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Zoology: Introduction to Felidae

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1. Introduction to Felidae

Felidae falls in the Carnivora order, which is made up of nine extant families (or ten if mongooses included, *Herpestidae*). Carnivores have two suborders: *Feliformia* (cat-like carnivores), which includes Felidae (the big and small cats); the Hyaenidae (hyenas); Viverridae (civets); Herpestidae (mongooses); and Caniformia (the dog-like carnivores) and includes Canidae (dogs); Ursidae (bears); Procyonidae (raccoons); Mustelidae (weasels); and two marine families: Otariidae (sea lions) and the Phocidae (seals). The role of carnivores is of a regulatory nature: to keep herbivore numbers in check (Pendragon and Winkler, 2014).

Felidae includes the entire big and small cat families (wild and domestic). Felids are slender, flexible and muscular with cryptically coloured fur for camouflage making them successful hypercarnivores. Felids range in size from the smallest African black footed cat (head-body length: 36-43cm) to the largest being the tiger (body length of up to 330cm) (Biology Online: Felidae). Their adaptations allow for high speed and extreme agility combined with great power (Bellani, 2020). Felidae are commonly known as cats, which references all types of cats, specifically domestic cats, but they are also referred to as felids (Wikipedia: Felidae).

Approximately 41 extant families of felids including family *pantherinae*: the lion, tiger, jaguar, leopard and snow leopard (the big 'cats' belonging to subfamily panthera) and clouded leopards and Sunda clouded leopard (medium cats of the neofelis subfamily). All other species are from the felinae family, consisting of 11 genera, 34 species, considered the small cats, including the bobcat, caracal, cheetah, cougar, ocelot and all domestic cats (Wikipedia: List of Felids). The term big cat was originally used to describe the four big

cats that roar: lions, tigers, jaguars and leopards but today it is used to describe the biggest wild cats (including snow leopards). commonly , big cats is used to reference all the cats of the pantherinae and neofelis subfamilies as well as the two biggest felinae cats: cougar and cheetah (Big Cats Wild Cats: Wild Cats Biological Classification). 36 of the felidae family are wild cats, however all felidae are similar, apart from size, they all have large eyes, round and flat faces, whiskers, large ears and nimble predators. Wild cats are naturally found all over the world except in Antarctica and Australia (Lamberski, 2014).

2. Felidae General Anatomy

Generally all cats (big and small) have the same anatomy, despite size and form all 'cats' are recognisable as part of the felid family. Species are distinguishable by colour patterns and body size, but their skeletal design remains mostly the same. Males are generally 5-10% larger than females but other sexual dimorphism is limited (Sicuro, 2011).

The felidae musculoskeletal system is built for agility, speed and successful predation. Their skeletons consists of cartilage and bone (Bozita) roughly 250 bones in adults (Grace, 2018). Very well-developed muscles are found in the jaw, legs and back contribute to excellent hunting skills, a very mobile spine creates flexibility and the tail, as an extension of the spine, helps with balance. Felidae are ambush hunters and, they are capable of easily getting over, under or between obstacles (Bozita) sleep in tight spaces, curled up for prolonged periods of time (Grace, 2018). Strong muscles in the back and hind legs allow for a straight, upward climb, such as up trees, aided by claws, however claws are not designed for climbing straight down (Bozita).

The flexibility seen in felids as well as their large stride is due to a floating clavicle bone, so if they can fit their heads through a tight

space, the floating clavicle allows them to squeeze the rest of their body through also (Grace, 2018). The muscular felidae system is tough, it contributes to their effective hunting skills and is designed for walking, running, jumping and twisting. Their muscular control and skeletal flexibility allows them to correct their body during a fall at an extremely rapid pace, a skill unique to cats (Cat Anatomy and Physiology, 2008).

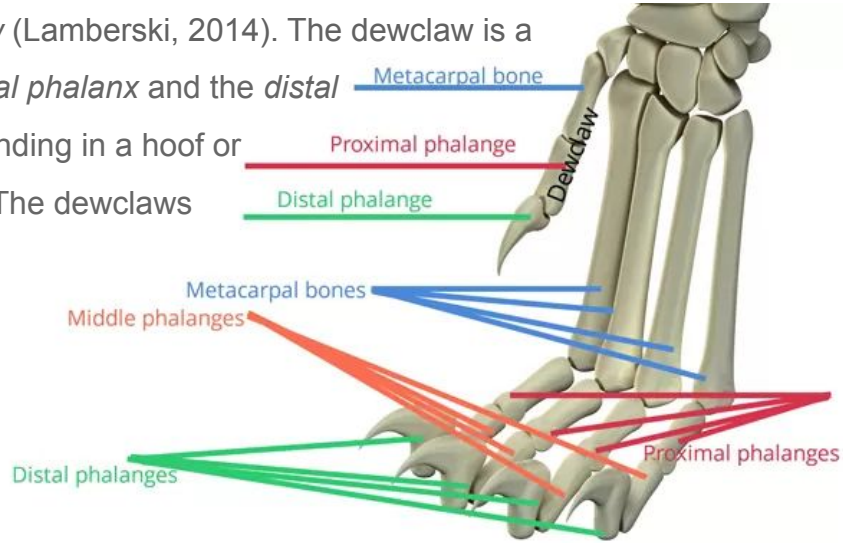
Extra bones are found mainly in the backbone: 52 to 53 vertebrae in a cat (as opposed to 32 to 34 in humans). The extra bones have additional padding inbetween, creating additional spacing and lending to flexibility for twists, turns and jumps (Grace, 2018).

There are 5 regions to the spinal column: the cervical, thoracic, lumbar, sacral and caudal. A total of 7 cervical vertebrae in the neck region, the first two cervical vertebrae are called the *atlas* and the *axis*. The thoracic or chest region consists of 13 vertebrae, each associated with a pair of ribs. The lumbar region (lower back) has 7 vertebrae ending at the pelvis, which contains 3 sacral vertebrae fused together (situated between the two hip bones). About 18 to 23 caudal vertebrae are found in the tail. The felidae spine is probably the most flexible of all mammals (Cat Anatomy and Physiology, 2008).

