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On the shoulders of giants: Reginald Innes Pocock and integrative mammal research in museums and zoos

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Abstract: Seventy years after his death, Reginald Innes Pocock's prominence in mammalogy is demonstrated by the continuing amount of citations in recent works and the final acceptance of some of his systematic proposals at generic and suprageneric levels. Pocock's ability to synthesize and integrate classical taxonomy with the then dominant polytypic species concept, utilizing both skull and external characters, of zoo and museum animals as unique opportunities for the advancement of mammal comparative biology – including the study of several extinct taxa – are an enduring legacy for mammalogy that deserves to be better appreciated especially among European zoologists.

Keywords: British Museum; integrative zoology; London Zoo; morphology; rhinoceros.

Introduction

Sometimes as zoologists and in particular mammalogists, we might dream of discovering new species of monkeys and felids, of studying near-extinct species, perhaps wishing to contribute to their survival, and meanwhile discovering little-known aspects of their morphology and physiology. In an era dominated by genetics and DNA, it is easy to forget that zoo and natural history museum visitors are mainly attracted by the diversity of animal morphology. And so while it is little appreciated how much work remains to be done in describing animal morphology (considering merely the increasing number of mammal species that have been recognized or discovered in recent

decades), it is safe to say that much of what we know about several of the rarest and recently extinct mammals of the world is due to the work of Reginald Innes Pocock (1863–1947), who was for 19 years Superintendent at the Zoological Society of London, and for many decades a regular collaborator of both London Zoo and the Natural History Museum. Seventy years after his death, we focus on Pocock's career as a mammalogist, although this was preceded by major taxonomic work with scorpions, spiders and other invertebrate groups (Hindle 1948).

Pocock was trained as a taxonomic zoologist and began working at the Entomological section of the British Museum (Natural History) in 1885; yet we believe that his early life in Clifton (Bristol), where he was exposed to the local zoo and museum, had an enduring effect on his interest in mammal taxonomy and behavior. In 1897, he published his first paper on mammals (Species and subspecies of zebras; Pocock 1897), which had been inspired by a zebra specimen at Bristol Museum, and later, when Oldfield Thomas had health problems, helped to complete the last volume of *Book of Antelopes* (Sclater and Thomas 1894–1900).

Pocock in the zoo

He dedicated further occasional notes and articles to mammals until 1904, when he became Superintendent at the London Zoo. Here, he decided from the beginning to make full use of the opportunity to study live animals, and one of his first papers dealt with a young female of the now critically endangered Hainan gibbon *Nomascus hainanus* (Thomas 1892), including descriptions of color changes and sexual cycle (Pocock 1905). Some of his early papers include rather “technical” descriptions of particular primate species, among them the distinctive *Cercocebus hamlyni* (Pocock 1907), while others deal with physiological and behavioral data on primates (Pocock 1906).

Among Pocock's most enduring contributions to mammalogy is the long series of papers devoted to the external morphology of most mammal groups, especially

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carnivores and ungulates, most of them titled “On the [some] external characters of the ...” (koala and some related marsupials, *Orycteropus*, South American edentates, lemurs and *Tarsius*, catarrhine monkeys and apes, Lagomorph rodents, beaver and some squirrels, some hystricomorph rodents, pangolins, several genera of carnivores, Felidae, mongooses, Mustelidae, Lutrinae, chevrotains, ruminant Artiodactyla Cervidae, etc.; we retain here the original names from titles). These studies benefited from his unique position at London Zoo, as remembered by Hindle (1948): “Whilst at the Zoo, where he occupied the old Curator’s house, he was able to observe the habits of the living animals and he found time in the evenings and at week-ends, which he often spent in the Prosectorium (dissecting room), to pursue his studies on those which died”. Among the taxa whose external morphology he described, we should mention in particular *Thylacinus* Temminck, 1824 (1926c), Tarsiidae (1918), *Galeopterus* Thomas, 1908 (1926a), *Daubentonia* É. Geoffroy, 1795 (1918, 1922b), Capromyidae (1926b, 1944a), *Pedetes* Illiger, 1811 (1922a), *Cynogale* Gray, 1836 (1915), *Hemigalus* Jourdan, 1837 (1933b), *Cryptoprocta* Bennett, 1833 (1916), *Orycteropus* G. Cuvier, 1798 (1924a), *Babyrousa* Perry, 1811 and *Hylochoerus* Thomas, 1904 (1943c), Tragulidae (1919), *Okapia* Lankester, 1901 (1936, 1943b), *Ailuropoda* Milne-Edwards, 1870 (1928), *Speothos* Lund, 1839 and *Chrysocyon* C. E. H. Smith, 1839 (1927), Manidae (1911b, 1924b) and some still little-known taxa such as *Lophiomys* Milne-Edwards, 1867 (1911a), *Felis bieti* Milne-Edwards, 1892 (1943a), *Cervus wallichii* G. Cuvier, 1823 (1912, 1942) and *Pardofelis marmorata* (Martin, 1836) (1932b).

Among the now-extinct taxa he studied, other than *Thylacinus*, we should highlight the Falkland fox *Dusicyon australis* (Kerr, 1792) (1913), Schomburgk’s deer *Rucervus schomburgki* (Blyth, 1863) (1943d), the quagga *Equus quagga* Boddaert, 1785 (1897, 1902, 1904, 1905, 1907) and the nearly or totally extinct Waldron’s red colobus *Piliocolobus waldroni* (Hayman, 1936) (not *waldronae* – see Brandon-Jones et al. 2007) (1935a). It was also in this period that he produced the series of papers which won him his Fellowship of the Royal Society, “On the specialized cutaneous glands of ruminants”, which appeared between 1918 and 1919 in the *Proceedings of the Zoological Society*.

