's 1699 work (copyright expired; freely available and adapted from http://flashbak.com/wp-content/uploads/2016/08/Tyson-chimpanzee-cowper.jpg)

refers to both the small size of the individual and the fact that the ancients, including Homer, used the name "pygmie" to refer to semi-human creatures (Groves, 2008). In fact, an important point that is usually not emphasized enough about Tyson's work is that "he has read practically everyone who had ever made some pertinent remark with reference to the man-like apes" and meticulously discussed those previous references in a total of 58 pages in four *Philological Essays* (Montagu, 1943, pp. 229–232). Tyson concluded that the "pygmies" of ancients probably referred to indirect, or at least not close, contacts with true apes, and argued that the "satyrs," "cynocephaly," or "sphinges" probably referred to monkeys or were merely mythological creatures (Montagu, 1943, pp. 229–232). In this sense, comparative anatomy also played a crucial role in the history of science and biology and of broader discussions on our place in nature. This is because it was critical to end with the confusion, speculation, and myths about human-like creatures that had been so deeply immersed in the minds of thinkers, philosophers, scientists, and the broader public for millennia. Similarly, the detailed anatomical studies of human fossils that started to be found in the 19th century—the first Neanderthal remains were discovered in Belgium, Gibraltar, and Germany in 1829, 1848, and 1856, respectively—were also crucial to inform and clarify discussions on those subjects (Corbey, 2005).

It is important to recognize that there were some erroneous assertions in Tyson's 1699 monograph. These mainly concerned the muscles, which were in reality dissected and described by William Cowper, who also assisted Tyson by doing the anatomical figures for that 1699 monograph (e.g., Figure 6) (Montagu, 1943). For example, in part probably also due to the young age of the chimp but in part due to incorrect observations and information, within the 34 features shared by the chimp and monkeys listed in that monograph two of them referred to the absence of facial muscles (e.g., occipitalis, frontalis, levator labii superioris, and small muscles attached to the ear) and hind-limb muscles (e.g., extensor digitorum brevis) that are actually usually present in chimps and monkeys (Diogo & Wood, 2011, 2012). These errors support Montagu's (1943, p. 307) idea that the few erroneous anatomical assertions done by Tyson were mainly due to three reasons: (1) "the age differences" (between the juvenile chimp versus the adult

humans and monkeys to which it was being compared); (2) "errors in observation" (e.g., incorrectly stating that muscles such as those listed just above were missing in chimps); and (3) "still others, chiefly relating to the muscles, which were due to Tyson's lack of comparative material" (e.g., incorrectly stating that those same muscles were also missing in monkeys). In fact, it is striking that although various authors—including Da Vinci—did dissect monkeys in some detail, with very few exceptions such as the works of Sylvius almost nothing was officially published about their muscles from Galen's studies of the muscles of *Macaca sylvanus* (see above) to Tyson's 1699 work, that is, for about 1500 years (Cole, 1975).

Despite the errors mentioned just above, the central conclusion of Tyson's work, that is, that he found more anatomical features shared by the common chimp and humans (48 according to him) than by this chimp and monkeys (34 according to his comparison), is completely right in view of current knowledge (Diogo & Wood, 2011, 2012). For instance, this was the first work to point out that the vocal (laryngeal) apparatus of apes is strikingly similar to that of humans, and that contrary to apes and other primates humans normally lack the upper limb muscles levator claviculae and dorsoepitrochlearis but have a distinct extensor pollicis brevis muscle for the movements of the thumb (see Figure 6, and Diogo & Wood, 2011, 2012). That is, Montagu's statement that, overall, Tyson's 1699 description of the common chimp bones as well as muscles and other soft tissues is remarkably detailed and generally correct, is completely accurate according to modern knowledge.

Moreover, Montagu (1943, p. 261) also noted that although Tyson incorrectly suggested that this chimp was "in all respects designed by Nature, to walk erect," Tyson never clearly stated that it actually did walk erect. Instead, the figures "exhibiting the musculature of the animal are placed in conventional positions, and are in no way intended to illustrate its normal posture. When standing erectly the chimpanzee's lower extremity are always somewhat bent at the knees, and the position in which the upper extremities and hands are held is characteristic" (Montagu, 1943, p. 261). Moreover, after describing the feet of the chimp, Tyson wrote that since "in the formation and its function too, being more like a hand, than a foot; for the distinguishing this sort of animals from others, I have thought, whether it might not be reckoned and call'd rather *quadru-manus* than quadrupes, i.e. a four handed, than a four-footed animal" (Montagu, 1943, p. 264). That is, Tyson correctly recognized that the great apes are not quadrupeds as non-hominoid primates are, nor "bimana" as humans are, referring instead to "quadrumana," a term that begun since then to be commonly used in the literature to refer to great apes (Groves, 2008).

Tyson's 1699 detailed comparisons between chimps, humans and monkeys paved the way for the development of primate comparative anatomy. These advances thus expanded as a field of biology in parallel with the expansion of European Empires because it became possible to obtain apes and other primates relatively easily and to join naturalist expeditions into new colonies. In particular, it was the "comparative method which Tyson introduced, that has since been adopted by all students of the comparative anatomy of primates. Huxley, in his *Evidence as to Man's Place in Nature* (1863), bodily adopted from Tyson the method of showing the resemblances and differences existing between monkeys, apes and men" and this method has been followed "since, but few who follow it are aware of the identity of the originator of this method" (Montagu, 1943, pp. 255–256). In fact, some authors argue that Tyson was the founder of comparative anatomy as a whole in England (see e.g., Montagu, 1943), and it is clear that after his work primate comparative anatomical works begun to be frequently published not only in England but also in France, Germany, Italy, Holland, and many other countries. For instance, in 1778 and 1782 Camper provided the first detailed anatomical descriptions of orangutans (*Pongo*) and comparisons with humans, and in 1787 Josephi published a detailed work on primates; both authors extensively cited Tyson's 1699 anatomical descriptions of chimps. Savage provided the first anatomical description of gorillas in 1847, although only later authors such as Barnard (1875), Bischoff (1870), Chudzinski (1885), and Eisler (1890) provided detailed descriptions of their soft tissues such as muscles and internal organs, while Bischoff (1880) provided detailed descriptions of these tissues in hylobatids. More details on the anatomy of different ape species continued to be published at a remarkable pace, for example, by Owen (1835), Duvernoy (1855−1856), Church (1861−1862), Champneys (1872), Chapman (1878, 1879, 1880, 1900), Deniker (1885), Deniker and Boulart (1885), Hartmann (1886), Duckworth (1898), Hepburn (1892), and Dwight (1895), among many others. In addition, detailed comparative anatomical works of non-anthropoid primates, that is, of strepsirhines and tarsiers, also started to be frequently published in the 19th century (Figure 7) (e.g., Allen, 1897; Burmeister, 1846; Cuvier & Laurillard, 1849; Huntington, 1897; Milne-Edwards & Grandidier, 1875).