2.1 Paws and Limbs:

Felids are digitigrade (walk on their toes) resulting in a rapid stride rate: five toes on each front paw and four on each back paw (Lamberski, 2014). The manus claws (front paws) are hook-shaped and the pedal claws (back paws) are blade-like, a difference associated with function: the manus claws have a larger radius of curvature and a smaller angle of arc compared to the pedal claws. Claws of digits 3 and 4 of the pes have a larger radius of curvature and a smaller arc (Bryan et al, 1996).

The first digit on each front foot (inside the limb at the wrist) is the *dewclaw* (Lamberski, 2014). The dewclaw is a digit that does not touch the ground and consists of two bones: the *proximal phalanx* and the *distal phalanx*. The distal phalange contains a pointed *ungual process* (a bone ending in a hoof or claw), surrounded by the claw and attached to the inner wrist by tendons. The dewclaws are always extended, they do not retract, and are used for additional grip for climbing and to hold prey (Wilson). All the other claws in felids retract; when the paw is relaxed claws pull back into a sheath, which prevents claws from becoming blunt (Etnyre et al, ADW). This highly developed retractable claw mechanism of felid is a distinguishing characteristic of felids (Bryan et al, 1996).



The exception to this is the cheetah, claws are only partially retractable. Unlike other felidae, cheetahs (*Acinonyx jubatus*) do not have the fleshy sheath protecting each claw (Lamberski, 2014). Felidae claws are innervated and rich in blood supply (Wilson: What is the dewclaw on cats?).

The powerful forelimbs are used in a supinate position to hold and capture prey in addition to locomotion. This increases mobility of the

Above: Felid paw bone anatomy. **Right:** Cat paw outer anatomy. **Image Credit:** Cat World

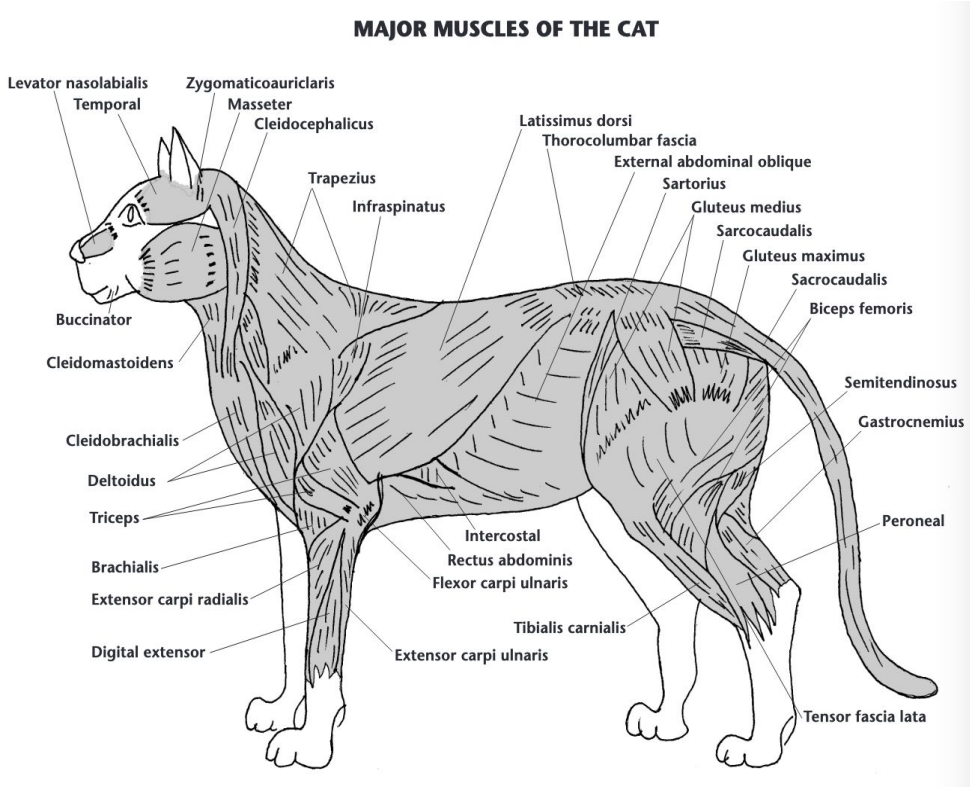
elbows and wrists but affects running, unlike canids that run faster due to their stiffer forelimbs (Lamberski, 2014).

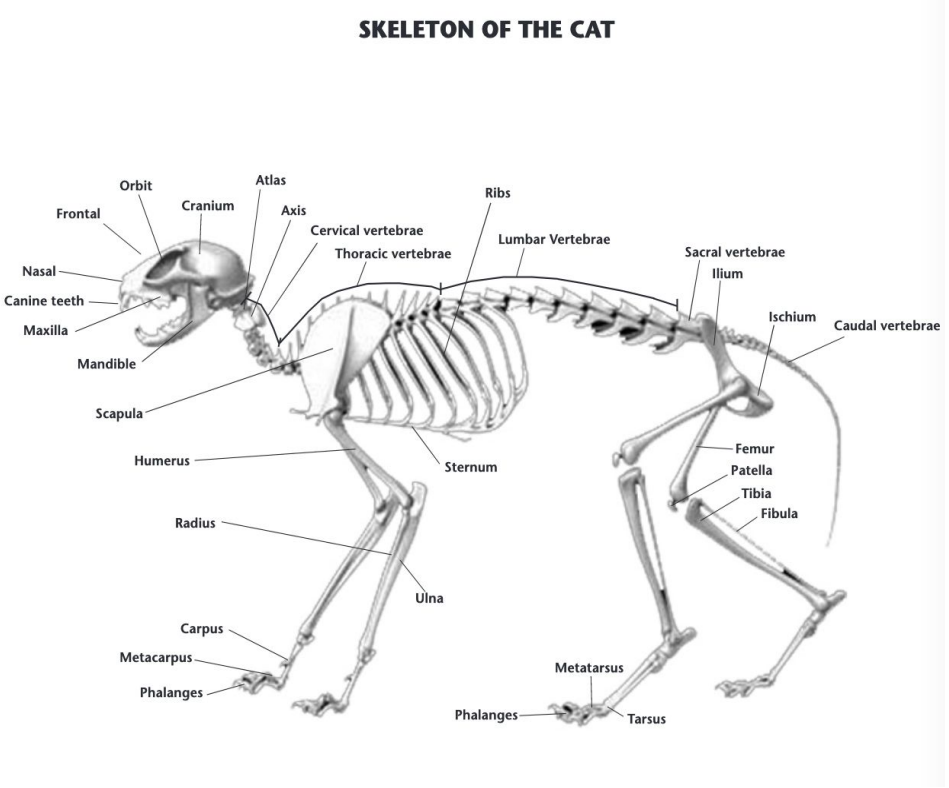
Felids are sprinters more than long distance runners, they move at high speeds for short bursts due fast-twitching muscles, which support their powerful limbs. Hindlimbs support body weight against gravity as well as postural changes from crouching to upright, they are also the main propulsors of locomotion in felids, so hindlimb muscles must provide power to generate forward acceleration. This force requirement is achieved through an increased volume of hip extensor muscles (muscles that bend or straighten the limb, ie pulling 2 bones together, in this case the hip and femur) in all mammal quadrupeds. This support requires a force-time impulse equal to that of the animal's body weight and stride time: faster speeds mean the foot has less contact with the ground (*short stance time*) for a smaller portion of the stride (*decreased duty factor*). At these high speeds and longer strides, peak limb force increases and muscles generate larger amounts of force and joint *moments* (the product of distance and physical quantity) to sustain limb force (Cuff et al, 2016).

