

Sarah Hartwell - Polydactyl Cats: Messybeast - <http://www.messybeast.com/poly-cats.html>

WHAT IS POLYDACTYLY?

Polydactyly, or extra digits, is a common trait among cats, particularly it seems, among Celtic cats and cats on part of America's Eastern coast and South West Britain. This distribution may well be linked. Except for Twisty Cats, polydactyly is not a product of bad breeding. It is simply a naturally occurring genetic variation and, as noted later on, polydactyly is found in fossil reptiles - meaning that five digits might be the abnormal form! Only one form of polydactyly is known to be harmful.

In a 1967 issue of Britain's "The Cat" magazine, Mary Collier of Axminster, Devon wrote *Can any readers of THE CAT give me any information about 6-toed cats, sometimes called 'Boxers' or 'Boxing Cats'? I have recently acquired a very fine kitten of this type [...] What I particularly want to know is their district or origin, or country if outside the British Isles and the date they may first have been recognised.*" In February 1978, the Daily Mirror carried a series of letters on polydactyl cats. Jennifer Wellstead, of Penzance, Cornwall, had asked if any other readers had cats with 6 toes on each paw. A "Mrs I" of Kettering, Northants, replied that 6-toed cats were favoured as witches' familiars of witches. Mrs Farley, of Havant, Hampshire, said she had 6 cats, 3 of whom had 6 toes and 2 had 4 toes on each foot in place of the 'normal' 5. She added that a recent litter had produced one kitten with 7 toes, 4 with 6 toes and 2 with the normal number of toes.

Polydactyly (six or seven toes) varies from the classic "mitten cat" through to cats which simply have more toes than normal, but no "thumb". A correspondent to the New Scientist noted that the innermost extra toes on the front paws are often opposable and some cats use them with quite startling proficiency to manipulate small objects with almost human dexterity. Some owners of polydactyl cats joke that their cats are more intelligent because of this and represent the next stage in feline evolution - the ability to open cartons and cans unaided.



Between one and three extra toes on the front feet

Polydactyl cats are known by various names - "mitten cats", "thumb cats", "six-finger cats", "Cardi cats" and "Hemingway cats". The latter is because of writer Ernest Hemingway who made his home on the small island of Key West, Florida. He shared the island with nearly 50 cats, including a 6-toed polydactyl given to him by a ship captain; the cats bred and the polydactyl trait became common, hence polydactyls are often known as "Hemingway Cats". Hemingway's colony of cats was free-breeding with the local cat population and the ratio of polydactyl cats to normal-toes cats was about 50/50. Another story suggests that the cat given to Hemingway was a female double-pawed cat and that the polydactyl cats on the island came from 19th Century ships' cats. The high rate of polydactyl cats in Boston, USA has also led to the nickname "Boston Thumb Cats". The nickname "double-pawed" cats is a misnomer since there is a specific double paw condition.

Polydactyly itself is also known as hyperdactyly or supernumary digits and occurs in many animals (including humans) as a spontaneous mutation or hereditary trait. The mode of inheritance - dominant or recessive - varies between species. Instances and illustrations of human polydactyly (for comparison purposes) are given at the end of this article.

AN ALL-AMERICAN TRAIT OR AN AMERICAN CONCEIT?

Some American cat lovers, cat publications and breeders (notably early advertising literature about PixieBobs) have claimed that polydactyly is unique to America. In early PixieBob promotional literature "Bigfoot is in the Building!" Brenda Weatherby and Carol Ann Brewer wrote that polydactyly first appeared in Boston in the early 17th century and that polydactyl cats are only found in North America. In actuality, polydactyl cats may have arrived in Boston from England. Polydactyly is emphatically not unique to North America. Any suggestions that polydactyl cats are not found outside of America are factually incorrect and perhaps an American conceit. The trait is found in Britain, some parts of mainland Europe and in Asia. Polydactyly is common enough in some areas of Britain for it to be almost unremarkable.

A polydactyl gene pool has become concentrated in south west Wales. Cats with extra toes are common in the area around Cardiganshire (Ceredigion) and are known as "Cardi-cats". Six-toed cats are apparently more common in Cardigan (Aberteifi) than elsewhere in Britain; seven-toed cats are also sometimes found in the area. Cardigan/Aberteifi sits on the Teifi estuary above Cardigan Bay and was once one of the busiest shipping ports in Wales which probably explains the high density of polydactyl cats in the area.