As noted by Lovejoy (1936, p. 231), in the 18th century decades after Tyson's 1699 anatomical work "the sense of the separation between man from the rest of the animal creation was beginning to break down." For instance, Rousseau asserted in 1753 that humans and great apes (orangutans and chimps, as gorillas were still not described then) are of the same species, language not being natural to humans but instead an art which one variety of this species (humans) has gradually developed (Lovejoy, 1936, p. 235). And in 1781 Bonnet stated that great apes have the size, members, carriage, and "upright posture" of humans, having a "true face" and being "entirely destitute of a tail" and "susceptible of education," to the point of acquiring even a sort of politeness (Lovejoy, 1936, p. 225). He stated that, whether we compare their minds or bodies with ours, "we are astonished to see how slight and how few are the differences, and how manifold and how marked are the resemblances" (Lovejoy, 1936, p. 225).

Paradoxically, on the other hand the discomfort caused by the human-chimp anatomical similarity revealed by Tyson actually led many other authors to instead re-emphasize an animal-human discontinuity in which the "true" gap was now not related to anatomy but to "civilization," that is, between European humans versus non-European humans plus other primates. For instance, in 1714, just 15 years after Tyson's work, Blackmore and Hughes, noting how "surprising and delightful it is" to trace "the scale or gradual ascent from minerals to man" placed the African Hottentots between "humans" and great apes (Lovejoy, 1936, p. 234). They wrote: "the ape or the monkey that bears

FIGURE 7 Non-anthropoid primates were the last primates to have their internal anatomy described in detail, with detailed gross anatomical descriptions of tarsiers (as *Tarsius tarsier*, shown here, from a plate of Burmeister's 1846 work) and strepsirhines mainly starting to be published in the 19th century (see text for more details) (copyright expired; freely available and adapted from https://archive.org/details/beitrgezurnh00burm)

the greatest similitude to man, is the next order of animals below him . . . as the Hottentot, or stupid native of Nova Zembla" (Lovejoy, 1936, p. 234).

Of course, there had been comparisons between nonhuman primates and Non-European humans much before the 18th century, including, strikingly, even comparisons between small/sized New World monkeys such as spider monkeys and human ethnic groups native to the West Coast of Africa, for example, by Oviedo in the 16th century (Veracini & Teixeira, 2016). Also, although this is often neglected in the literature, during the Middle Ages various Muslim scholars have also compared certain human groups with nonhuman primates and even explicitly stated that humans derived from other primates (e.g., Malik, Ziermann, & Diogo, 2017; Montagu, 1943). However, the profusion and morphological detail of such comparisons only truly emerged in the 18th century with the so-called "anatomical racial studies," which became particularly prominent in comparative anatomy and anthropology in the 19th and the first half of the 20th centuries and were deeply related with justifications for slavery and/or colonialism (e.g., Bancel et al., 2014; Diogo, 2010; Gould, 1981, 2002).

Linnaeus' 1735 *Systema Naturae* is a landmark example of the impact of Tyson's 1699 monograph and the growing tension between two different ideas. One is the human-chimp similarity and continuity suggested in Tyson's monograph. The other is the trend toward the creation of a new dichotomy between "truly civilized humans" versus other humans plus animals that was in great part due to the discomfort caused by the human-chimp similarities described by Tyson. In fact, as

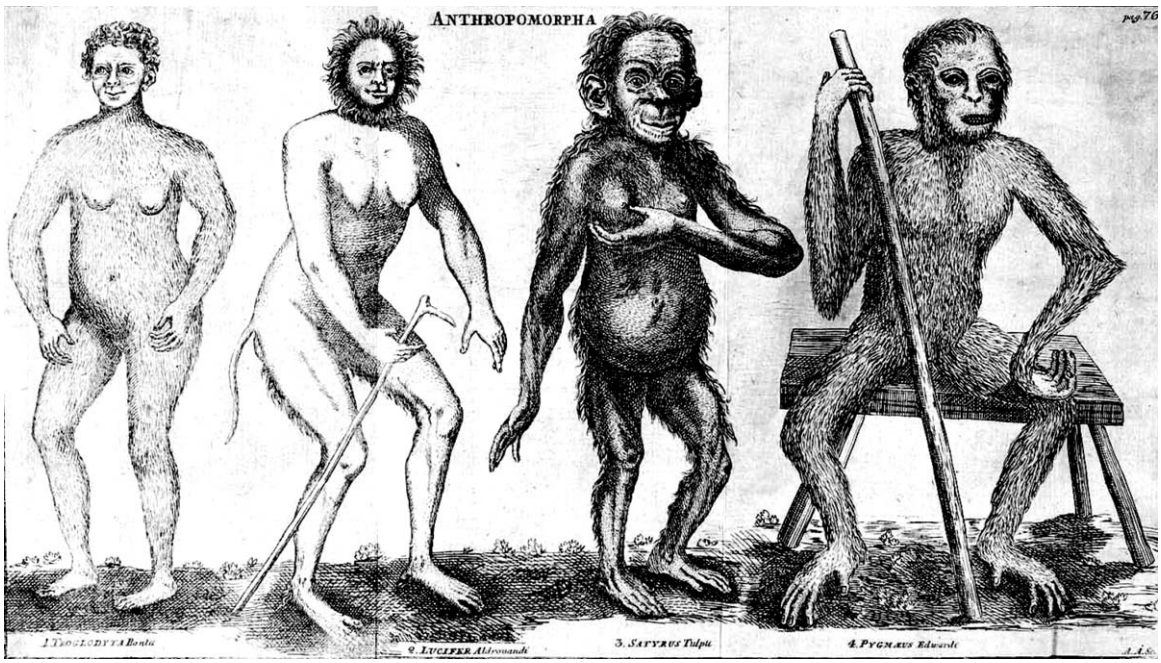

FIGURE 8 The "Anthropomorpha" of Linnaeus (1735): *Troglodyta*, *Lucifer*, *Satyrus* and *Pygmaeus*, which is a mix between scientific descriptions such as those of Tyson and imaginary human-like creatures mentioned by earlier authors (copyright expired; freely available and adapted from https://upload.wikimedia.org/wikipedia/commons/8/8a/Hoppius_Anthropomorpha.png)