At the swing phase the hindlimbs must protract quick enough to reposition in time for the next stance. Limb protraction is limited by limb inertia, internal muscle architecture, maximal contraction velocity of muscle fibres as well as moment arms of the muscles. Fast running tetrapods usually have reduced muscle mass towards the distal ends of limbs and distal muscles transmit their force down along the tendons. Tapering and reduced muscle mass along the limbs reduces the amount of power required by the muscles to swing the limb, therefore energy is saved by using tendons but also contributes to bouncing dynamics and enables muscles to remain optimally isometric during steady-state locomotion (Cuff et al, 2016).

2.2 Dentition:

Felidae dental anatomy consists of 30 (sometimes 28) teeth with the following dental formula: incisors: I3/3; canines: C1/1; premolars: P2-3/2; molars: M1/1. This formula depicts the top/bottom teeth, there are 14 teeth at the top and 16 teeth at the bottom





Above left and right: General muscular (right) and skeletal anatomy of felidae. **Images Credit:** Cat Anatomy and Physiology, 2008

totalling 30 teeth altogether (Lamberski, 2014). The upper premolar is significantly reduced in most felidae species but in the Lynx genus it is missing altogether (Etnyre et al, ADW) so they have 28 teeth. Incisors are the small front teeth used for ripping flesh from carcasses; canines are canonical and long, with a groove in the enamel, and used to puncture prey tissue with minimal force (Lamberski, 2014; Etnyre et al, ADW); the upper premolars (carnassial teeth) are used to slice meat. A reduced number of teeth allows for a reduced skull length and mandibles, improving efficacy of the muscles when closing the jaw, resulting in the most powerful bite relative to muscle mass than other carnivores, except mustelids (weasels, badgers, otters, minks) (Lamberski, 2014).

3. Felidae Sensory System

As with most mammals, Felidae have the same 5 senses: sight, hearing, taste, smell and touch; and all work in the same way as other mammals (Cat Anatomy and Physiology, 2008), however felids do have exceptional vision and hearing. Being crepuscular (active at dawn and dusk), the tapetum lucidum helps intensify limited light for hunting. Several species have large semi-rotating ears. The felid tongue has a sandpaper-like texture due to posteriorly directed papillae (often referred to as barbs) on its surface. These barbs help retain food in the mouth and remove tissue/hair from the body and bones of prey (Etnyre et al, ADW).

3.1 Vision:

The cat eye has the same anatomy as other mammal eyes and they experience the same eye problems as humans (cataracts, glaucoma, etc) (Galett, 2020). Due to the position of the eyes, they have a wider field of view, around 200 degrees (as opposed to our 180 degrees). They also have larger eyes relative to their head size so they can take in more light in dimmer hours of the day

(Through Glowing Eyes, 2020).

A cat eye sits in the *orbit*, which is made from several bones, and includes muscles, nerves, blood vessels and structures to produce and drain tears. At the back of the eye lies the *retina*, which contains 2 types of photoreceptors: *cone* and *rod* cells. Cone cells allow for excellent visual acuity and binocular vision (to judge speed, distance and see more detail) and are also responsible for colour vision, however it is uncertain whether cats see in colour.

Felids have 6 to 8 time more rod cells than humans, which allows them absorb that much more dim light but they have less cone cells than rod cells, rod cells are also used for see quick movements and cats have heightened, visual acuity when it comes to small movements but they are short sighted, seeing only up to 6 metres ahead of them (humans see 30 to 60 metres). The lenses in cat's eyes don't filter out all UV light and it is thought that they can see a colour spectrum outside of the human range (Through Glowing Eyes, 2020).

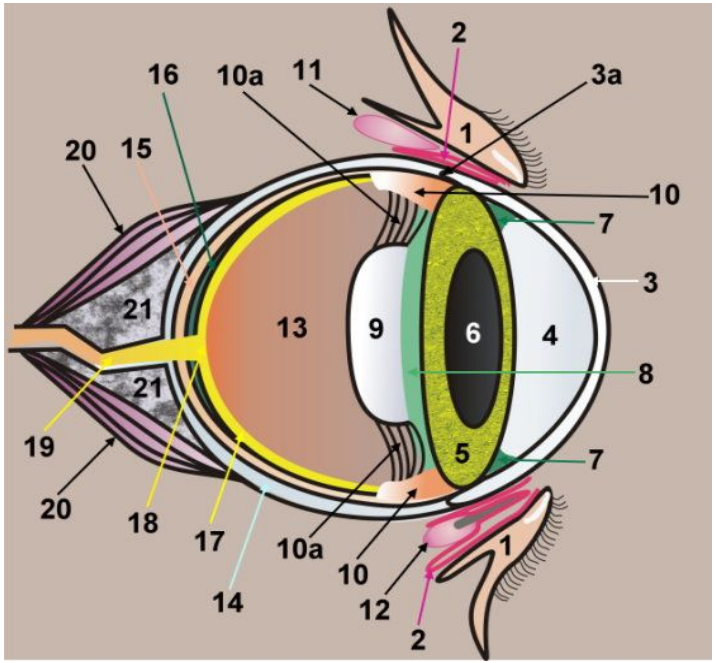
Behind the retina is a layer of reflective cells called the *tapetum lucidum*, that magnifies incoming light (Galett, 2020). Light that has already passed through the tapetum lucidum, reflects light through the retina a second time (Through Glowing Eyes, 2020). This re-reflection increases light to photoreceptors and allows cats to see better in the dark. Sometimes a portion of light bounces off the *tapetum lucidum*, misses the retina and bounces back out of the cat's eyes, which is why the cat's eyes have greenish-bluish reflection or 'glow' (Carnegie Museum: Meowfest).