Pocock the taxonomist

Papers or monographs written after Pocock’s time at the zoo rank among the classical works on mammalian morphology and taxonomy. They include his “Catalogue of the genus *Felis*” (Pocock 1951), “The Fauna of British India

including Ceylon and Burma – Mammalia” Vols. 1 and 2 (Pocock 1939, 1941), “The leopards of Africa” (Pocock 1932a) – an overlooked issue today – and “The panthers and ounces of Asia” (1930).

Pocock not only described several species and subspecies but also made important efforts to disentangle supraspecific relationships from the taxonomic (for details, see Tables 1 and 2) and phylogenetic point of view, regularly attempting to homologize particular characters (e.g. antlers in cervids – Pocock 1933a). Through the integrative study of craniometric and morphological data, he laid the basis for understanding felid phylogenetic relationships (Pocock 1917), and he was the first to propose the overall classification of Primates into two subgroups Strepsirrhini and Haplorrhini (tarsiers + “pithecoïd primates”) which is still in use today (Groves 2008). He recognized correctly the uniqueness of the African palm civet (*Nandinia* Gray, 1843) and placed it in the monotypic family Nandiniidae (Pocock 1929), a conclusion which is fully supported by new evidence (Gaubert et al. 2005, Wible and Spaulding 2013).

In the light of recent discussion concerning the 20th century history of systematic mammalogy in Europe (Gippoliti and Groves 2012), it is interesting to note that while Pocock was certainly a “lumper” with an overly indulged belief in the subspecies category, his revisionary work always grew out of a classical specimens-based approach. After his death, the majority of his opinions regarding alpha taxonomy were accepted by the classic “Checklist of Palaearctic and Indian Mammals 1758–1946” (Ellerman and Morrison-Scott 1951), although most of the genera proposed were not accepted (following Simpson 1945). Specifically, Simpson (1945), in the review section of his monograph, explicitly expressed an adherence to some of Pocock’s classifications, though some divisions were scaled down in rank, but also an opinion that some of Pocock’s classifications (e.g. pangolins, procyonids) were unnecessary and inconvenient taxonomic inflations, especially if these higher taxa were monotypic. Concerning Pocock’s genera and higher taxa (see Tables 1 and 2) in the classification section of Simpson’s monograph (1945), 16 taxa were omitted, 15 were synonymized, six were scaled down in rank and five were accepted. The motivation to raise some previously recognized species groups/subgenera to genera was often motivated, as he acknowledged himself (e.g. Pocock 1935b), by a desire to stabilize the contentious generic nomenclature.

The fact that 50 of Pocock’s papers are cited in the latest edition of *Mammal Species of the World* (Wilson and Reeder 2005), and a search of his name across the same monograph results in 268 records (for comparison: Elliot 214; Thomas 2901; Matschie 315; Miller 675; Schwarz 90;

Table 1: List of suborder, families, subfamilies, tribe, genera, subgenera, species and subspecies created by Pocock and still valid in Wilson and Reeder (2005).

Order	Suborder	Family	Subfamily	Tribe	Genus	Subgenus	Species	Subspecies	Year
Pilosa		Cyclopedidae							1924
Primates	Haplorrhini								1918
Primates			Callicebinae						1925
Primates					<i>Allenopithecus</i>		<i>nigroviridis</i>	<i>cephodes</i>	1907
Primates					<i>Cercopithecus</i>		<i>cephus</i>		1907
Primates					<i>Cercopithecus</i>		<i>doggetti</i>		1907
Primates					<i>Cercopithecus</i>		<i>hamlyni</i>		1907
Primates					<i>Cercopithecus</i>		<i>hamlyni</i>	<i>hamlyni</i>	1907
Primates					<i>Cercopithecus</i>		<i>sclateri</i>		1904
Primates					<i>Chlorocebus</i>		<i>tantalus</i>	<i>budgetti</i>	1907
Primates					<i>Macaca</i>		<i>sinica</i>	<i>aurifrons</i>	1931
Primates					<i>Papio</i>		<i>ursinus</i>	<i>griseipes</i>	1911
Primates					<i>Semnopithecus</i>		<i>ajax</i>		1928
Primates					<i>Semnopithecus</i>		<i>hector</i>		1928
Rodentia			Callosciurinae						1923
Rodentia				Marmotini					1922
Rodentia		Thryonomyidae							1922
Rodentia			Dolichotinae		<i>Myoprocta</i>		<i>pratti</i>		1913
Rodentia						<i>Paramanis</i>			1824
Pholidota						<i>Uromanis</i>			1924
Carnivora					<i>Felis</i>		<i>chaus</i>	<i>kelaarti</i>	1939
Carnivora					<i>Felis</i>		<i>chaus</i>	<i>prateri</i>	1939
Carnivora					<i>Felis</i>		<i>margarita</i>	<i>airensis</i>	1951
Carnivora					<i>Felis</i>		<i>margarita</i>	<i>meinertzhageni</i>	1938
Carnivora					<i>Felis</i>		<i>silvestris</i>	<i>foxi</i>	1944
Carnivora					<i>Felis</i>		<i>silvestris</i>	<i>tristrami</i>	1944
Carnivora					<i>Leopardus</i>		<i>geoffroyi</i>	<i>euxanthus</i>	1940
Carnivora					<i>Leopardus</i>		<i>geoffroyi</i>	<i>leucobaptus</i>	1940
Carnivora					<i>Leopardus</i>		<i>geoffroyi</i>	<i>paraguayae</i>	1940
Carnivora					<i>Leopardus</i>		<i>pajeros</i>	<i>budini</i>	1941
Carnivora					<i>Leopardus</i>		<i>pajeros</i>	<i>steinbachii</i>	1941
Carnivora					<i>Leopardus</i>		<i>pardalis</i>	<i>steinbachii</i>	1941
Carnivora					<i>Leopardus</i>		<i>wiedii</i>	<i>boliviae</i>	1941
Carnivora					<i>Leopardus</i>		<i>wiedii</i>	<i>salvinus</i>	1941
Carnivora					<i>Leptailurus</i>		<i>serval</i>	<i>lipostictus</i>	1907
Carnivora					<i>Leptailurus</i>		<i>serval</i>	<i>panstictus</i>	1907
Carnivora					<i>Prionailurus</i>		<i>bengalensis</i>	<i>trevelyani</i>	1939
Carnivora					<i>Prionailurus</i>		<i>rubiginosus</i>	<i>philipsi</i>	1939
Carnivora					<i>Puma</i>		<i>concolor</i>	<i>cabreriae</i>	1940
Carnivora			Pantherinae						1917
Carnivora					<i>Panthera</i>		<i>pardus</i>	<i>delacouri</i>	1930
Carnivora					<i>Panthera</i>		<i>tigris</i>	<i>sumatrae</i>	1929
Carnivora					<i>Paguma</i>		<i>larvata</i>	<i>neglecta</i>	1934