Tyson's work, Linnaeus' work also profoundly influenced the publications of Blumenbach's and Camper, whom are usually considered the "fathers of physical anthropology" and of "racial anatomical studies" (Corbey, 2005; Montagu, 1943). That is, on the one hand Linnaeus went one step further than Tyson did because in the great scheme of classification of the living world proposed in the tenth edition of *Systema naturae* (1758) he further developed his previous classifications (see e.g., Figure 8) and listed two *Homo* species: *H. sapiens* ("*H. diurnus*") and *H. troglodytes* ("*H. nocturnus*"), the latter including the great apes ("*H. sylvestris Orang-Outang*," that is, Bontius' orangutan and Tulpius' and Tyson's chimpanzees, as gorillas have not been officially described by then: for example, van Wyhe & Kjaergaard, 2015). However, this suggested human-animal continuity was accompanied, on the other hand, by an apparent discontinuity between humans themselves. This is because Linnaeus divided humans into different "variations" that were defined by both anatomical and social/moral traits, suggesting that these "variations" were in reality somehow fixed. These human "variations"—which, therefore, became to be commonly defined as "races" by subsequent authors—were: (1) American: red, bilious, straight—governed by customs; (2) European: white, sanguine, muscular—governed by customs; (3) Asian: sallow (pale), melancholic, stiff—governed by opinion; and (4) African: black, phlegmatic, stiff—governed by chance.

Numerous authors have discussed the connection between Linnaeus work and the development of the term "race" and of racism in the 18th and 19th centuries, as well as about the many nuances related to these topics and their links. A comprehensive, updated discussion on these topics is provided in the recent book *The Invention of Race* (Bancel et al., 2014). In particular, the chapter by Hoquet summarizes, in my opinion, the most critical points within this discussion. Namely, Hoquet (2014, p. 28) states that despite the numerous nuances concerning this topic—and the fact that as noted above Linnaeus actually referred to "variations" and not to "races"—there is no doubt that "Linnaeus description, due to the strict union of the physical and the moral, goes beyond a physical characterization of race: it includes the moral character of peoples." That is why for Hoquet, more than the works and terms used by other authors that are often said to have invented the modern sense of the word "race" such as Bernier and Buffon, "the categories developed by Linnaeus ultimately do indeed correspond to what we call 'races': they are physical and moral categories that divide humans by color and by continental zones, and are unified by Hippocratic temperaments."

This is because for most authors previous to, or living in the same epoch as Linnaeus—including those that, as Buffon, defended that the differences between human groups were due to "degeneration" from an "ideal type"—such differences were mainly due to climate/environmental changes, grounded in humoralism, and were, therefore, in theory *reversible* (Hoquet, 2014; Meijer, 2014). By connecting the social/moral with anatomy, Linnaeus thus paved the way for authors such as Meiners, Blumenbach, Camper, and Broca and the so-called "anatomical race studies" that became so frequent in the 19th and the first half of the 20th centuries to undertake a "biologization of the social" (Reynaud-Paligot, 2014). I would say that this was in fact truly an anatomization of the social/moral, stressing again the fact that the direct, profound connection between comparative anatomy and the history of the concept of "race" and of racism is not always emphasized as it should be in the literature and in discussions on these subjects.

