Comparative anatomy of the coccyx

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COMPARATIVE ANATOMY OF THE COCCYX

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INTRODUCTION

Comparative anatomy of the coccyx refers to the presence or absence of a tail. The question is whether we can consider the presence of a human-type coccyx as the absence of a tail. This subject does not seem to have appealed to many researchers, and the most complete works mainly date back to the 19th century. We will try to describe the animals that have a coccyx, identify possible homologies, and examine the phylogenetic aspects and the evolutionary benefits as part of bipedalism.

THE TAIL

Anatomy

-General anatomy: What does a tail comprise [9]?

The superior end, or anterior end in zoology, is the sacrum, and is generally defined as the set of vertebrae joined to the hipbones. The idea that the coccyx is a rudimentary representation of a tail is old but not clearly defined; and hence requires clarification [8]. The tail is an extension of the spine beyond this particular bone and is composed of several fused vertebrae joined to the pelvis and called the sacrum. The number of caudal vertebrae varies according to the length of the tail. In some hominoids including humans, some rudimentary vertebrae are fused together, forming the coccyx.

There are two 2 types of caudal vertebrae: anterior and posterior.

There are few anterior caudal vertebrae, between 2 and 11, with a very similar morphology to the lumbar vertebrae; they have a neural arch, articular apophyses, and spinous apophysis. They sometimes comprise the entire tail, as seen in the Myrmecophagidae (Anteaters), Pholidota (Pangolin), Potamogales (insectivorous mammal), Sirenia (Manatee) [Fig 2], and Cetaceans, and are sometimes completely absent as in the Chiroptera (Bats) [Fig 3] and Hyracoids (Hyraxes). Conversely, the posterior caudal vertebrae are cylindrical, biconvex, without a neural arc and with rudimentary processes; there are remnants of only the transverse and spinous apophyses. The joints are formed by vertebral discs.
Gradually, as we progress towards the end of the tail, all the vertebral features disappear [Fig 4] [Fig 5], and the vertebrae essentially take the form of a fused length of bone, like the tailbone of the Hominoids. This bone remains exclusively in Chiroptera (Bats) [Fig 6] and Hyracoids (Hyraxes). Some Monodelphes and Edentata have coccygeal vertebrae fused to the sacrum. [20]. However, their morphology differs from that of primates whose sacral part is not concave, is higher than it is wide and forms an angle with the lumbar spine. Some breeds of sheep and dogs also have very small caudals that resemble a coccyx [13].

The tail is therefore an organ whose anatomical structures show a decreasing complexity from the proximal to distal direction. Its distal portion cannot be equated to the equivalent of a coccyx, in that it has greater mobility, owing to the disappearance of the articular processes, reduction in the thickness of the joint capsules, and large size of the intervertebral discs.

Figure 2

Figure 3

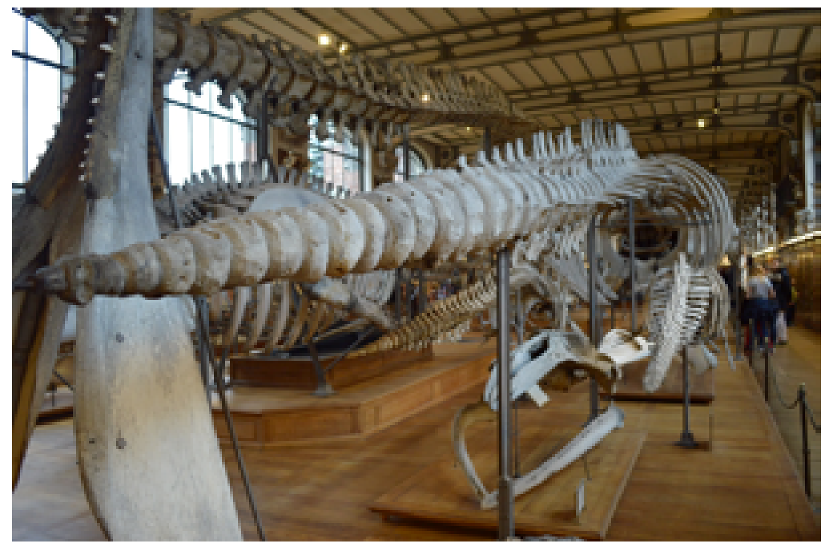

Figure 4

Figure 5

Figure 6

-According to the classes of animals, the study of caudal vertebrae in the different classes of vertebrates, excluding fish [Fig 7] due to the absence of pelvis, allows the following general features to be included:

The caudal vertebrae of the Anura (some amphibians) fuse to form a styliform bone called the urostyle or coccyx [24] [Fig 8] unlike the other class of Amphibians, the Urodela, which have a real tail [Fig 9].