The most sensitive area of the retina is called the *area centralis*, which contains thousands of tightly packed photoreceptors. Each

photoreceptor is attached to a nerve fibre, the nerve fibres bundle together to form the optic nerve, which carries electrical impulses to the brain from the photoreceptors (Galett, 2020).

Upper and lower eyelids of thin skin cover the eye and blink reflexively to protect the eye, spread tears over the surface of the eye keeping it moist and clear away small particles. Eyelids are similar to those of human eyelids but cats have an additional, semi-transparent nictitating membrane (or the third eyelid) (Through Glowing Eyes, 2020). The third eyelid is found under the other 2 eyelids, on the nose side of each eye, and extends upwards to protect the eyeball from scratches or in response to inflammation (Galett, 2020).

Tears comprise water, oil and mucus. *Lacrimal glands*, located at the top outer edge of each eye, produce water. Nictitating eyelids also produce a portion of water for tears. *Goblet cells* in the conjunctiva produce mucus and the *meibomian glands* produce the oily portion of tears. This mixture of water, oil and mucus is more protective and evaporates slower. Tears drain into the nasolacrimal ducts, into the nose (Galett, 2020).



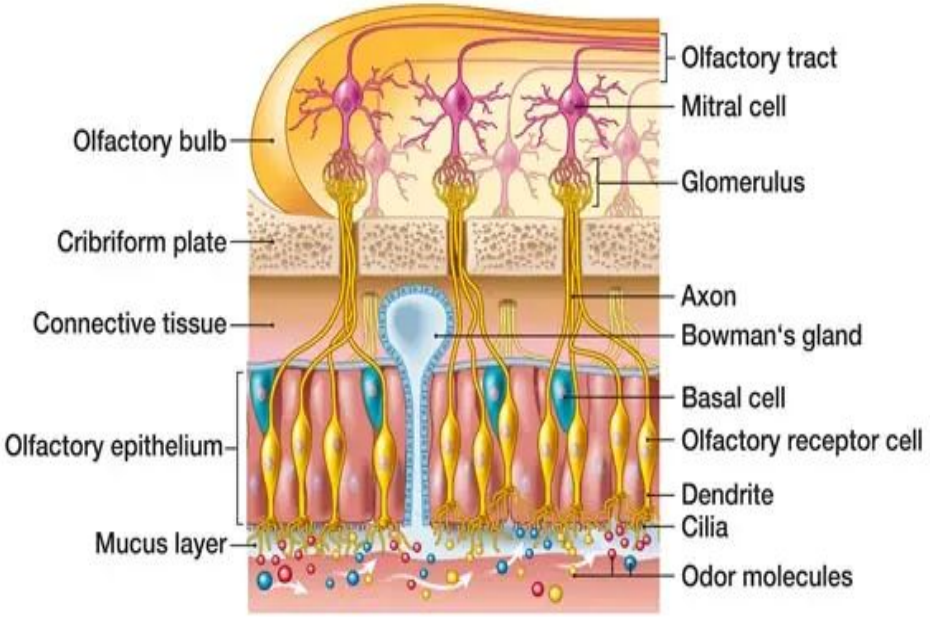
Above: Felidae eye anatomy (1) Eyelids (2) Conjunctiva/nictitating membrane (3) Cornea (3a) Limbus: joins the cornea to the sclera (4) Aqueous fluid filled, anterior chamber between the cornea and the iris (5) Iris (6) Pupil (7) Canthus with trabecular meshwork: a loose sponge-like tissue responsible for drainage of the anterior chamber (8) Posterior chamber: filled with the aqueous fluid (9) Lens (10) Ciliary Body: produces the aqueous fluid (10a) Suspensory ligaments that hold the lens and direct curvature of the lens (11) Lacrimal gland (12) Nictitating gland (13) Vitreous humor: maintains shape of the eye (14) Sclera (15) Choroidea: contains blood vessels responsible for the retina's metabolism. (16) Tapetum lucidum (17) Retina (18) Optic nerve papilla: location of the optic nerve on the retina (19) Optic Nerve (20) Eye movement muscles (21) Lipid Tissue. **Image Credit:** EverGreen

3.2 Hearing:

Felidae ears are internally, morphologically like those of most mammals, with three structural areas: the outer, middle and inner ear. Felidae can hear from different directions without turning their heads due to their rather large, rotating cupped pinnae (the outer ear flap) independently (Etnyre et al, ADW). Felids are highly sensitive to sound and have a broader hearing range above and below the range of human hearing as well as higher frequencies than dogs, they have the broadest range of hearing of all mammals (Cat Anatomy and Physiology, 2008; Paws Chicago: Cat Senses; Wikipedia: Cat Senses). The outer ear is connected by 27 muscles and this allows felidae to determine where sound is coming from, by sensing differences in the time of arrival and intensity of the sound received by the two ears (Paws Chicago: Cat Senses).

3.3 Olfaction:

Kittens are born blind but their sense of smell is very well developed (Wilson: Sense of Smell in Cats). Olfaction (the sense of smell) is an important sense in felidae as it provides information on pheromones: females in heat, territorial markings; dangers such as predators, fire, spoiled food; taste and appetite. Cats have a large olfactory epithelium (a membrane in the nasal cavity which is about



Above: Structure of the olfactory system. **Image Credit:** Wilson: Sense of Smell in Cats

20cm^2 in humans) this means that their sense of smell is rather acute. Felidae have close to 200 million odor-sensitive cells in their noses compared to humans that have only 5 million (Wikipedia: Cat Senses).

As a cat inhales, air travels to the olfactory area situated at the back of the mouth, the rest goes into the lungs. The felidae nasal cavity is lined with a mucociliary blanket that is innervated and contains blood levels and cilia. As odour molecules enter the nasal passages, they dissolve in the mucus lining of the olfactory epithelium and guided to the cilia of the olfactory neurons located in the epithelium. The odour molecules bind to protein receptors of the olfactory neurons, which convert chemical stimuli to electrical signals through the olfactory nerve to the olfactory bulb located in the front part of the brain, which is processes smells and sends signals to the brain where they are interpreted as odours (Wilson: Sense of Smell in Cats).