Table 1 (continued)

Order	Suborder	Family	Subfamily	Tribe	Genus	Subgenus	Species	Subspecies	Year
Carnivora					<i>Paguma</i>		<i>larvata</i>	<i>nigriceps</i>	1939
Carnivora					<i>Paradoxurus</i>		<i>hermaphroditus</i>	<i>scindiae</i>	1934
Carnivora					<i>Paradoxurus</i>		<i>hermaphroditus</i>	<i>vellerosus</i>	1934
Carnivora					<i>Paradoxurus</i>		<i>jerdoni</i>	<i>caniscus</i>	1933
Carnivora					<i>Cynogale</i>		<i>bennettii</i>	<i>lowei</i>	1933
Carnivora			Prionodontinae						1933
Carnivora					<i>Civettictis</i>				1915
Carnivora					<i>Genetta</i>		<i>johnstoni</i>		1907
Carnivora					<i>Poiana</i>		<i>leightoni</i>		1907
Carnivora					<i>Viverricula</i>		<i>indica</i>	<i>baptistae</i>	1933
Carnivora					<i>Viverricula</i>		<i>indica</i>	<i>klossi</i>	1933
Carnivora					<i>Viverricula</i>		<i>indica</i>	<i>mayori</i>	1933
Carnivora					<i>Viverricula</i>		<i>indica</i>	<i>wellsi</i>	1933
Carnivora					<i>Mungotictis</i>				1915
Carnivora					<i>Mungotictis</i>		<i>decemlineata</i>	<i>lineatus</i>	1915
Carnivora		Nandiniidae							1929
Carnivora					<i>Herpestes</i>		<i>fuscus</i>	<i>rubidior</i>	1937
Carnivora					<i>Herpestes</i>		<i>vitticollis</i>	<i>inornatus</i>	1941
Carnivora					<i>Paracynictis</i>				1916
Carnivora					<i>Canis</i>		<i>lupus</i>	<i>arabs</i>	1934
Carnivora					<i>Canis</i>		<i>lupus</i>	<i>arctos</i>	1935
Carnivora					<i>Canis</i>		<i>lupus</i>	<i>orion</i>	1935
Carnivora					<i>Vulpes</i>		<i>rueppellii</i>	<i>sabaea</i>	1934
Carnivora					<i>Ursus</i>		<i>thibetanus</i>	<i>laniger</i>	1932
Carnivora					<i>Aonyx</i>		<i>cinerea</i>	<i>nirnai</i>	1940
Carnivora					<i>Hydrictis</i>				1921
Carnivora					<i>Lutrogale</i>		<i>perspicillata</i>	<i>sindica</i>	1940
Carnivora					<i>Arctonyx</i>		<i>collaris</i>	<i>consul</i>	1940
Carnivora					<i>Martes</i>		<i>flavigula</i>	<i>robinsoni</i>	1936
Carnivora					<i>Mellivora</i>		<i>capensis</i>	<i>pumilio</i>	1946
Carnivora					<i>Mellivora</i>		<i>capensis</i>	<i>signata</i>	1909
Carnivora					<i>Mustela</i>		<i>eversmannii</i>	<i>admirata</i>	1936
Carnivora					<i>Mustela</i>		<i>putorius</i>	<i>anglia</i>	1936
Carnivora					<i>Mustela</i>		<i>putorius</i>	<i>rothschildi</i>	1932
Carnivora					<i>Vormela</i>		<i>peregusna</i>	<i>syriaca</i>	1936
Carnivora					<i>Bassaricyon</i>		<i>beddardi</i>		1921
Perissodactyla					<i>Equus</i>		<i>hemionus</i>	<i>blanfordi</i>	1947
Artiodactyla					<i>Cervus</i>		<i>elaphus</i>	<i>kansuensis</i>	1912
Artiodactyla					<i>Rucervus</i>		<i>duvaucelii</i>	<i>branderi</i>	1943
Artiodactyla					<i>Tragelaphus</i>		<i>scriptus</i>	<i>fasciatus</i>	1900
Artiodactyla					<i>Tragelaphus</i>		<i>scriptus</i>	<i>ornatus</i>	1900
Artiodactyla					<i>Naemohedus</i>		<i>baileyi</i>		1914

Number of created taxa (86): Pilosa (1); Primates (13); Rodentia (5); Pholidota (2); Carnivora (59) [Feliformia (42), Caniformia (17)]; Perissodactyla (1); Artiodactyla (5).