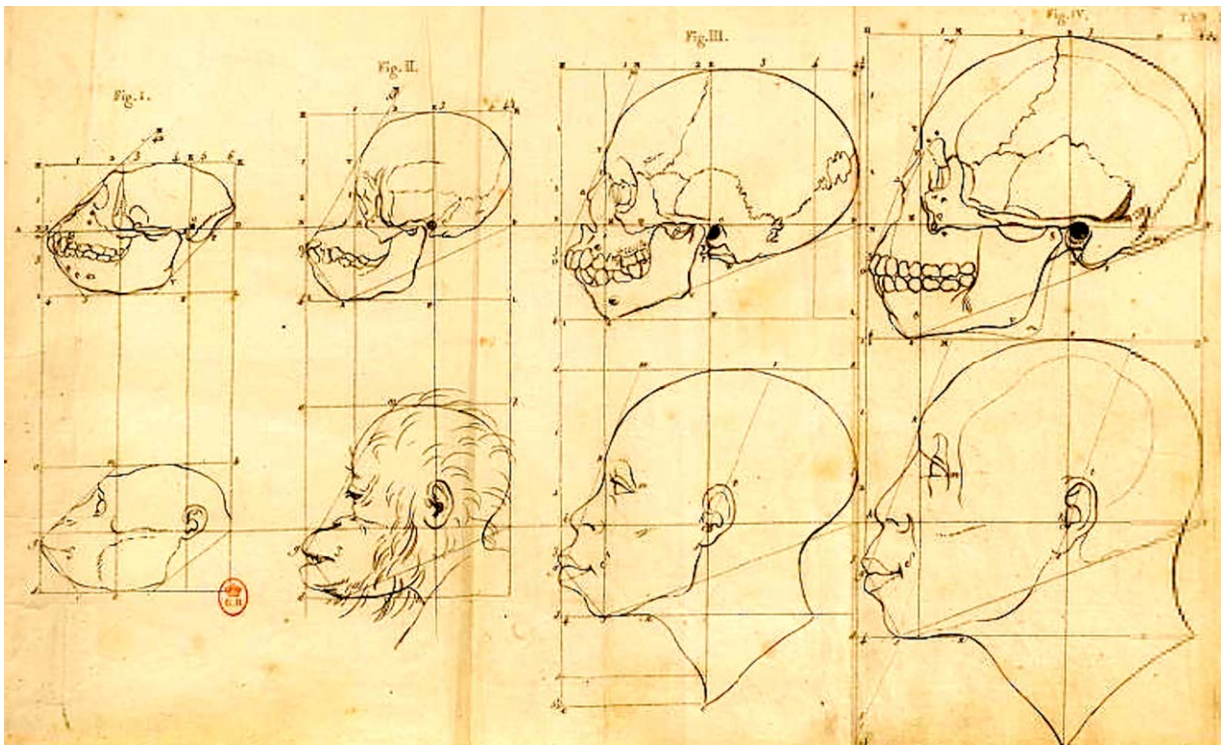

FIGURE 9 Skulls and facial angles of a monkey, an orangutan, an African moor and an Asian as shown in a plate of 1791s French translation of Camper's work on the facial angles (copyright expired; freely available and adapted from http://gallica.bnf.fr/ark:/12148/bpt6k1054470t/f179.item)

This direct and profound connection is further emphasized by the fact that the person that is for many the "father of physical anthropology" was Petrus Camper. This Dutch anatomist provided, in 1772, the first detailed anatomical description of orangutans (*Pongo*) and evidence that both orangutans and chimpanzees are actually not bipedal, contrary to Tyson's suggestions. Camper's work was crucial for discussions on the place of humans in nature by both confirming Blumenbach's distinction between the African chimpanzees and the Asian orangutans, and for being the first detailed craniology "human anatomical racial study." As noted by Guedron (2014), Camper started a tradition in which the design of human anatomical plates and illustrations become to be used within the broader discourse of racial hierarchization. Some authors defend that Camper's engravings that initiated craniology and became infamous for suggesting that protruding jaws (prognathism) indicated an "objective" anatomical and racial hierarchy in nature (Figure 9) should not be isolated "from the rest of Camper's work, the original context about organic interconnectiveness, human head shapes' plasticity and their mutual reciprocity" (Meijer, 2014, p. 33). Meijer (2014, p. 44) accurately noted that Camper stated, for instance, that "prioritizing whiteness was narcissism, for those who gave precedence to whites were always white themselves." However, many if not most authors consider that Camper clearly contributed to the rise of racism in the 18th and 19th centuries and paved the way for the creation of the "negro" (Panese, 2014). Namely, with the help of the facial angle, Camper differentiated "between the Negro, the 'Calmouque', and the European, noting 'analogies' between the head of the Negro and that of the monkey" (Figure 9), and specifically stated that "the whitest" humans were "also the most beautiful and well-proportioned in the known world" (Panese, 2014. p. 51).

Guedron's (2014) chapter clearly shows how crucial comparative anatomical illustrations, in particular those including human sequential images, were for the development of the concept of "race" and racism. Guedron argues that Camper's works were crucial catalyzers for that development, independently of the discussion on whether Camper himself agreed, or not, with those ideas of "race" and the views defended in the "racial anatomical studies" that become particularly frequent after his work. This is because almost all figures used in those subsequent studies to display the idea of an hierarchization of "race" were based on Camper's writings on the facial angle and in particular in the sequential illustrations published in the French translation of those writings (i.e., in Camper, 1791: see e.g., fig. 9). Guedron (2014, pp. 62–63) explains that "at first glance there is no narrative link between the different skulls . . . yet the horizontal organization of the first two plates suggests to the reader that he must read left to right." He further notes that "Camper is careful to warn us that we must not jump to hasty conclusions (based on these images) . . . still, the sequence implies evolution, with the white race nearing perfection - Europeans were placed next to Greek gods - and the African in proximity with the monkey (nonhuman primates)."

Therefore, "it is not difficult to understand how such images came to be interpreted as a kind of teleological demonstration, from the beast to the divine," as actually Camper's "words could not have been also clearer: the upper and lower jaws protrude in the same way in all black people . . . in this way, they are more like monkeys than us, or the

faces from antiquity" (Guedron, 2014, p. 63). Guedron wisely points out that such illustrations are a crucial part of the biologization, or anatomization, of the social, as they recall old conceptions of the human body—the split between the spiritual and material, the soul and the beast. He notes: "the top of the head was considered to be more developed among whites . . . meanwhile, the inferior part of the face (considered to be more developed in non-Europeans) . . . was related to . . . violence and instinct, which were associated with primitive peoples." Sequential illustrations similar to those provided in Camper (1791) appeared in countless publications that followed, well before Darwin's 1859 *The Origin of Species*. A few relevant examples are Cuvier's 1797 very influential *Tableau elementaire de 'histoire naturelle des animaux*, White's 1799 *An account of the regular gradation in Man*, Blumenbach's 1804 *De l'unite du genre humain*, and Cloquet's 1821–1831 *Anatomie de 'homme*, among many others. Linked with the typical association between anatomical and social/moral features that mainly started with Linnaeus's classification (see above) and the types of racial ideas that emerged from it, such anatomical illustrations were, therefore, crucial to lead to the racial determinism that become so widespread among scholars in the 19th century. This determinism was related to the idea of biological transmission, through blood and heredity, of not only anatomical but also intellectual and moral attributes within a given people (Reynaud-Paligot, 2014).

An emblematic example of this, and of the fundamental—but too often neglected as noted above—role played by comparative anatomy in discussions on apes, human "races," the chain of being and our place in nature in general, concerns Sarah Baartman, nicknamed the "Hottentot Venus." She was taken on board of a British ship in South Africa by a surgeon of the Royal Navy in 1810 and then arrived in London before being sent to Paris. Although she was not the first person to be displayed in exhibitions in Europe, by quickly starting to be an object, all at once, of entertainment, media interest, "sexual fantasy," and science, she marked in a sense the beginning of a new way of thinking about "the Other" in the West (Boetsch & Blanchard, 2014). This particular interest about her is at least partly explained because she was preceded by a mythical figure of the "African Hottentot" in the European imagination: "Hottentots' were a source of fascination, and were earmarked to fill the role of a 'missing link' (in the chain of being) . . . a symbol of an 'intermediate race' between human and animal . . . or at the very least act as proof of degeneration within the human species" (Boetsch & Blanchard, 2014, p. 189).