Anal glands produce strong-smelling pheromones that are deposited on vertical surfaces when spraying, which is a form of territorial marking and is used by all male cats. Females in heat release sex pheromones from the cheek glands and in their urine. The Felidae sense of taste is tied to its sense of smell, they have about 470 taste buds (humans have 9 000; 1 700 in dogs) but their poor taste is made up by the heightened sense of smell. If a cat has a blocked nose, they lose their appetite due to loss of smell. These highly efficient predators use their exceptional sense of hearing, vision and sense of smell to detect prey (Wilson: Sense of Smell in Cats).

3.3.1 Jacobson's Organ:

Jacobson's organ (or vomeronasal organ) is a scent analysing organ (chemoreception) located in the roof of the mouth (between the hard palate and the soft nasal tissue). The organ contains ducts leading to the mouth and to the nose, used to analyse pheromones (scent chemicals) from other cats, especially those in urine (Cat Behavior Associates: What is the Vomeronasal Organ?).

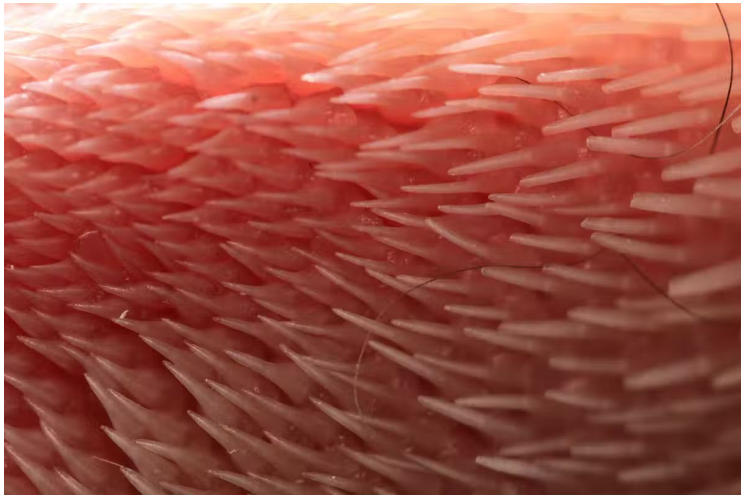
When the animal picks up a scent it will wrinkle its top lip with its mouth partially open and the tongue to hang slightly in order to allow passage to the vomeronasal organ. This is called gaping and is the equivalent of the Flehmen response, which is the gathering of chemical messages in other mammals (Wikipedia: Cat Senses; Cat Behavior Associates: What is the Vomeronasal Organ?). The Jacobson's organ is connected to the region of the brain associated with feeding, social and sexual behaviours by receptor cells.

Olfaction is vital to cats as it provides essential cues to find a mate, food and detect danger. Pheromones are used for communication between felidae and they have nine pheromone producing glands: the *pinna*; the *temples*; cheek; *perioral* (or corners of the mouth); *submandibular* (underneath the jaw); *interdigital* (between the toes); *sides of the anus*; *supra-caudal* (base of the tail); *caudal* (along the tail). It is for this reason that all cats rub their heads on each other and on objects, to deposit pheromones in order to mark their territory (Wilson: Sense of Smell in Cats).

When studied microscopically, examination of several transverse sections of the vomeronasal organ, findings showed that the wall of the vomeronasal duct bears 4 different types of epithelium (simple columnar; respiratory; receptor; stratified squamous). Other soft tissue components are associated with epithelium types. Where the duct wall is lined with receptor epithelium, nerves and connective tissue are present between the epithelium and the vomeronasal cartilage. The majority of glands and blood vessels are found lateral to areas lined with respiratory epithelium in the duct wall. Numerous basal cells were present in the sensory epithelium (Salazar et al, 1996).

3.4 Taste:

The tongue of Felidae is long and flat, tapering slightly in front and more so towards the back of the mouth. The surface of the tongue is covered with backward pointed papillae that are barb-like, enabling the animal to scrape meat off bones or lick hair and fur off its prey as well as clean its coat by licking. Taste buds are present, especially at the tip and near the throat, which react to chemical stimuli to produce sensations of taste (Cat Anatomy and Physiology, 2008).



Above: The surface of a cat's tongue, showing rigid, hollow papillae near the tongue tip (right of image) and soft, conical papillae near the throat (left of image). **Image Credit:** The Conversation: Cool for Cats

In 2005, it was discovered that the entire 'cat' family lacks the *TAS1R2 protein*, one of two sweetness sensory receptors. The deletion of TAS1R2 gene causes a shift in the genetic reading frame that leads to the transcription not detecting mRNA or protein produced for this sensation. Another protein, *TAS1R3*, that is present with relevant taste buds present, however is inactive. Such a genetic marker is found in the entire family but not other animals, so it is inherited by all descendants (Wikipedia: Cat Senses).

3.5 Touch:

Both skin and fur play an important role in the sense of touch in felidae. Skin and fur is designed for protection and it is very dense. When fur reaches its full length, it doesn't grow anymore. The Felidae coat consists of three different hair types, whether it's a short-

or long-haired 'cat' and all three coats have different functions (Bozita, including below list):