Table 2: List of families, subfamilies, genera, species and subspecies created by Pocock (with the original version of names), but not valid in Wilson and Reeder (2005).

Order	Family	Subfamily	Genus	Species	Subspecies	Year	Synonym of
Das.			<i>Notoctonus</i>			1926	<i>Dasyurus</i> É. Geoffroy 1796
Das.			<i>Satanellus</i>			1926	<i>Dasyurus</i> É. Geoffroy 1796
Das.			<i>Stictophonus</i>			1926	<i>Dasyurus</i> É. Geoffroy 1796
Pri.			<i>Hapalemur</i>	<i>schlegeli</i>		1917	<i>Hapalemur griseus griseus</i> (Link 1795)
Pri.			<i>Leontocebus</i>	<i>leoninus</i>		1914	<i>Leontopithecus rosalia</i> (Linnaeus 1766)
Pri.			<i>Cercopithecus</i>	<i>rufotinctus</i>		1907	<i>Cercopithecus albobularis albobularis</i> Pousargues 1896
Pri.			<i>Cercopithecus</i>	<i>albobularis</i>	<i>beirensis</i>	1907	<i>Cercopithecus albobularis erythrarchus</i> Peters 1852
Pri.			<i>Cercopithecus</i>	<i>stairsi</i>	<i>mossambicus</i>	1907	<i>Cercopithecus albobularis erythrarchus</i> Peters 1852
Pri.			<i>Cercopithecus</i>	<i>kolbi</i>	<i>hindei</i>	1907	<i>Cercopithecus albobularis kolbi</i> Neumann 1902
Pri.			<i>Cercopithecus</i>	<i>albobularis</i>	<i>rufilatus</i>	1907	<i>Cercopithecus albobularis monoides</i> I. Geoffroy 1841
Pri.			<i>Cercopithecus</i>	<i>stuhlmanni</i>	<i>nirigenis</i>	1907	<i>Cercopithecus mitis mitis</i> Wolf 1822
Pri.			<i>Cercopithecus</i>	<i>stuhlmanni</i>	<i>carruthersi</i>	1907	<i>Cercopithecus mitis stuhlmanni</i> Matschie 1893
Pri.			<i>Cercopithecus</i>	<i>neglectus</i>	<i>brazziformis</i>	1907	<i>Cercopithecus neglectus</i> Schlegel 1876
Pri.			<i>Cercopithecus</i>	<i>ezrae</i>		1908	<i>Cercopithecus neglectus</i> Schlegel 1876
Pri.			<i>Cercopithecus</i>	<i>nictitans</i>	<i>laglaizei</i>	1907	<i>Cercopithecus nictitans nictitans</i> (Linnaeus 1766)
Pri.			<i>Cercopithecus</i>	<i>pygerythrus</i>	<i>johnstoni</i>	1907	<i>Chlorocebus pygerythrus hilgerti</i> (Neumann 1902)
Pri.			<i>Cercopithecus</i>	<i>pygerythrus</i>	<i>whytei</i>	1907	<i>Chlorocebus pygerythrus rufoviridis</i> (I. Geoffroy 1843)
Pri.			<i>Cercopithecus</i>	<i>tantalus</i>	<i>alexandri</i>	1909	<i>Chlorocebus tantalus tantalus</i> (Ogilby 1841)
Pri.			<i>Cercopithecus</i>	<i>jamrachi</i>		1906	<i>Lophocebus albigena johnstoni</i> (Lydekker 1900)
Pri.			<i>Cerocebus</i>	<i>hamlyni</i>		1906	<i>Lophocebus aterrimus</i> (Oudemans 1890)
Pri.			<i>Cerocebus</i>	<i>nemestrina</i>	<i>blythii</i>	1931	<i>Macaca leonina</i> (Blyth 1863)
Pri.			<i>Macaca</i>	<i>mulatta</i>	<i>mcmahoni</i>	1932	<i>Macaca mulatta</i> (Zimmermann 1780)
Pri.			<i>Macaca</i>	<i>radiata</i>	<i>diluta</i>	1931	<i>Macaca radiata</i> (É. Geoffroy 1812)
Pri.			<i>Macaca</i>	<i>sinica</i>	<i>inaurea</i>	1931	<i>Macaca sinica sinica</i> (Linnaeus 1771)
Pri.			<i>Cercopithecus</i>	<i>talapoin</i>	<i>ansorgei</i>	1907	<i>Miopithecus talapoin</i> (Schreber 1774)
Pri.			<i>Presbytiscus</i>			1924	<i>Rhinopithecus Milne-Edwards</i> 1872
Pri.			<i>Pithecius</i>	<i>entellus</i>	<i>achates</i>	1928	<i>Semnopithecus dussumieri</i> I. Geoffroy 1843
Pri.			<i>Pithecius</i>	<i>entellus</i>	<i>elissa</i>	1928	<i>Semnopithecus dussumieri</i> I. Geoffroy 1843
Pri.			<i>Pithecius</i>	<i>entellus</i>	<i>lulus</i>	1928	<i>Semnopithecus dussumieri</i> I. Geoffroy 1843
Pri.			<i>Pithecius</i>	<i>entellus</i>	<i>priamellus</i>	1928	<i>Semnopithecus dussumieri</i> I. Geoffroy 1843
Pri.			<i>Pithecius</i>	<i>entellus</i>	<i>aeneas</i>	1928	<i>Semnopithecus hypoleucos</i> Blyth 1841
Pri.			<i>Pithecius</i>	<i>entellus</i>	<i>achilles</i>	1928	<i>Semnopithecus schistaceus</i> Hodgson 1840
Pri.			<i>Trachypithecus</i>	<i>pyrrhus</i>	<i>stresemanni</i>	1935	<i>Trachypithecus (T.) auratus auratus</i> (É. Geoffroy 1812)
Pri.			<i>Pithecius</i>	<i>pyrrhus</i>	<i>atrior</i>	1928	<i>Trachypithecus (T.) barbei</i> (Blyth 1847)
Pri.			<i>Trachypithecus</i>	<i>obscurus</i>	<i>corax</i>	1935	<i>Trachypithecus (T.) obscurus flavicauda</i> (Elliot 1910)
Rod.			<i>Tamiodes</i>			1923	<i>Funambulus</i> Lesson 1835
Rod.			<i>Marmotops</i>			1922	<i>Marmota Blumenbach</i> 1779
Rod.			<i>Arvicanthis</i>	<i>niloticus</i>	<i>naso</i>	1934	<i>Arvicanthis niloticus</i> (É. Geoffroy 1803)
Rod.						1922	<i>Thryonomidae</i> Pocock 1922
Rod.						1922	<i>Erethizontinae</i> Bonaparte 1845
Eri.			<i>Paraechinus</i>	<i>dorsalis</i>	<i>albior</i>	1934	<i>Paraechinus aethiopicus albatrus</i> Thomas 1922