The shape of the body of "Venus" was considered peculiar, because of her steatopygia (buttock and hip hypertrophy) and macronymphia (protruding sexual organs), and it was also because of these supposedly extraordinary anatomical features that she became an object of so much sexual and scientific interest. In 1815 Saint-Hillaire published a report in which he compared her face with that on an orangutan and her posterior with that of a female mandrill monkey, while Cuvier stated that he had never "seen a human head that more closely resembled that of a monkey" (Boetsch & Blanchard, 2014, p. 191). Just 24 hours after her death on the 29th of December 1815, Cuvier dissected her body, removing her sexual organs and anus for preservation and then having her other anatomical parts removed, including the brain, and putting them in jars to be kept in the museum archives as a "reference anatomical specimen," as was commonly done for nonhuman animals (Boetsch & Blanchard, 2014). Cuvier's comments about her dissected body emphasize both the importance of comparative anatomy for the invention of race and how by Darwin's time it was effectively usually accepted that the anatomical and the social/moral were profoundly linked. For instance, taking in particular her sexual anatomical features as proof of a "primitive" sexual appetite in African women, Cuvier said that "races with depressed, compressed skulls are forever condemned to inferiority" (Boetsch & Blanchard, 2014, p. 191).

It is also worthy to mention that the works of Jena zoologist Ernst Haeckel—who is often named as the "German Darwin" because he was the leading public exponent of Darwinism not only in Germany but also in central Europe as a whole—also included similar racial comments and so-called classifications. For example, in his popular 1868 "*Natürliche Schöpfungsgeschichte*" he showed how humans had risen from primates and proposed that whites had risen from the other 11 species of people: he illustrated it infamously in the Frontispiece, and revised it for the second German edition in 1870. Haeckel's "*Anthropogenie*" (1874) included an influential "monkey table" (no. XI), also showing a racist classification, and in the English edition of "The History of Creation" (1887) he also laid out his so-called "evolutionary taxonomy of humans," for example, he proposed a basic division between "straight-haired men" and "woolly-haired men," the common ancestor of which was speechless "ape-like men,"or *Pithecanthropus*. This latter book lacks the infamous illustration of his earlier books referred to just above, but the text is clear about his racist ideas anyway. The life and works of Haeckel were the main focus of a particularly interesting book, written by Richards (2008), to which the readers should refer, for more details on this subject. In fact, it is important to note that, due to space limitations, I could not discuss here many other works that provide interesting discussions on the topics covered in this section of the present article. For those readers that are interested in knowing more details about these topics, the following publications—not cited in the paragraphs above—and the references cited therein are among those that are also particularly interesting: Vogt (1870), Lewis (2001), Hoßfeld (2010), and Marks (2012).

4 | FROM DARWIN TO TODAY

Although it is clear that many authors had defended that organisms can change during time, and even that humans "derived" from nonhuman primates well before Darwin and Wallace (e.g., Gould, 2002; Malik et al., 2017; Mayr, 1976), it is also evident that Darwin's (1859) *On the Origin of Species* had an astonishing influence on discussions about our place in nature. As this subject has been discussed in countless papers and monographs, I will not repeat or discuss everything that has been pointed out and discussed in those innumerable works. For the purpose of the present work it is instead more important to stress the following points. First, Tyson's detailed anatomical comparisons between humans, apes and monkeys were crucial to pave the way for Darwin's

publications. Second, Darwin provided a naturalistic, rational way—instead of supernatural or vitalistic ideas—to explain how evolution occurs, including how humans derived from nonhuman primates, through natural selection. Third, unfortunately Darwin's work and in particular his insistence in the notion of a "struggle of nature" based on the Malthusian theory of population did provide ammunition to extremist views within racist works, including those proposed by eugenicists.

The first point was already emphasized in the sections above. Regarding the second point, it has been widely discussed in the literature. It is well known how Darwin's ideas and in particular their implications about the phylogenetic relationships between humans and other primates provoked passionate and even violent reactions from not only theologians but also from the broader public and from researchers from various fields of science, including the most renown comparative anatomist of that time, Richard Owen. The discomfort created by Darwin's ideas was not merely due to the fact that one would no longer need to evoke supernatural beings to discuss and/or explain our place in Nature. It was also due to the fact that his ideas of evolutionary randomness and chance put in question a perhaps even more intricate human feature: our tendency to create teleological narratives about the final "purpose," or "goal" of human existence (Gould, 2002). This despite the fact that in reality Darwin could not completely restrain himself from still being teleological in a way, often referring for instance to "perfection" and "progress" in evolution. The idea that we are merely one of many primate species, and that our evolution was not related to a noble "goal" or "purpose," was inconceivable for a great part of the society and even of the scientific community. This is one of the reasons why Darwin's opponents were particularly furious with his 1871 book *The Descent of Man*, and with Huxley's 1863 *Evidence as to Man's Place in Nature*.

Paradoxically, as happened with Tyson's 1699 work, these two books and other similar subsequent publications had the double effect of leading many scholars to defend even more vigorously the animal-human discontinuity (i.e., within Darwin's opponents) and the discontinuity between European humans and other human groups (i.e., within those following, and often misinterpreting or at least exaggerating, Darwin's ideas). For instance, more and more scholars started to defend polygenism, that is, the idea defended by some pre-Darwin authors that for instance the different color or other traits of different human groups is not due to degeneration (monogenism) but instead to the fact that these groups form different species. For instance, these scholars argued that blacks are part of a "species" that in many ways is more similar to chimpanzees than to the "species" including whites (Gould, 1981; see also below). Of course, one cannot make Darwin's directly responsible for how some eugenicists used his work, and one should also clarify that eugenics is a very wide term as countless biologists could be somehow considered to be eugenicists in the early 1900s. Moreover, many of these eugenicists did not necessarily approve negative measures such as sterilization or even murder, being instead more focused on using science to "improve" qualities via, for example, the production of positive traits (Buklijas & Gluckman, 2013). However, as noted above, by stressing over and over the notion of "struggle for life," Darwin's did unfortunately gave a line of argument to those that started and/or wanted to use his ideas to support their extremist negative views. This includes those within the eugenics movements that became highly influential in the United States and then in Germany before and during the second world war (Gould, 1981). In fact, nowadays when scholars refer to Darwin's 1859 book, they almost always refer to its title as "*On the origin of species by means of natural selection*." However, the full title was actually "*On the origin of species by means of natural selection, or, the preservation of favored races in the struggle for life."* Taking this subtitle into account, and the numerous references to "struggle for life" in the book as a whole, as well as the numerous references to the book by those scholars that promoted the most negative views/measures within the eugenics movements, it is difficult to accept that the argument that linking Darwin's book to those scholars' ideas is far too stretched.