I saw several polydactyls each year at the Chelmsford Cats Protection rescue shelter as well as having owned a polydactyl. I found a superb bobtailed polydactyl cat in rural Malaysia (close to Kuantan) where "six-finger cats" are considered lucky. Being an unneutered tomcat, the trait would be perpetuated.



Two polydactyl kitten from Lake Chini near Kuantan, Malaysia; the father was a bobtailed polydactyl had produced a dynasty of multi-toed kittens on local female cats.

An article from Cornell University, Cat Watch (1998), cited studies into polydactyl cats from the 1940's through to the 1970's. The study indicated that the trait may have occurred in cats taken to Boston by English Puritans during the 1600s and speculated that the mutation developed in cats already in the Boston area rather than in cats in England. The progeny of these cats may have travelled on trading ships from Boston to Yarmouth, Massachusetts and Halifax, Nova Scotia, two areas which also have a high incidence of polydactyly. Charles Darwin wrote of polydactyl cats in his book "The Variation of Animals and Plants Under Domestication" published in the 1850's "I have heard of several families of six-toed cats, in one of which the peculiarity had been transmitted for at least three generations" pre-dating claims elsewhere that the first scientific recording of feline polydactyly was in 1868.

Polydactyl cats are said to be virtually non-existent in Europe, because "unusual looking cats" were destroyed due to witchcraft superstitions, practically eliminating the trait (Kelly, Larson,1993). I do not know whether Britain was

included in the generic term "Europe" or whether it meant mainland (continental) Europe only. In Norway, polydactyl cats are known as "ship's cats" as the extra toes supposedly gave them better balance on ships in stormy weather; they are not uncommon and polydactyl kittens are sought after pets. Polydactyl random-bred cats have been reported in Sweden though other European cat lovers (locations not reported) had apparently never seen a polydactyl. They are common enough in Britain to be considered unremarkable.

Polydactyl cats were considered "lucky" by sailors. Sailors also believed polydactyl cats to be superior mousers and ratters. Employed as ships' ratters and lucky mascots, they would have reached America with early British settlers hence their greater frequency in Eastern states. A disproportionately high number of "lucky" polydactyl cats, compared to normal-toed cats, would have found their way there. This would lead to a greater proportion of polydactyls than usual for a random-breeding cat population. Back in Britain, with its large cat population of which the polydactyl formed only a small part, the trait remained less common (though there have been localised pockets of higher than average incidence). There is a higher incidence of polydactyly in South-West England, possibly associated with ports from which ships set sail for the New World.

Bjørn B Svingen, owner of a polydactyl cat, provided the following information on polydactyl cats in Norway and their association with ships: *"I have heard people say that these genes came to Norway long ago. The story was that the genes were inherited from Spanish or Portuguese ship cats with this 'disorder'. These cats were supposedly common on ships trading on the Norwegian coastline. They have again become popular, at least in our area, and are plentiful in Trøndelag in mid Norway."* As a result, they are also known there as "Skipskatt" (ship-cat).

In a survey and detailed account of cats he found in Singapore in 1959, Searle had not noted any polydactyls. The only polydactyls I noted in the Malaysia/Singapore region were the Lake Chini cats.

THE GENE(S) FOR POLYDACTYLY

There are two forms of polydactyly described by embryologists. Pre-axial polydactyly refers to extra digits on the inside edge (thumb-side) of the paw. Post-axial polydactyly refers to extra digits on the outer side (little finger side) of the paw and is uncommon.