The tails of reptiles decrease in size and simplify from the front to the back. [Fig 10]

Birds are special due the presence of a synsacrum [Fig 11] (except Ratites which have tails) in common with the Ornithischian dinosaurs. This is the fusion of the last thoracic, lumbar, and first caudal vertebrae. These are rudimentary, with suppression of the vertebral features, forming a vertical bony plate [24].

In non-hominoid mammals, there is generally a marked transition between the thoracic and lumbar segments that are much more developed than the caudal part. The tail is consistent with general anatomy description, but the phenomena of coalition and reduction of the caudal vertebrae may also occur in quadrupeds with a developed tail.

Figure 7

Figure 8

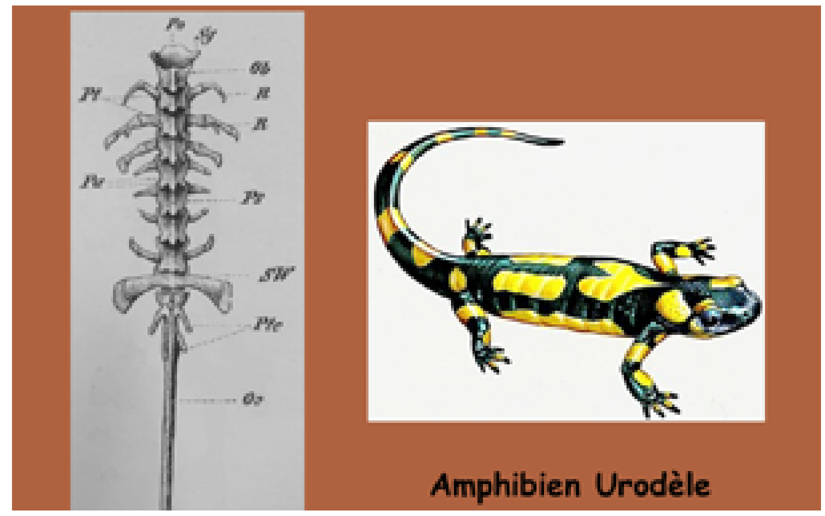

Figure 9

Figure 10

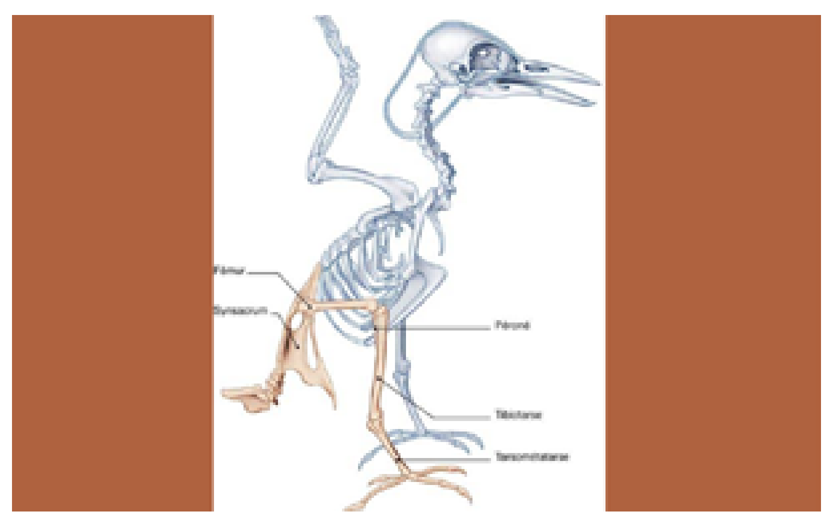

Figure 11

In humans, the human embryo aged 5 weeks has a tail and a larger number of vertebrae than adults (38), which reduce during its growth [4, 24]. The foetal coccyx is entirely cartilaginous in the third month [Fig 12] This is the coccyx of near-term fetus [Fig 13].