Table 2 (continued)

Order	Family	Subfamily	Genus	Species	Subspecies	Year	Synonym of
Car.		Acinonychinae				1917	Felinae Fischer de Waldheim 1817
Car.			<i>Acinonyx</i>	<i>rex</i>		1927	<i>Acinonyx jubatus jubatus</i> (Schreber 1775)
Car.			<i>Badiofelis</i>			1932	<i>Catopuma</i> Severtzov 1858
Car.			<i>Felis</i>	<i>bieti</i>	<i>vellerosa</i>	1943	<i>Felis silvestris ugandae</i> Schwann 1904 ^a
Car.			<i>Felis</i>	<i>lybica</i>	<i>brockmani</i>	1944	<i>Felis silvestris ocreata</i> Gmelin 1791
Car.			<i>Felis</i>	<i>lybica</i>	<i>pyrrhus</i>	1944	<i>Felis silvestris mellandi</i> Schwann 1904
Car.			<i>Felis</i>	<i>lybica</i>	<i>lowei</i>	1944	<i>Felis silvestris lybica</i> Forster 1780
Car.			<i>Felis</i>	<i>lybica</i>	<i>lynesi</i>	1944	<i>Felis silvestris lybica</i> Forster 1780
Car.			<i>Felis</i>	<i>silvestris</i>	<i>euxina</i>	1983	<i>Felis silvestris silvestris</i> Schreber 1777
Car.			<i>Felis</i>	<i>lybica</i>	<i>foxi</i>	1944	<i>Felis silvestris silvestris</i> Schreber 1777
Car.			<i>Colocolo</i>			1941	<i>Leopardus</i> Gray 1842
Car.			<i>Lynchailurus</i>	<i>pajeros</i>	<i>huina</i>	1941	<i>Leopardus colocolo colocolo</i> (Molina 1782)
Car.			<i>Lynchailurus</i>	<i>pajeros</i>	<i>garleppi</i>	1941	<i>Leopardus pajeros thomasi</i> (Lönnberg 1913)
Car.			<i>Leopardus</i>	<i>wiedii</i>	<i>pardictis</i>	1941	<i>Leopardus wiedii wiedii</i> (Schinz 1821)
Car.			<i>Leopardus</i>	<i>wiedii</i>	<i>pirrensis</i>	1941	<i>Leopardus wiedii amazonicus</i> (Cabrera 1917)
Car.			<i>Felis</i>	<i>servalina</i>	<i>poliotricha</i>	1907	<i>Leptailurus serval pantastictus</i> (Pocock 1907)
Car.			<i>Panthera</i>	<i>pardus</i>	<i>saxicolor</i>	1927	<i>Panthera pardus nimr</i> (Hemprich and Ehrenberg 1833)
Car.			<i>Panthera</i>	<i>pardus</i>	<i>jarvisi</i>	1932	<i>Panthera pardus nimr</i> (Hemprich and Ehrenberg 1833)
Car.			<i>Panthera</i>	<i>pardus</i>	<i>sindica</i>	1930	<i>Panthera pardus nimr</i> (Hemprich and Ehrenberg 1833)
Car.			<i>Panthera</i>	<i>pardus</i>	<i>bedfordi</i>	1930	<i>Panthera pardus japonensis</i> (Gray 1862)
Car.			<i>Panthera</i>	<i>pardus</i>	<i>millardi</i>	1930	<i>Panthera pardus fusca</i> (Meyer 1794)
Car.			<i>Panthera</i>	<i>pardus</i>	<i>adersi</i>	1932	<i>Panthera pardus pardus</i> (Linnaeus 1758)
Car.			<i>Panthera</i>	<i>pardus</i>	<i>adusta</i>	1927	<i>Panthera pardus pardus</i> (Linnaeus 1758)
Car.			<i>Panthera</i>	<i>pardus</i>	<i>brockmani</i>	1932	<i>Panthera pardus pardus</i> (Linnaeus 1758)
Car.			<i>Panthera</i>	<i>pardus</i>	<i>puella</i>	1932	<i>Panthera pardus pardus</i> (Linnaeus 1758)
Car.			<i>Panthera</i>	<i>pardus</i>	<i>shortridgei</i>	1932	<i>Panthera pardus pardus</i> (Linnaeus 1758)
Car.			<i>Panthera</i>	<i>tigris</i>	<i>styani</i>	1929	<i>Panthera tigris amoyensis</i> (Hilzheimer 1905)
Car.		Arctogalidiinae				1933	<i>Paradoxurinae</i> Gray 1864
Car.			<i>Paradoxurus</i>	<i>hermaphroditus</i>	<i>laneus</i>	1934	<i>Paradoxurus hermaphroditus hermaphroditus</i> (Pallas 1777)
Car.			<i>Paradoxurus</i>	<i>hermaphroditus</i>	<i>cantori</i>	1934	<i>Paradoxurus hermaphroditus musanga</i> (Raffles 1821)
Car.			<i>Hemigalus</i>	<i>derbyanus</i>	<i>invisus</i>	1933	<i>Hemigalus derbyanus derbyanus</i> (Gray 1837)
Car.			<i>Viverra</i>	<i>civetta</i>	<i>matschiei</i>	1933	<i>Civettictis civetta schwarzi</i> Cabrera 1929
Car.			<i>Poiana</i>	<i>richardsonii</i>	<i>liberiensis</i>	1908	<i>Poiana leightoni</i> Pocock 1907
Car.			<i>Moschothera</i>			1933	<i>Viverra</i> Linnaeus 1758
Car.		Fossinae				1915	<i>Eupleridae</i> Chenu 1850
Car.			<i>Galidictis</i>	<i>eximius</i>		1915	<i>Galidictis fasciata fasciata</i> (Gmelin 1788)
Car.			<i>Mungotictis</i>	<i>substriatus</i>		1915	<i>Mungotictis decemlineata decemlineata</i> (Granddier 1867)
Car.		Mungotidae				1919	<i>Herpestidae</i> Bonaparte 1845
Car.			<i>Hyaena</i>	<i>hyaena</i>	<i>sultana</i>	1934	<i>Hyaena hyaena</i> (Linnaeus 1758)
Car.			<i>Canis</i>	<i>lupus</i>	<i>rex</i>	1935	<i>Canis lupus hattai</i> Kishida 1931
Car.			<i>Cuon</i>	<i>alpinus</i>	<i>adustus</i>	1941	<i>Cuon alpinus alpinus</i> (Pallas 1811)