Within the various publications discussing this subject, one that is particularly lucid is Todes' 1989 book *Darwin Without Malthus*. He explains how Darwin was influenced by Malthus and by his free-competition ideas in the specific capitalistic context of the industrial revolution in overpopulated regions of England and that was embedded in the specific context of the discussions of human's place in nature that were held in England at the time (Todes, 1989, pp.17–19). This notion of a continuous, suffocating struggle in nature led for instance to tremendously influential bias and erroneous concepts that affected and continue to affect evolutionary biology. These include the adaptationist framework and the neglect of features that are actually crucial within biological evolution such as the existence of ecomorphological mismatches and the importance of altruism and cooperation, for instance (for recent reviews, see Diogo, 2017a,b). However, for the purpose of the present work a point that is more important and particularly critical about the dynamics of Darwin's struggle for existence was that it "was (supposedly) . . . most severe between the individuals of the same species, for they frequent the same districts, require the same food, and are exposed to the same dangers . . . (as) Darwin wrote" (Todes, 1989, pp. 10–11). Darwin used "the words 'struggle' and 'competition' interchangeably . . . the metaphor 'struggle for existence', and in such phrases as 'the great battle for life' and the 'war of nature' contributed a certain rhetorical power to his argument" (Todes, 1989, p. 11). It is, therefore, not difficult to see how Darwin (1859), by sacrificing precision for eloquence, and defending that within this struggle "death is generally prompt, and that the vigorous, the healthy and the happy survive and multiply" unintentionally gave easy ammunition for eugenicists around the globe (Todes, 1989, p. 11). This includes those within the Third Reich that defended the notion of "us *versus* them" and ultimately "us *or* them," as only one group could possibly survive such an incessant Darwinian struggle (Diogo, 2017a). As put by Corbey (2005, p. 76), "the Darwinian perception of nature as competition provided new support to the age-old icon of a beastly, humanlike, and now preferably apish Other."

It is, therefore, not a coincidence that particularly in the end of the 19th century many ethnographical books started to portray non-European men carrying weapons, to emphasize aggressive practices like war and hunting (Andreassen, 2014). As explained by Andreassen (2014,

FIGURE 10 Austrian poster to advertise the 1933 movie King Kong (copyright expired; freely available and adapted from https://knoji.com/images/user/kingkong austrianposter.jpg)

p. 121), "Darwin's arguments about the survival of the fittest became central to theories about racial hierarchies and human development." He noted that "many scientists began to see the different races competing against one another; the stronger and more intelligent would thrive, while the weaker and less intelligent races declined . . . racial Darwinism." For instance, at the end of the 19th century "indigenous people were literally being exterminated by white colonizers in Australia, but their extermination was not understood as a result of the atrocities being committed against them but rather as a result of biological determinism that mandated that the stronger (white) race survive while the weaker race (of color) disappeared" (Andreassen, 2014, p. 122). It is thus also not a coincidence that at the same time that non-Europeans were increasingly represented as aggressive and as carrying weapons in the Western media and literature, the exact same pattern was applied to great apes in the end of the 19th and first half of the 20th century, as emblematically illustrated by the 1933 movie King-Kong (Figure 10) (e.g., Corbey, 2005; Sorenson, 2009). Particularly during colonial expansion in the second half of the 19th and first half of the 20th centuries, there was a tendency to use overlapping textual and visual representations of both apes and so-called "lower human races" conceived as living ancestral forms that were wild, savage, and aggressive. Such a view clearly contrast with the views of earlier writers such as Rousseau who tended to emphasize the peaceful behavior of both of them to create different images of the "natural man" (Sorenson, 2009).

As put by Corbey (2005, p. 10), as the so-called "lower human races," great apes and particularly gorillas "came to be seen as powerful personifications of wildernesses to be fought heroically and conquered by civilized Westerners." One of the most influential channels through which the "beast-in-man stereotype" spread from the 19th into the 20th century scientific and cultural discourse was Sigmund Freud's psychoanalysis (Corbey, 2005). In fact, such overlap continues to have atrocious consequences nowadays at numerous levels, including in American popular culture, as archival content analysis shows for instance that news articles create implicit associations between black criminals and apes and that those identified as more "ape-like" are more likely to be executed (Sorenson, 2009). A particularly upsetting but illustrative example of the links between the discovery of nonhuman primates by Westerners, science, comparative anatomy, colonialism, and also animal abuse concerns the colonial propaganda film made in the 1950s in the Belgian Congo. This film was made on behalf of the Belgian government that circulated broadly in Belgian cinemas, programmed on Sunday afternoons for families with children. As described by Corbey (2005, p. 10), "the footage shows in great and, by present-day standards, shocking detail how scientists of the Royal Belgian Institute of Natural Sciences shoot and kill an adult female gorilla carrying young; subsequently the body is skinned and washed in a nearby stream, with the distressed youngster sitting next to it; the adult's skeleton, skin and other body parts were collected for scientific (anatomical) study and conservation, while the live young gorilla was sent to the Antwerp zoo."