Ossification begins in the ninth foetal month with appearance of the central core of the first caudal vertebrae [8]. The human coccyx is formed of 4 to 6 parts. It is obvious that the ontogenesis does not strictly reflect the phylogenesis [11], but this suggests that our distant ancestors could have had a tail. Recent clinical and pathological work has allowed the differentiation of the persistence of a true tail. This derives from the most distal portion of the embryonic tail, and contains fat, connective, muscle, and nerve tissue and is covered in skin. Unlike the pseudo-tail, it consists of a low lumbar-sacral protrusion just resembling the previous one [6]. Pathologically, one can observe a persistence of the embryonic tail; [Fig 14] shows a fetus 13 weeks and 5 days gestation with a unossified cauda. This is a fetus «interrupted» for failure of neural tube closure of anencephaly kind.

Figure 12

Figure 13

Homologies

How can we draw parallels between the tail of mammals and the human coccyx? The coccyx consists of 4–6 atrophied vertebrae (5 in 15% of cases, 3 in 3% of cases), offering insertion to the sacrosciatic ligaments and ischiococcygeus muscle. The sacrum is composed of five sacral vertebrae [Fig 15] The upper segment (necessary sacrum of Broca) comprises the first two (three according to Broca [3]), which are articulated via the atrial surface with the hipbone. The mechanical transmission is made by this intermediary, allowing one side to tighten when walking, while the other one releases, alternately. The lower segment is composed of the other 3 sacral vertebrae which are held in place by sacrosciatic ligaments, helping to limit the movement of the sacrum [16]. According to Raymond Dieulafé, Broca [8] refers to the lower non-articular area as "an additional or superimposed sacrum", and is characteristic to humans and anthropoids. It is formed by the true caudal vertebrae (extension of the spinal canal), which follow the false caudals (sortened towards their bodies) in the form of the coccyx.

Figure 14

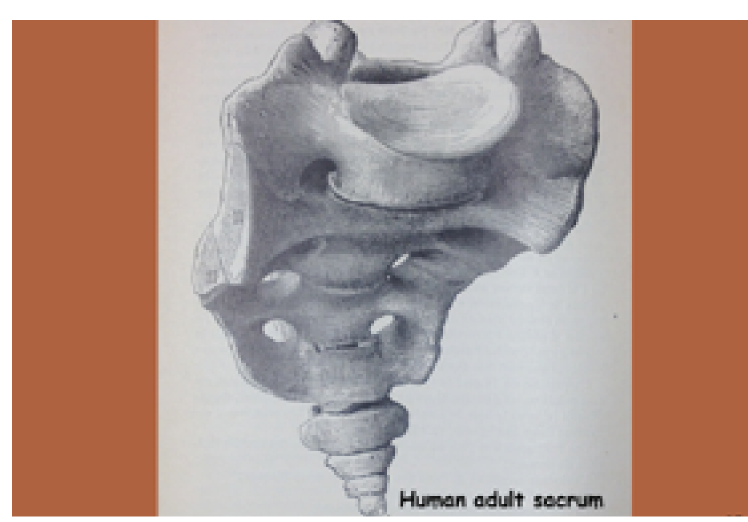

Figure 15

The homology is in this way established between the tail of mammals and the distal end of the spine. This is how Paul Broca [3] explained the transitions between mammalian tails and the human coccyx.

Specific roles of the tail

The tail of vertebrates has a variety of species-specific roles:

-It may be primarily of a locomotory nature [9]. In the kangaroo, it serves as a pendulum and keeps the core balanced when jumping. In felines, it serves as a balance when changing direction while running/ chasing. The cat uses it in order to land on all fours in a fall. In cetaceans, it helps in propulsion. It aids in arboreal movements in some animals with long prehensile tails: Marsupials (Opossum, Phalangers), Carnivores (Binturong), Vermilingua (Tamandua, Cyclops, Manis) Rodents (Coendou), Primates (Cebidae as Ouistiti [Fig 16]).

-Ruminants [2] mobilise their tails to chase parasitic flies away.

-In groups of social animals such as monkeys, the tail is an indicator of hierarchy or age [2], depending on its position.

-Finally, it may reflect the emotional state or mood as with dogs.