Table 2 (continued)

Order	Family	Subfamily	Genus	Species	Subspecies	Year	Synonym of
Car.	Ailuropodidae	Taxidiinae	<i>Cuon</i>	<i>javanicus</i>	<i>fumosus</i>	1936	<i>Cuon alpinus alpinus</i> (Pallas 1811)
Car.			<i>Cuon</i>	<i>javanicus</i>	<i>infuscus</i>	1936	<i>Cuon alpinus alpinus</i> (Pallas 1811)
Car.			<i>Cuon</i>	<i>javanicus</i>	<i>laniger</i>	1936	<i>Cuon alpinus alpinus</i> (Pallas 1811)
Car.			<i>Cuon</i>	<i>javanicus</i>	<i>jason</i>	1936	<i>Cuon alpinus hesperius</i> Afanasjev and Zolotarev 1935
Car.						1916 ^b	Ursidae Fischer de Waldheim 1817
Car.			<i>Arcticonus</i>			1917	<i>Ursus</i> Linnaeus 1758
Car.						1920	Mustelidae Fischer 1817
Car.			<i>Plesiogale</i>			1921	<i>Mustela</i> Linnaeus 1758
Car.			<i>Putorius</i>	<i>putorius</i>	<i>aureus</i>	1936	<i>Mustela eversmannii eversmanni</i> Lesson 1827
Car.			<i>Vormela</i>	<i>peregrusna</i>	<i>euxina</i>	1936	<i>Vormela peregrusna peregrusna</i> (Güldenstädt 1770)
Car.			<i>Vormela</i>	<i>peregrusna</i>	<i>ornata</i>	1936	<i>Vormela peregrusna pallidior</i> Stroganov 1948
Per.			<i>Equus</i>	<i>burghelli</i>	<i>selousii</i>	1897	<i>Equus burghellii antiquorum</i> (C. H. Smith 1841)
Per.			<i>Equus</i>	<i>burghelli</i>	<i>wahlbergi</i>	1897	<i>Equus burghellii antiquorum</i> (C. H. Smith 1841)
Per.			<i>Equus</i>	<i>burghelli</i>	<i>crawshayi</i>	1897	<i>Equus burghellii crawshayi</i> De Winton 1896
Per.			<i>Equus</i>	<i>grevyi</i>	<i>berberensis</i>	1902	<i>Equus grevyi</i> Oustalet 1882
Per.			<i>Microhippus</i>	<i>hemionus</i>	<i>bahram</i>	1947	<i>Equus hemionus onager</i> Boddaert 1785
Per.			<i>Equus</i>	<i>quagga</i>	<i>dantelli</i>	1904	<i>Equus quagga</i> Boddaert 1785
Art.		Odocoileini				1923	Capreolinae Brookes 1828
Art.		Pudinae				1923	Capreolinae Brookes 1828
Art.	Madoquinae Oreotraginae		<i>Procapra</i>			1923	<i>Muntiacus</i> Rafinesque 1815
Art.			<i>Thacervus</i>			1943	<i>Rucervus</i> Hodgson 1838
Art.						1910	Antilopinae Gray 1821
Art.						1910	Antilopinae Gray 1821
Art.			<i>Gazella</i>	<i>rufifrons</i>	<i>hasleri</i>	1912	<i>Eudorcas rufifrons laevipes</i> (Sundevall 1847)
Art.			<i>Rhynchotragus</i>	<i>hodsoni</i>		1926	<i>Madoqua guentheri smithii</i> Thomas 1901
Art.			<i>Prodocas</i>			1918	<i>Procapra</i> Hodgson 1846
Art.			<i>Limnotragus</i>			1900	<i>Tragelaphus</i> de Blainville 1816
Art.			<i>Tragelaphus</i>	<i>delamerei</i>		1900	<i>Tragelaphus scriptus sylvaticus</i> (Sparman 1780)
Art.			<i>Capricornis</i>	<i>sumatraensis</i>	<i>robinsoni</i>	1908	<i>Capricornis sumatraensis</i> (Bechstein 1799)
Art.			<i>Capricornis</i>	<i>sumatraensis</i>	<i>jamrachi</i>	1908	<i>Capricornis thar</i> (Hodgson 1831)
Art.			<i>Capricornis</i>	<i>sumatraensis</i>	<i>rodoni</i>	1908	<i>Capricornis thar</i> (Hodgson 1831)
Art.			<i>Capricornis</i>	<i>sumatraensis</i>	<i>humei</i>	1908	<i>Capricornis thar</i> (Hodgson 1831)
Art.			<i>Naemorhedus</i>	<i>hodgsoni</i>		1908	<i>Nemorhaedus goral</i> (Hardwicke 1825)
Art.			<i>Aegoryx</i>			1918	<i>Oryx</i> de Blainville 1816
Art.			<i>Oryx</i>	<i>leucoryx</i>	<i>latipes</i>	1934	<i>Oryx leucoryx</i> (Pallas 1777)