One of the earliest inheritance studies was by Poulton (probably 1880s/90s) which is mentioned by Thomas Hunt Morgan (Professor of Experimental Zoology, Columbia University) in *Experimental Zoology* (Publ. Macmillan & Co, London, 1910): *Poulton has given some records of polydactyl cats that appear to be explicable, so far as they go, along Mendelian lines. Three young were produced from a polydactyl female by an unknown father. They were all polydactyl. If polydactylism dominates over the normal condition, this result is simple dominance. One of these individuals (F1) produced three litters (by unknown fathers), in which four normal and six abnormal kittens appeared. If the father was normal, five normal and five polydactyl young would be expected. Thus:- (P + N) + (N + N) = (2NP + 2NN) [P being poly foot and N being normal foot]*

Sis & Getty (1968) describe polydactyly as an monogenic autosomal dominant trait affecting the pre-axial part of the limb. This is the typical and harmless form of polydactyly though other forms may exist. Both Danforth and Chapman & Zeiner proved in their research that normal feline polydactyly is a simple incomplete dominant gene with variable expression. According to geneticist and TICA Genetics Committee Chair Dr Solveig Pflueger "most polydactyl cats... have a form of pre-axial polydactyly with the extra digits(s) on the thumb side of the foot..." The Pd gene causes the entirely harmless form of polydactyl.

The main studies on feline polydactyly are Danforth's studies *Heredity of Polydactylism* (1947) and *Morphology of the Feet in Polydactyl Cats* (1947) plus Chapman & Zeiner's study *The Anatomy of Polydactylism in cats with Observations on Genetic Control* (1961). The Danforth and Chapman & Zeiner studies observed examples of both mitten-foot and patty-foot polydactyly in their studies (some refer to the patty foot as "snowshoes" but I avoid that term as there is a cat breed called the Snowshoe). Danforth, and Chapman & Zeiner, stated that polydactyly was never observed in the hind feet except when it was also present in the front feet. A hind-foot polydactyl must have extra digits on the front feet, though sometimes these are not readily discernible and can only be found by x-ray.

The gene(s) for polydactyly specifically affects the tissue formed at the very end of the limb (apical cap) of a developing embryo. This is the area where the toes will form. Danforth studied the way normal pre-axial polydactyly developed in embryos based on data from 150 cats. He discerned evidence of polydactyly in the 20th day of gestation in the form of excess development on the edges of the limb buds that would form the forelimbs. If the

apical cap is larger than normal, extra toes will develop from it. It is worth noting that physical damage to the apical cap might also trigger the development of extra toes. Branching of the apical cap will lead to complete double paws or, if it branches early enough, to doubled limbs.

The first major study into classical polydactyly (thumb cats) was conducted in 1947. For his study "Heredity of polydactyly in the cat" (Journal of Heredity 38, 107, 1947) Danforth studied two female polydactyl cats that he housed at his laboratory, The cats came from locations 85 km from each other in California, but the possibility of them being related could not be ruled out. He mated these females with different males and recorded the dates of mating and the physical traits of the kittens. He collated additional information from friends with polydactyl cats.

He noted that the effects of polydactyly could always be seen on the front paws and sometimes also on the hind paws. On the front paws, the first digit was at least enlarged in one front paw and might be doubled or tripled. If the hind paws were also affected, there was at least a rudimentary dew-claw and sometimes additional claws. Where there was a doubled first digit, it was sometimes incompletely formed with the additional digit between the first digit and the other claws. The position of the first digit was also changed a little from normal to resemble a thumb. The four images show different footprints: a normal-footed front paw and 3 expressions of polydactyly:



Danforth mated all possible combinations of his cats: Poly x Poly, Poly x Non-Poly, Non-Poly x Non-Poly. This confirmed that polydactyly was a dominant gene, because in every mating where at least one parent was polydactyl there were polydactyl offspring. In matings between two normal-footed cats there were never any polydactyl offspring. In 3 matings, all offspring were polydactyl and therefore one or both parents were probably homozygous for polydactyly.

In guinea pigs, one form of polydactyly is lethal when homozygous. Danforth's studies indicated that this was not the case in cats. In a mating Pp x Pp (heterozygous parents) on average 25 % of the young will be homozygous for polydactyly, 50 % heterozygous for polydactyly and 25 % normal-footed. If the gene was lethal, the 25% of homozygous offspring would die before birth and the litters therefore would be smaller than expected. Danforth found the average litters to be almost the same size (4.12 with offspring homozygous for polydactyly compared to 4.35 for litters where no offspring could be homozygous). This also affected the ratio of polydactyl and normal-footed offspring in a litter. If the gene was lethal when homozygous, there would be (on average) 2 poly kittens for every normal-footed kitten. Danforth's cats produced a ratio of 77 poly kittens to 22 normal-footed kittens.