Figure 16

MUSCULATURE [10]

The episomatic musculature:
In tetrapods with a transverse limb, it was especially developed to the side of the ilium, and reduced to vertebral gutters and iliac tuberosities in reptiles. In mammals, the iliac spine relationship is very powerful, and among these muscles, the long dorsal (iliocostalis dorsi) and spiny transverse (intertransversarii dorsales caudae = abductor caudae dorsalis) form the dorsal and lateral muscles of the tail, respectively. In the absence of a tail, the iliocostalis (lumbosacral) muscle predominates.

The hyposomatic musculature:
The first group of hyposomatic muscles is inserted on the pelvis and the proximal femur. It is a powerful muscle mass, antagonist to the episomatic muscles flexing the spine and tail. It remains in the absence of the tail inserted into the ilium and femur (quadratus lumborum and small psoas).

The second group is the musculature of the belly and the tail (sacro-caudalis, flexor caudae), also acting in flexion; it remains confined to the ventral and perineal area. The ischiococcygeus muscle [13] (also called the M. coccygeus, levator coccygis, triangularis coccygis, levator coccygis, coccy-ischial, ischiocaudal) is often missing, probably due to the likely regression of the caudal portion of the spine in Homo sapiens.

However, the abductor muscles are most often present in contrast to the flexor and extensor of the tail, because they participate in the closing of the ano-caudal region. According to the authors, the ischiococcygeus muscle is contiguous to/runs alongside the levator ani muscle, where it forms a continuous blade, representing the pelvic floor, regardless of whether the muscular origin is pelvic or spinal. This can be interpreted as an adaptation to the erect position.

The appendicular musculature:
The extrinsic muscles are few because iliosacral mobility is is very restricted. In reptiles, the ischiocaudal and femorocaudal (caudo-femoralis, caudo-ischio-femoralis) musculatures are responsible for the mobility of the tail base. In mammals, the homology-based study seems to find these muscles in the thigh muscles and glutes.

COCCYX AND BIPEDALISM [9]

Is bipedalism associated with the presence of a coccyx, or with the absence of a tail?

To find out, we must list the bipedal animals.

Bipedalism, even occasional, exists only in a few species other than primates. The most common is in the jumpers: Marsupials (Antechinomys, Macropus [Fig 17]), insectivores (Macroselides), rodents (Jerboas [Fig 18], Zapus Dipus, Allactaga, etc.), primates (Indris Galago Tarsius, etc.).
The second category of bipeds consists of walkers: carnivores (Bear), primates (Humans, Gorilla, Gibbon, Orangutan etc.).

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The anatomical similarities between these two groups are the characteristic spine and the sacrum. The cerebrocaudal increase in pressure forces in bipeds results in continuous increase in height and diameter of the vertebral body from top to bottom, and in rigidity of the sacrum itself, which often consists of a greater than average number of vertebrae in the group studied. The strengthening and lengthening of the muscles are consistent with the increased differentiation of the transverse and spinous processes.

Aside from these similarities, we must differentiate the jumpers from the runners.

Jumpers like the kangaroo have a long, developed, and powerful tail, which is used to balance the core, and keeps a certain obliquity. There is no difference between the anterior and posterior caudal vertebrae, i.e. no distal conversion to rudimentary structures, as is usually the case in the tail of quadrupeds [Fig 19].

This is exactly the opposite in all non-jumper bipedal walkers with an almost straight trunk and no tail as the bear [Fig 20].

Figure 17

Figure 18

Figure 19

Figure 20

Amongst these bipeds, casual or permanent, walkers or jumpers, terrestrial or arboreal, only hominoid primates have a coccyx. This applies to both current forms and fossils.

With respect to the rest of the spine, the lumbar curve is characteristic of humans, as is their spine's hypermobility and length. There are traces of the same features in other walker bipeds, but not in quadrupeds. Conversely, among the jumpers, the spine is very convex and compacted on the pelvic area with a chest hypermobility allowing the weight of the body to be thrown backwards at the time of jumping in order to not tip forward.

It is likely [8] that the morphology of the sacrum and the frequency of the sacrococcygeal synostosis, associated with the ligament and muscle development, are an adaptation to the erect stance. Indeed some tail muscles are integrated in the pelvic floor, a true musculoskeletal frame. According to Paul Broca [3], the progressive atrophy of the tail in Anthropoids is connected with the need to provide a more resistant visceral pelvic floor, in relation to the upright position. Huxley [12] had the same opinion.