Importantly, once again, within the discussion of these subjects, and in particular within the complex interplay between the agendas and biases of researchers, politicians, financial markets, media, and the broader public (e.g., Bancel et al., 2014; Gould, 1981), comparative anatomy played a chiefly important role in the rise of racism and eugenics in the last decades of the 19th and first half of the 20th century (Diogo, 2010). One of the more illustrative examples, among an endless number of others that could be cited here, is Huber's 1931 work on the comparative anatomy and evolution of the facial musculature, which defended that blacks and Australian natives are more similar not only morphologically but in a way also mentally to chimpanzees than to whites (see Figure 11). As noted by Huber (1931, p. 5) the "first three decades of the 20th century" were a particularly "active period of racial anatomical research on facial musculature." As I explained in detail in an earlier paper (Diogo, 2010), as other eminent and influential comparative anatomists Huber used the "results" of his "racial anatomical studies" (Figure 11) to defend that some of the facial muscles of Europeans are not differentiated in nonhuman primates, and that in

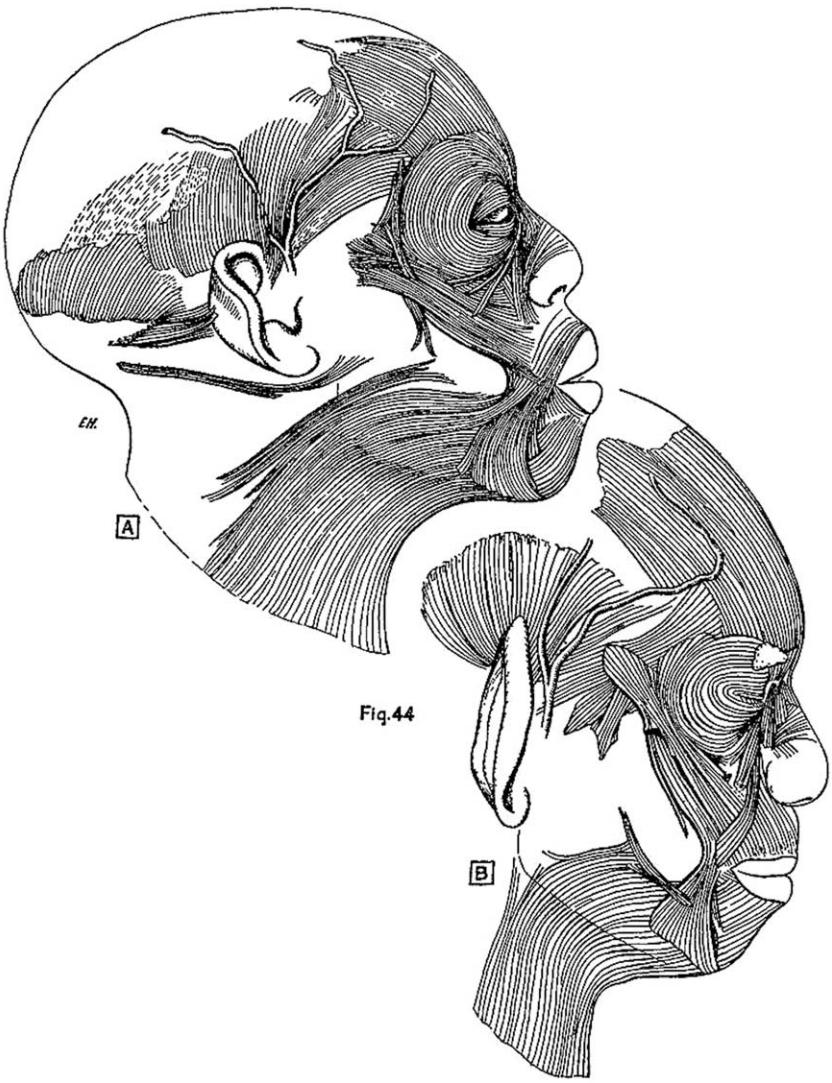

FIGURE 11 Drawing of the facial muscles by Huber, showing what he considered to be "significant racial differences" between a so-called "adult male negro" (on the left) and a so-called "adult male Australian" (on the right) (copyright expired; freely available and adapted from Huber, 1931)

many aspects non-Europeans resemble more these primates than Europeans.

Namely, Huber (1931, p. 101) stated: "the facial musculature of the adult American Negro is generally composed of bundles which are much coarser and also darker in color than are those of the White; there is, moreover, in the Negro, a lack of differentiation into well defined individual muscles in some regions of the face . . . in a prevailing percentage of White cases, the zygomaticus musculature has reached a higher stage in evolution" (see Figure 6). As an illustrative example of how racial determinism and the deep links between anatomy and the social/moral were commonly accepted at the time, he wrote: "in the responsive faces of Whites we notice, especially in the upper region of the face and about the mouth, a great range of varied expressions with many modulations; the mouth, even closed, may serve as an admirable index of character or mental state through a slightly increased tonus of its musculature . . . the smile turns into a happy, hearty laugh" (Huber, 1931, pp. 159–160). In contrast, "apparently nerve impulses that are less finely graded reach the respective mimetic muscle groups, thus setting them into sudden, strong contraction which rather suggests more primitive muscle actions (of the 'negroes'); the expression is characteristic . . . the large white teeth show in vivid contrast to the dark face; instead of grades laugh typical of the white we notice the characteristic grinning of the negro, and through sounds, often simultaneously uttered, which differ in tone of voice from those of the white, the negro's grinning becomes even more characteristic." In turn, "the Polynesians, like the negroes—a dark skinned, yet profoundly different somatically and psychologically, a highly intelligent race—show a distinctly different facial expression, very similar to that of the white; I should never forget the intelligent, pleasing and charming features of the kindly Hawaiian faces."

What is particularly striking is effectively that this kind of quotes were not written by a few, somewhat unknown researchers, but instead by the most eminent, respected and influential comparative anatomists of the first half of the 20th century. That is, although almost

all these comparative anatomists of that time accepted evolutionary ideas, they were still in reality more concerned to stress the "astonishing" differences between the "civilized" Europeans versus the "uncivilized" Non-Europeans plus nonhuman primates than to focus on the animal-human continuity. And what is particularly disturbing is that those comparative anatomists were so biased by their prejudices that they could inclusively provide wrong data to support their ideas, either unconsciously because of those biases or even intentionally, to the point of faking data (Diogo, 2010). In fact, we now know, for example, that the facial muscles that Huber and other comparative anatomists of the first half of the 20th century said to be uniquely present in Europeans are in fact present in most individuals of *all* studied extant human groups as well as in at least some extant nonhuman primates. Even the muscle risorius, which was said to be only present in the "civilized" whites and that was mainly responsible for their "gracile" smile is in reality often present in chimpanzees (Diogo & Wood, 2011, 2012; Diogo et al., 2013a, 2017).