Number of created taxa (117): Dasyuromorphia (3); Primates (32); Rodentia (5); Erinaceomorpha (1); Pholidota (2); Carnivora (52); [Feliformia (39); Felidae 27, Viverridae 7, Eupleridae 3, Herpestidae 1, Hyainidae 1; Caniformia (13): Canidae 6, Ursidae 2, Mustelidae 5]; Perissodactyla (6); Artiodactyla (18).

Das., Dasyuromorphia; Pri., Primates; Rod., Rodentia; Eri., Erinaceomorpha; Car., Carnivora; Per., Perissodactyla; Art., Artiodactyla.

^aRather synonym of *Felis bieti*.

^bRather 1921.

Groves 435), gives further evidence of his enduring role in the field of mammalogical systematics. Comparing his “taxonomic rating”, expressed here as the number of valid species and subspecies of African and Asian primates described and recognized by him, he stands with 35% between Matschie and Elliot (both 16%) and Miller (44%) and Thomas (54%) (for details see Groves 2008, and Tables 1 and 2). For some additional points, see the section “Critical evaluation”.

Pocock’s numerous studies are characterized not only by extensive descriptions and dichotomous analyses useful for the recognition of specific characters, but they are also figurative studies. As was the custom in the scientific literature of the 1800s and the early 1900s, the texts were accompanied by a rich iconographic complement, which over time would be replaced by photography and come to be much reduced in specialized journals. In this way, he was able to apply his talent in painting and drawing to the need to provide clear pictures of the characteristics of the animals studied, with a style that recalls the field manuals and guides much in use today. Pocock specified the morphology of investigated taxa comprehensively – muzzle, rhinarium, palate, tongue, sublingual area, ear, facial vibrissae, cheek-pouch, claws, fore and hind foot, pouch (in marsupials), anal and genital area, penis, baculum, glands, tail, mammae or mammary area (marsupials) – and so contributed to the standardization of data collecting on mammals (Brown 1971, Brown and Yalden 1973, Ansell 1965).

Some might consider Pocock to be the author of rather technical morphological and taxonomic reports, but his papers often include interesting biological interpretations: recognition marks in antelopes, warning colorations in insectivores and carnivores, coloration in perissodactyls, juvenile colorations in lions (see, e.g. Pocock 1908, 1909, 1911c) and also the description of behavior, such as vocalizations of the siamang (Pocock 1910). For a basic overview and a complete list of Pocock’s papers, see Hindle (1948).

Pocock and the rhinoceros

The rich material of the British Museum at the time allowed Pocock to examine in detail some of the peculiar features of the skull of the Asian rhinoceroses, which have been dramatically extirpated from most of their original ranges over the last few centuries (Amin et al. 2006). Other British zoologists had studied these animals, using mostly the materials preserved at the then British Museum or at the Royal College of Surgeons.