COCCYX AND OBSTETRIC STRESSES

There are any morphological and embryological arguments in favour of the first coccyx part belonging to the sacrum. Besides in the majority of cases in adults, one can observe the ossification of the sacrococcygeal articulation with persistence of the medio-coccyx articulation.

The usual fusing of the first coccyx piece with the complementary sacrum is in relation to the muscles and ligaments that govern the vertical position by increasing their insertion surface (such as sacrosciatic ligaments, gluteus maximus muscle). Obstetric constraints on the mobility of this structure delay the mid-caudal fusing (between the first and the second coccyx part), and its prevalence in women is augmented with age [20].

The second part of the coccyx retains more mobility with age than the first, explaining possible dislocations and, in case of merger, fractures during childbirth. [13]

The coccyx is effectively the rigid skeleton of the posterior part of the pelvic floor; childbirth requires its removal to the rear, while the mid-caudal mobility persists the most.

COCCYX AND SEATED POSITION [9]

The ability to sit depends on the articular mobility and proportions of the lower limbs, as well as the sagittal mobility of the spine. It is interesting that the only animals able to sit on the hindquarters by freeing the forelimbs for grooming and gripping are squirrels [Fig 21], primates and bears [Fig 22], and that only primates have a coccyx [9].

Figure 22

Figure 21

COCCYX AND EVOLUTION

The Miocene Hominoids

The recent discovery of the five-caudal vertebrae of Nacholapithecus kerioi proves that at least one branch of hominoids has existed without a tail since the Middle Miocene (15 Ma) [14]. Morphological similarities between the coccyx and that of modern monkeys suggest that it is a derived characteristic (synapomorphy). Different interpretations exist on the presence of a tail in Proconsul heseloni [18], dating from the Lower Miocene. This proved, therefore, that the loss of the tail occurred at the beginning of hominoid existence, still three million years before Nacholapithecus.

Figure 23

Australopithecus (3–4 Ma)

The remains of Australopithecus show the presence of a modern human coccyx. This is especially visible in Australopithecus afarensis [17] and A. sediba [Fig 23]. However, most studies only concern the number of lumbar and sacral vertebrae.

Furthermore, the sacrococcygeal region has an anthropometric dimension. Studies show that the height of the sacrum and coccyx individually as well as added together are an indicator of the stature of an individual [15], more precisely the measurements of the head and foot. This measurement is indicative, though the measurement of long bones is the most accurate indicator. Some studies confirm that the morphology of the sacrum, (the width of the spinal canal in particular) and the considerable development of the spinous and transverse processes and articular processes, are indicators of tail length, as much in primates as in other families. Since the tail is rarely found in the paleontological remains, the sacrum can thus give valuable morphological indications for the presence and morphology of a tail and the phylogeny of the hominoids [18, 19].

Modern monkeys

The length of the tail in primates may vary considerably between species and among the population of the same species. Some monkeys, Catarrhines in particular (therefore not Hominoids), have an extreme reduction of the tail [Fig 24] [14]; these are the macaques Macaca nigra and M. Sylvanus, whose morphology of the sacrum and post-sacral vertebrae is very different from that of existing hominoids. Among the Old World monkeys (Catarrhine monkeys), the length of the tail is considered an important characteristic which reflects functional adaptations and their phylogeny [22, 23].

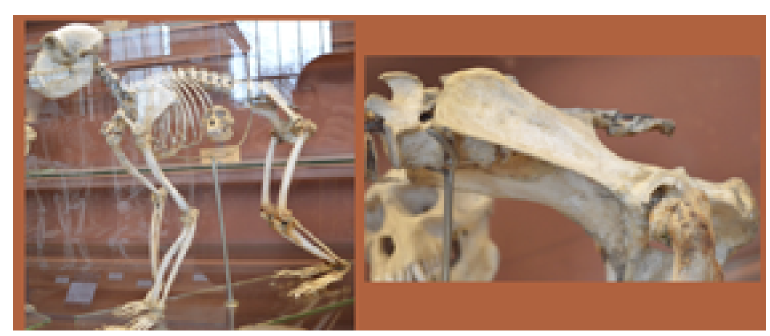

Figure 24

The prehensile characteristic of the tail, which can suspend the entire weight of the body, has evolved among the New World monkeys (Plathyrrhines) in Atelidae (Alouatta, Ateles [Fig 25], Brachyteles, Lagothrix) and New World monkeys (Cebus, Sapajus). These prehensile tails share morphological characteristics that distinguish them from non-prehensile tails. These characteristics include the size of the proximal portion of the tail, the development of structures from the haemal arc, the resistance of the vertebral bodies to torsional stresses and bending, and the role of the musculature.