Fortunately, since the 1950s, there has been a dramatic change of view toward a vision of continuity and unity both between all extant human groups and between them and other primates. This change in mindset was in great part influenced by the aim of not repeating the errors that lead to ideas that were used to justify atrocities committed during World War 2. For instance, the UNESCO Statement on Race—an official declaration against racism, which attempted to break the connection between "race" and biological determinism—was published in 1950, becoming an extremely important turning point within this change in mindset. On the other hand, this change was also in great part influenced by less biased comparative anatomical, genetic and behavioral works on primates. In fact, in many countries eugenics was already losing some ground as early as the 1930s because geneticists could not confirm any of the key conceptual tenets defended by eugenicists, and also because of the socioeconomic crisis that affected many of these countries in that decade (for more details, see e.g., Kevles' 1998 book *In the Name of Eugenics*).

Regarding comparative anatomy, a major difference is that researchers now commonly use actual photographs—instead of the type of schematic drawings used by authors such as Huber, which can be more easily the reflection of or biases and/or manipulated—and more and more even other visual tools such as MRI-scans and 3D-images to document morphology. For instance, the first photographic atlases of apes, which include such scans and 3D-images and even newer techniques such as photogrammetry have just been published in the last 7 years (Diogo, Pastor, Hartstone-Rose, & Muchlinski, 2014; Diogo et al., 2010, 2012, 2013a, 2013b, 2017). Concerning behavior studies, the contributions of researchers such as Dian Fossey, Birute Galdikas and Jane Goodall in the second half of the 20th century—which were themselves probably the reflection of the changes that begun mainly after the second world war—were crucial for the strikingly fast changes that have occurred since then. As recently emphasized by De Waal (2016), one crucial consequence of those changes is that many researchers such as him are now accepting, for instance, that a major problem within their field has been not the anthropomorphization of nonhuman primates, but instead the nonacceptance that these primates are in fact so much like us in numerous aspects. For instance, they use tools, display complex behaviors, have similar emotions and facial expressions, plan tasks in advance, are able to deal with abstract concepts, and so on. A clear and broader reflection of the change of mentality that has occurred since the second world war is *The Great Ape Project* calling for great apes to be accorded the same basic rights as humans, and even to proposals for placing humans and chimps in the same genus (e.g., Diamond, 1991).

As noted for the above Section of this article, I could not discuss here many other publications providing discussions on the topics covered in this Section, so I am providing here an additional list of works that include interesting discussions and relevant references therein, for those readers that are interested in knowing more details about these topics: Erb (1998), Tattersall (2002), Brattain (2007), Bliss (2012), and the Unesco reports "on race" and "the new statements on race" (1950, 1951, 1952), as well as the scientific works of the Swiss-American primatologist Adolph H. Schultz in the 1950s (e.g., 1950, 1953, 1957).

5 | GENERAL REMARKS

There has been a crucial connection, for more than 2000 years, between studies of the comparative anatomy of humans and nonhuman primates and discussions about our place in nature, the chain of being, and the differences between human groups. This connection mainly started with Galen's descriptions of the "Barbary ape"—an Old World monkey species with a vestigial tail—to infer human anatomy following the notion of human-animal continuity implied by the Greeks' idea of a *scala naturae*. Notably, these monkey anatomical descriptions were subsequently used, for more than one millennium, as the "basis of human anatomy." The rise of Christianity lead to a change in mindset within Europeans, in which nonhuman primates then became to be usually seen in a very negative way, even as the symbol of Satan himself. When nonhuman primates started to be directly studied by Westerners in their non-European environments and in particular in Europe after becoming to be sent to and regularly seen in many European cities, from the 14th century on, this negative view started to change to a more positive one. This more positive vision culminated in Tyson's 1699 work showing that chimps display gross anatomy features that are more similar to ours than to those of monkeys. However, many authors were profoundly discomforted by this human-chimp similarity, and this uneasiness lead to a new tendency to re-emphasize the animal-human discontinuity, which then usually became related to "civilization" instead of anatomy, that is, between Europeans versus non-Europeans plus other primates. Due to the existing tension between the anatomical and the moral/social, quickly after Linnaeus *Systema Naturae* and the emergence of so-called "anatomical racial studies" influenced particularly by Camper's pioneer craniology studies, a new emphasis was placed on anatomy again. However, this emphasis was now more focused on the gap between "civilized" and "noble" Europeans versus "uncivilized," "brute" non-Europeans plus other primates, therefore, dangerously connecting anatomy with the social and moral. This was

the so-called biologization—or as I would prefer to call it, the anatomization—of race.

Unfortunately, this dangerous trend was further reinforced by the biased "results" of the so-called "anatomical and psychological racial studies" and by ideas based on Darwin's "struggle for life and survival of the fittest," which became a crucial part of the propaganda that lead to extremist racist ideas and the rise of eugenics in the end of the 19th and first half of the 20th centuries culminating in Nazism. These historical facts contradict the idea that there is a "progress" in science and society. This is because 2000 years after Galen emphasized the anatomical similarities between nonhuman primates and humans, in the first half of the 20th century the most eminent comparative anatomists were so focused instead on—in some cases literally obsessed by—the differences between not only humans and nonhuman primates, but also between humans themselves. Since the 1950s there has been a remarkable change of view. But, again, one should never take any kind of change toward so-called "progress" in science and society as guaranteed. This is in particular shown by the re-appearance of attitudes and patterns—across the globe—that are in some ways so disturbingly similar to those commonly seen in the first half of the 20th century. Unfortunately, history tends instead to repeat itself, and that is why historical reviews such as this one are particularly timely, useful and necessary in present times.

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