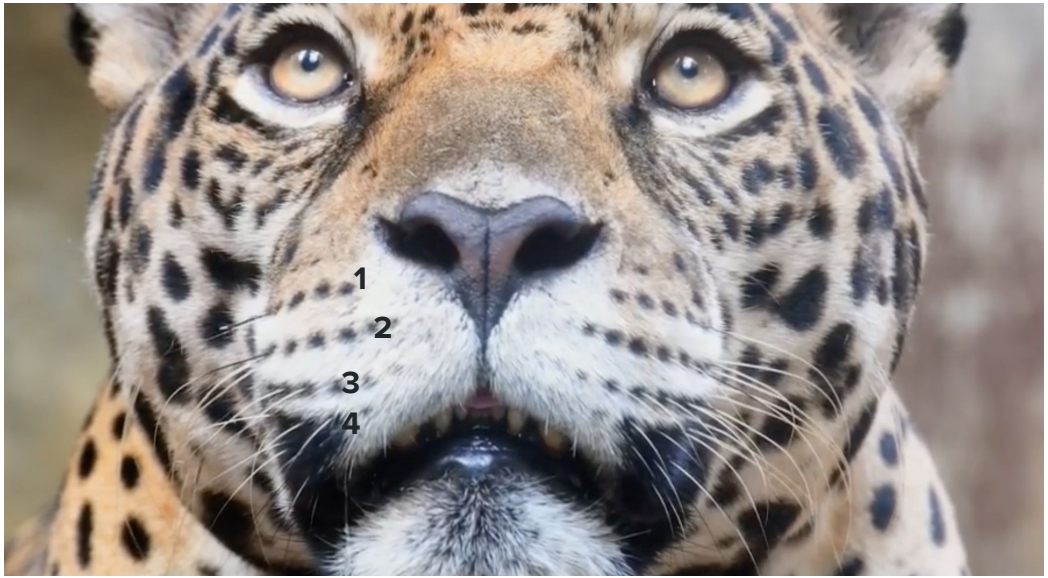
- **Guard hair:** This top layer consists of straight, even hairs, which give the fur its colour and protection from getting wet.
- **Awn hair:** Under the guard hair, is an extra layer of protection and is made up of middle hair, middle wool and wool hair.
- **Undercoat:** This is closest to the body and made up of thin, soft hair that keeps the animal warm.

Fur also serves as insulation against heat and cold as well as insect bites, stings, thorns and other potential dangers. Hair is shed according to climatic conditions all year round but mostly in spring and autumn and is also be a health indicator. The cats sense of touch comes from the skin, which anatomically, is like human skin, consisting of 2 layers: the outer (epidermis) and the inner dermis (Cat Anatomy and Physiology, 2008).

Whiskers (or vibrissae) play a large role and enhance the sense of touch, they are strategically placed on the face in rows that transmit critical sensory information and even plays a role in balance. Some animals also have whiskers on other parts of their bodies, but the pattern changes from one species to another (Texas A&M University: The Cat's Five Senses, 2019). Some have additional whiskers on the cheeks and above the eyes, some on the back of their front legs. It seems that the entire Felidae family have 4 rows of whiskers on each side of their face on the top lip, varying in length (Wikipedia: Cat Senses).

The barrel cortex in the brain receives information from the whiskers in a similar fashion to that of the visual cortex and allows the cat to form a 3D map of its surroundings, however this is not considered a type of vision, it is still a touch sensation. Vibrissae also aid in sensation and navigation (Evans et al, 2019).

The 2 upper rows of whiskers can be moved independently from the lower two rows for precision when measuring. Whiskers are thicker than ordinary hairs and roots three times deeper than other hairs. The numerous nerve endings at the base of each whisker gives the animal extraordinary detailed information about air movements and nearby objects with which the whiskers may make physical contact, enabling the cat to know that it is near obstacles without seeing them. Whiskers also aid in hunting. When a cat is unable to see its prey due to close proximity to its mouth, its whiskers move to encircle around its muzzle to allow detection of prey location with precision. When a cat's whiskers have been damaged they may bite the wrong part of its prey, indicating that whiskers provide detailed information about the shape and activity of the prey (Wikipedia: Cat Senses).



Above: 4 rows of whiskers in varying lengths on the jaguar can be clearly seen in this photo (numbered 1 to 4). **Image Credit:** Sidder 2016

4. Felinae vs Pantherinae

Felidae is the family of animals that falls under the order Carnivora. Felidae is divided into 2 groups: Felinae and Pantherinae. Felidae is divided by roar or purr as well as round pupils (panthera) and slit pupils (felinae) (Etnyre et al, ADW). The only big cat that

does not roar is the snow leopard, they mew, growl, yowl and prusten (also known as chuffing, which is blowing through the nose) (WWF: Where do snow leopards live?). Neofelis are different: they have elliptical pupils that when dilated are round; their dentition is also different in that they do not have a premolar tooth and their hyoid is ossified as with felinae and therefore unable to roar like the rest of the pantherinae family. Compared to the felinae family, panthera have long or very long tails (Bellani, 2020).

4.1 The Purr and The Roar:

The mammalian voice box (larynx) is situated in the same place for all mammals, when air passes the structure it it creates sound, of which the vocal cords and hyoid bones are essential for creating sound. The difference is in the structure: ossified or cartilaginous and how they are attached to the base of the skull (directly or with ligaments) (Welsh, 2021).

The small cat species (felinae) have an ossified hyoid, which enables them to purr. In felinae, the hyoid is a horseshoe shaped bone, anteriorly situated, directly attached to the base of the skull and supports the larynx and tongue (Wikipedia: Felinae). During breathing, felinae dilate and constrict the glottis (the area around the vocal cords), in a rapid and rhythmic manner, as air flows over the larynx the laryngeal muscles vibrate and a purring sound occurs (Hambly: Why do Cats Purr?). Felinae can purr during both inhalation and exhalation in a continuous, rhythmic fashion. The neural oscillator in the brain controls purring, which gets the laryngeal muscles twitching and in turn produces sound at least 25 times per second. These bursts of sound strung together are the familiar purr we all know (la Fontaine, 2021).

The frequency at which purring occurs is 25 to 150Hz but it is not considered a form of vocal communication. Initially it was thought

that cats purr when they are happy, however studies have shown that purring also occurs after an injury or a stressful event, it is a form of self-medication, pain relief and helps the animal to heal. The low level purring frequencies of felinae, including the bigger species (like cheetahs, cougars and pumas), builds bone density, which gives the animal a 90% chance of survival, like a built in physical therapy after severe trauma. This may also explain why they spend much of their life sleeping. These low level frequency vibrations are used in studies for astronauts that suffer from bone density loss in low gravity conditions (The SciShow, 2013).

The reasons for purring are many: contentment, pain, stress, self soothing and healing. Kittens are blind and deaf until two weeks old but purr after just two days, to let their mothers know where they are and attract their attention at feeding time. This continues into adulthood. Domestic cats often purr when stroked by humans, which leads to the association of purring with pleasure in humans (Hambly: Why do Cats Purr?).