Figure 25

However, the interpretation of the shape of the intervertebral articular surfaces [6] is less clear insofar as the morphology observed in these prehensile tails is similar to that of some large terrestrial monkeys, as Mandrill [Fig 26] (Catarrhine) with a non-prehensile Papio-type tail.

Figure 26

Summary

In view of this, in terms of evolution, the absence of a tail and the presence of a coccyx in anthropoids probably have a phylogenetic significance and a value indicating the evolutionary adaptations. The presence of a coccyx currently dates the divergence between monkeys and hominoids to around the Middle Miocene.

However [13], statistics show that in humans and quadrupeds, there are far more numerical variations in the bony elements of the sacrococcygeal region than there are in the rest of the spine, and in mobility between parts, making it difficult to award an absolute taxonomic value.

CONCLUSION

The tail and coccyx constitute the terminal portion of the spine. The comparative anatomy research thus far allows us to establish homologies and designate an evolutionary link and the presence of a common ancestor.

The coccyx is specific to hominoid primates. Its presence is not associated with all forms of bipeds. However, the osteological, ligament, and muscle transformations associated with it are an evolutionary advantage in standing upright, for supporting the pelvic viscera, and for childbirth.

ANNEX: COCCYX AND COMPARATIVE ANATOMY OF PRIMATES [5, 10]

Lemurs: 25 caudal vertebrae, with many variations
Tarsiers: between 27 and 29 caudal vertebrae
Platyrrhines: 30–34 caudal vertebrae
Catarrhines:
Cynomorphes (= monkeys): 27 caudal vertebrae in species with long tails up to 5 in only some macaques that are terrestrial quadruped species
Great apes: extreme reduction of the caudal vertebrae,
Hylobates and Symphalangus: 2–3 [Fig 27]
Pan: 3 but sometimes 6 [Fig 28-29]
Gorilla: 3 [Fig 30]
Orangutan: 3 [Fig 31]
Human: the caudal vertebrae are less reduced than in the Orangutan, from 4 to 5, 7 to 9 in the embryo, and from 4 to 6 in adults, even in ancient Homo as Homo ergaster (1 to 1.8 Ma [Fig 32])

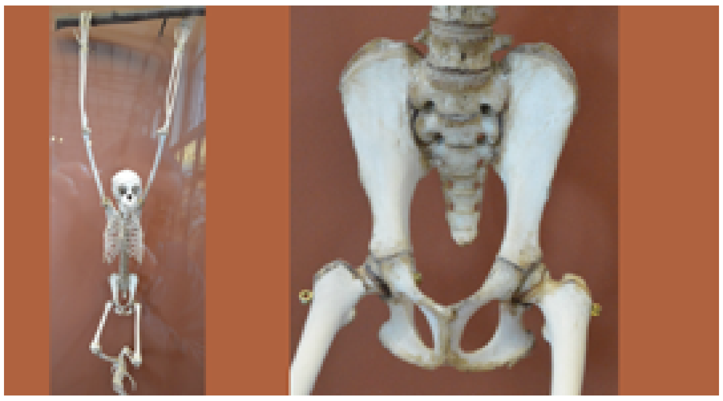

Figure 27

Figure 28

Figure 29

Figure 30

Figure 31

Figure 32

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<tr><td colspan="7">Prosimians</td></tr>
<tr><td rowspan="9">Anthropoids</td><td colspan="6">Platyrrhines</td></tr>
<tr><td rowspan="8">Catarrhines</td><td rowspan="2">Cercopithecus</td><td colspan="4">General</td></tr>
<tr><td colspan="4">Macaques</td></tr>
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<tr><td rowspan="5">Hominidae</td><td colspan="3">Pongidae</td></tr>
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<tr><td>Australopithecus</td></tr>
<tr><td>Pan</td></tr>
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