Edward Blyth had published a memoir on the Asian rhinoceroses (Blyth 1862), and a few years later, Gray

described the characters of the skull of both Asian and African species (Gray 1867) and published two catalogs of the specimens preserved in London (Gray 1869, 1873a). In 1873, Gray studied specifically the dental morphology of rhinoceroses (Gray 1873b); similar work was taken up by Flower and dealt more fully with the diagnostic characters of the skulls of the three Asian species (Flower 1876). These studies converged in Pocock’s first publication on rhinoceroses (Pocock 1944b), in which he expanded the discussion of diagnostic features of the skulls of the three Asian species, focusing on the peculiar shape of the premaxillae, providing important information for taxonomy and, in particular, describing and illustrating the intraspecific variability of these bones in younger and older specimens. One year later, he published an accurate description of the nasal bones of Asian rhinoceroses, describing an old male skull of *Rhinoceros sondaicus inermis* Lesson, 1838 from the Sundarbans with its unusual ossified septum and illustrating this peculiar characteristic (Pocock 1945a,b). This latter taxon, exterminated before 1925 and known from only 11 specimens preserved in the world’s museums (Rookmaaker 1997), is another example of the documentation of an extinct taxon by Pocock. In the same year, Pocock’s studies expanded the diagnoses for the recognition of the Asian species (Pocock 1945a,b) and, as he himself writes in the preface, correcting some observations previously made by Flower in 1876 and taking into account the publication of the American paleontologist Colbert (Colbert 1942); the mesopterygoid fossa and vomer are well documented, as are the molars.

Two of Pocock’s last publications (Pocock 1946a,b) concern a significant detail of features of the second upper premolar in *Rhinoceros sondaicus* Desmarest, 1822, showing the importance that this type of investigation has in mammalian taxonomy, and contain a brief discussion of sexual dimorphism. It was a tough job, considering the still not very clear difference between sexes as observed in the skulls of the three Asian rhinoceroses at different age stages. All these studies were realized, thanks to the richness of the material stored at the British Museum (Natural History).

Critical evaluation

Although we consider Pocock’s contribution in general as enormous and inspiring, it is correct also to note some critical points concerning his work and personality. As pointed out by Brandon-Jones (1993, 2004 and personal communication), Brandon-Jones et al. (2004), Groves (2008) and Gippoliti (2017), some parameters in his work

Table 3: List of eponyms, responsible authors and status according to Wilson and Reeder (2005).

List of eponyms	Authors	Status
<i>Cercopithecus erythrogaster pococki</i>	Grubb et al. 1999	Valid
<i>Mus mayori pococki</i>	Ellerman 1947	Synonym of <i>Mus (Coelomys) mayori</i>
<i>Rattus pococki</i>	Ellerman 1941	Valid
<i>Leptailurus serval pococki</i>	Cabrera 1910	Valid
<i>Pocockictis</i>	Kretzoi 1947	Synonym of <i>Mustela</i>
<i>Equus burchelli pococki</i>	Brasil and Pennetier 1909	Synonym of <i>Equus burchellii antiquorum</i>

were ill-founded, even considering the extensiveness of his scientific field and productivity:

1. His rather lumping approach in alpha-taxonomy overlooked some distinct taxa, and his views have been accepted/fixed by others much more easily due to his influence; he worked, however, in a historical period where biology was shifting taxonomy toward oversimplification (Gippoliti 2017, Gippoliti et al. 2018);
2. He made some revisions based on very limited material and geographic coverage; but it is fair to remember that multi-museum revisions were not common at the time;
3. He made mistakes (e.g. Robertson et al. 2017) – although this could be considered usual in every scientific work. He appears at times to have been arrogant and egotistical, ignoring the work and taxa description of his predecessors and contemporaries and replacing them by new names of his own, as in his work on *Semnopithecus* Desmarest, 1822 (Brandon-Jones 2004).

No wonder that these points have led some modern renowned taxonomists to recognize him often as a superb morphologist, but a poorer taxonomist, and reproach him for being overly ignorant about biogeography.

Conclusion

Pocock's contribution to mammalogy was enormous and in many ways laid the foundation for the work of following generations of zoologists and morphologists. His life and work (for more details see Hindle 1948, Groves 2008, Jayaraman 2012) can be a source of contemplation and inspiration (see also Table 3).

His studies are often used in current total-evidence phylogenetic analyses as sources of data in attempts to detect phylogenetic relationships and conflicts among data partitions for particular taxa, and are also used to reconstruct the evolution of particular morphological characters (e.g. Wozencraft 1989; Salles 1992, Mattern

and McLennan 2000, Vrba and Schaller 2000, Zrzavý and Řičáňková 2004, Goswami and Friscia 2010). Additionally, his studies provide a source of diagnostic characters of recognized groups or species (e.g. Groves and Grubb 2011, Kryštufek et al. 2016). Nonetheless, it must be admitted that too often we are left with an absence of the basic information on many species that would be necessary for integrative phylogenetic evaluations (Wiens and Collins 2004, Guillerme and Cooper 2016). As the work of Pocock was closely associated with the Zoological Gardens, we could wish for a better documentation of species held and bred in *ex situ* institutions, alive or after their demise, by storing them in museum collections. Unfortunately this is still not common practice (Groves 1982, Kitchener 1997, Gippoliti and Kitchener 2007).

As the quality of phylogenetic analyses and meta-analyses is closely related to the number of taxa sampled and the number of positively scored characters, scientific journals and reviewers should encourage publications of primary morphological data in this current era, so dominated by genetic works.

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