Some sports medicine doctors use high-frequency vibrations to repair bones, joints, muscles, tendons, ligaments and even heal wounds. It is known that bone growth can occur with vibrations of 25-50Hz and soft tissue heals at 100Hz. Vibrations at high frequencies increase production of natural anti-inflammatories in the body as well as minute contractions and relaxation in muscle fibers, which stimulate growth of bone cells (la Fontaine, 2021). While the neofelis species fall under the panthera family, their hyoid is ossfied as with the felinae species (Bellani, 2020).

Only 4 of the panthera species roar: the lion, tiger, jaguar and leopard, because a bone in the hyoid (the *epihyal*) is replaced by a ligament (Mills, 2014). They also have a single vocal fold with a thick mucus lining, a large vocal muscle (*thyroarytenoid muscle*) and

a large *cricothyroid* muscle (the only tensor muscle in the larynx) consisting of long, narrow membranes. When vocal folds are longer than 19mm enables the roar in the panthera genus (Wikipedia: Pantherinae). The deeper the *epihayoids* extends, the deeper the roar (Mills, 2014). A major difference between roaring and purring can be found in the voice box: purring occurs with extremely rapid twitching of the vocalis muscle (in the vocal folds). The roaring species not only have longer, stretchier ligaments, they are fleshier and fattier, which makes them strong and flexible allowing for the roar (Welsh, 2021).

Big cats and medium wild cat sounds can be heard here, where various territorial roars to meows, growls and chuffing are featured (YouTube: Big Cat Rescue). Production of a roar is complex behaviour generated by airflow from the respiratory system vibrating the vocal folds to produce sound, this sound production by flow-induced vocal fold oscillation exposes the tissue to mechanical stress (Klemuk et al, 2011).

Findings from research undertaken by Klemuk et al on vocal folds of 3 species (bengal and siberian tigers and a lion) showed:

(a) Panthera have highly organised vocal folds: a deep layer of *lamina propria* (connective tissue) containing adipocytes (fat cells) embedded in collagen and elastin fibres. The lumen-side is fat free with a compact extracellular matrix and *hyaluronan* (a lubricant). Finger-like projections between the lamina propria and the epithelium creating a large surface area between the epithelium and connective tissue, which improves the exchange of nutrients, oxygen and waste as well as increase physical binding sites that connect the epithelium to the lamina propria, in turn helping tissue withstand the greater force of a roar.

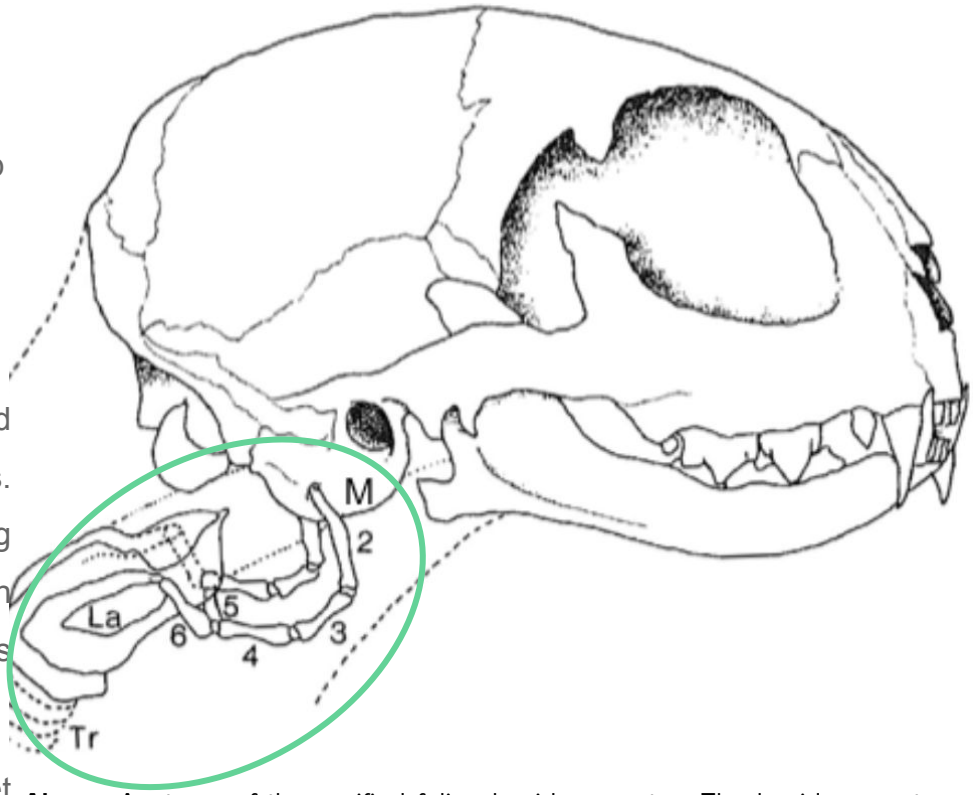
(b) Vocal fold viscoelasticity (both elastic and viscous properties) contributes to vocal differences in individual, sex and species level. The animals in this study were elderly and outside of mating season at the time of death. Age or season (mating versus

non-mating) at this point had not been tested, but likely reflected in viscoelasticity of vocal folds.

(d) Elastic and viscous properties of panthera vocal folds help to ease the vocal pressure and muscular activity. Findings in this research support that morphology and vocal function of vocal folds are linked.

Klemuk et al suggest that the fat around the panthera vocal cord area helps to shape the vocal folds rather than add mass. Panthera vocal folds are thick and have a flat surface making them rectangular in shape, which contributes to lower phonation pressure as well as low frequencies and acute sound intensities (or acoustic *intensity*: power carried by sound waves).

Furthermore, fat provides a protective function in its deep set position, serving as a cushion; it is also more easily distorted than densely packed fibro-elastic tissue, therefore can absorb deformations. Fat is widely found as a cushion material to absorb



Above: Anatomy of the ossified feline hyoid apparatus. The hyoid apparatus joins the larynx (La) to the middle ear capsules (M; auditory bullae - where the ear apparatus reside) via two parallel chains of seven 'bones'. The fifth bone links the two chains, forming the central basihyoid. The first and seventh members of the chains are always cartilaginous therefore are not displayed in the diagram. In panthera, bones in position 3 are cartilaginous and elongated allowing for the roar. Tr = trachea. **Image Credit:** Pendragon and Winkler, 2011

compression stress (as in the sole, the knee or in the buttocks). Deep fatty layers of the lamina propria contain large blood vessels, more so than the fat-free layers. Fluid and blood circulation is generally problematic in oscillating areas because blood vessels are sensitive to severe bending and can easily rupture. The large fat cells help vessels remain intact. In addition, accumulation of fat in connective tissue is a source for repair mediated by stem cells. Since the oscillation of tissue during roaring in lions and tigers can possibly cause tissue damage, the advantage of fat reservoir cells is that fast tissue repair is possible with guaranteed stable phonation (Klemuk et al, 2011).

5. Felidae Social & Territorial Behaviour

Felidae are all solitary animals with the exception of lions (*Panthera leo*) and sometimes the social behaviour of domestic cats (*Felis catus*), varies depending on the availability of food and density of the group. Domestic cats retain their wild routes as solitary hunters whether in the wild or in artificial situation. Generally, living arrangements of free-living, domestic cats can be females that form small groups, vaguely resembling a lion pride, and others remain solitary in their own territories (hunting and mating grounds), which is typical of most wild felids (*Felis silvestris*) (iCatCare: The Social Structure of Cat Life, 2018), often only coming together to mate, compete over prey or territory (Four Paws International: Territorial Behaviour of Cats, 2021).

While solitary animals, cats are capable of forming bonds with humans and other cats and the complexity of their social life is not fully understood. The concept of a solitary cat society has recently changed, it is now understood that cats can live in large, dynamic groups with an evident loose social structure on condition that there is abundant food. Two social structures are apparent: one is a type of despotic hierarchy (one dominant leader and everyone else an equal second) and the occasional pariah cat/s; second, a far

more dynamic and interactive hierarchy that involves actions by the leader cats demonstrating their dominance, asserting their position, time sharing and prioritisation. Cats in these social groups have preferred associates and cats who actively avoid each other, a dynamic very similar human social behaviour (Centre for Canine Behavior: Feline Social Structure & Aggression, 2019).

When cats form social groups, they only work when members of the group are familiar and there is no competition for food and other resources. Strong social relationships form with familiar individuals, especially between kittens of the same litter and with their mother. In feral cat colonies kittens are often be nursed any of the lactating queens, which helps to form social bonds from a young age. Often a larger central colony of females exists, which is associated with a food source and smaller peripheral groups may develop around that central colony, that also have access (although poorer) to the food source, but will be poorer in health and in reproductive performance (iCatCare: The Social Structure of Cat Life, 2018).

The immediate area around a cat's sleeping space is aggressively defended. Different habitats and living conditions in which cats live, increases social bonds between cats, but each one still has its own patch that is to be respected. Claiming territory is a natural felidae behaviour (both indoor, outdoor and wild cats). The territory size and how it is defended, varies from cat to cat. Territory is marked by depositing urine and excrement in high-up locations (Four Paws International: Territorial Behaviour of Cats, 2021).

Territories of tomcats may overlap in certain areas as the areas they patrol are much larger than neutered males' areas. A tomcat's territory often includes multiple territories that belong to female cats so this allows tomcats to check which female is in heat. Overlaps are usually non-problematic because cats avoid each other or visit neutral areas at different times, however an encounter most often includes no more than threatening gestures, serious confrontations are avoided, although they observe each other's signals. Fighting

occurs mostly during an encounter between very confident individuals and neither backs down and so hierarchy is settled by fighting (Four Paws International: Territorial Behaviour of Cats, 2021).

Lions (*Panthera leo*) on the other hand, are the most social of all the felidae family, with matriarchal prides formed from 6 to 7 related females with no evident hierarchy. Females explore territory and hunt cooperatively by either forming subgroups or spending time alone. Prides have fission-fusion social dynamics with keystone individuals maintaining cohesion and individuals have preferential associations. Lions are resident animals and both males and females patrol their territory, females patrol closer to the natal area (or home range) whereas males patrol the outer areas of their territory. Territories are protected by patrolling, roaring and scent marking by both males and females. The home range size is influenced by abundance of prey, prey movements and geography: home range increased when there is less prey and are smaller when more prey is available. Home ranges vary in size: 25 to 1000+ km^2 (averaging 100-200 km^2). Lions are most active (hunting, playing, grooming, aggressive behaviour) at dawn and more so at dusk, although this can also happen during the day should the opportunity arise. They usually spend most of the day (up to 20 hours) resting in the shade to conserve energy and avoid heat but cubs and subadults (sometimes even males) follow the females (San Diego Zoo Wildlife Coalition: African and Asian Lions: Behavior & Ecology).

Male lion coalitions, up to 7 per pride, challenge each other coalitions enabling them to keep hold of territory and mating rights in female prides. Social interactions between pride members includes rubbing cheeks, chins and foreheads as a greeting; licking and grooming usually between mother and cub or 2 females; head rubbing is usually reserved for males greeting other males. Expectant mothers give birth synchronously but leave

the pride to keep their young cubs safe until they can see, walk and start venturing outside of the den. Cubs are raised in a communal crèche and females nurse one another's cubs. The male cubs from the same crèche are known to sometimes form lifelong alliances. Territorial behaviour includes vocalization and scent marking to deter trespassing lions. On average, males hold residency with a pride for only 2-3 years before new males take over the pride, when intruder males take over a pride, they may commit infanticide, which secures paternity, causing females to go into an infertile 'testing period' thought to cultivate social bonds with the strange males. Considering the frequency of mating, conception rates in the wild are low (San Diego Zoo Wildlife Coalition: African and Asian Lions: Behavior & Ecology).

6. Conclusion

Felidae is a diverse order of animals where the of the species is 100 times bigger than the smallest, but the characteristics, genome, behaviour is the same throughout. As pets they are loved the world over!

'Cat' is one of the first one hundred words that children learn. These popular pets descended from the African wildcat (*Felis silvestris)* and domesticated initially for agricultural defense purposes against rodents; also worshipped in Egyptian religion and in the middle ages became a dark omen but now are companion animals. Today's domestic cats come from generations of artificial selection for coat colour, appearance and behaviour, leading to the 40-odd cat breeds we have today (O'Brien, 2004).

The roaring *Panthera* genus sit at the top of the trophic chain in every ecosystem they occupy. All 36 felidae species are loved above all other carnivores. It's tragic that the vast expanse required by wild cats to survive has resulted in every species of felidae officially considered endangered or threatened in the wild today by CITES, IUCN Red Book and other monitors (O'Brien, 2004).

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