Probable Mating	Offspring polydactyl		Offspring normal		Total
	Observed	Expected	Observed	Expected	
PP x Pp	8	8	0	0	8
PP x pp	11	11	0	0	11
Pp x Pp	69	68.25	22	22.75	91
Pp x pp	33	31.5	30	31.5	63
pp x pp	0	0	61	61	61

From these studies, Danforth concluded that polydactyly was a variable expressed dominant gene with no reason to suspect it was lethal when homozygous: "these data lend no support to the assumption that polydactyly in the cat is lethal when homozygous" nor was it associated with the cat's gender "The trait is not related to sex, and no

evidence is found that its gene is lethal" He did not find evidence of split foot or radial hypoplasia (also called radial hemimelia) in his studies though his second study into feline polydactyly ("Morphology of the Feet in Polydactyl Cats", 1947) found that cats with 6 metatarsals (toes) tended to have fusion at the ulna which caused varying degrees of rotation of the joint of the radius.

Useful Formula For Describing Polydactyl Front Paws	
Normal front foot	4
Foot with extra toes that do not form a thumb (patty foot)	5; 6 (etc)
Mitten foot with thumb (single digit)	4+1
Mitten foot with 2 or more extra toes	4+2; 4+3 etc
Mitten foot where extra claws are tucked between the normal foot and "thumb": (the numbers in brackets mean extra claws that aren't on a fully developed toe)	4+(1)+1; 4+(2)+1; 4+(1)+2 (etc)

In 1955, Albert C Jude, author of "Cat Genetics" (a book that had as much about mice and rabbits than cats!) documented two forms of polydactyly. He wrote that polydactylism (extra digits), and oligodactylism (reduction of toe number) were sometimes reported by the fancy, but were the exception (not selected for) rather than the rule within cat breeding. This meant little data was available on feline polydactyly to permit proper scientific study. He noted that polydactyly involving only the preaxial side of the limb had been documented in cats by Danforth in 1947 and was dominant over the normal form. Most cases of polydactylism in cats observed by Jude had affected the front feet only.

Jude also described another form of polydactyly, the type we now call "mitten cats" but which he called "posterior reduplication", in his 1955 book: Another interesting deformity - only very occasionally seen in cats, but more frequently seen in some other animals - is known as "posterior reduplication." The condition was found in a stock of mice by Danforth in 1923, and a description was published by him in 1930. This deformity is mentioned here mainly to show how information of a helpful nature can be given by fanciers. In this instance it came from Mrs. A. Winsor of Hull, a well-known English Abyssinian breeder. Before the war, says Mrs. Winsor, "I had two little black she-cats. One came into season, and a strange gray tom came to investigate. His feet were really amazing. His front legs were very thick and stout, big feet, with normal number of toes. On the inner side of each foot was another smaller foot. A sort of stalk grew from the ankle, as if the ankle bone had been split, and this ended in a complete foot which rested on the ground alongside the normal foot, and turned slightly inward, When sitting he had to advance one leg, as he could not possibly put all his four feet side by side, and when walking he sort of lifted one foot over the other. He mated my queen who was calling at the time and there were two black kittens whom we put to sleep, and two gray-striped, both females. One had just thumbs; the other had seven toes - four ordinary, and three extra where the thumb would be. There was no stalk, but these three toes had a separate pad; they were about the same length as the others, and her feet spread out like paws. She also had a sort of "thumb" half-way up each hind foot, with a claw on the end. The other gray-striped female - the one that had just thumbs - we kept for eight years and then she died. I managed to get a granddaughter who is now seven years old. She has had countless kittens, and about half of every litter have the 'Family Feet.'"

It is interesting that Jude differentiated between the 2 types of polydactyly in 1955; differentiating between the two forms has recently become a concern for cat breeders due to the occurrence of Twisty Cats.

According to the late Roy Robinson in his book "Genetics for Cat Breeders", polydactyly has been officially (scientifically) recorded as early as 1868, though it had been observed earlier and seen frequently since. The distinguishing feature is the presence of extra toes, most noticeably on the front feet. Robinson explains that there is considerable variation in the number of extra toes and in how well-formed they are. The trait ranges from an enlargement of the inside digit into a "thumb" to the formation of three apparently well formed extra toes (i.e. 7 toes on the affected foot). A cat may even have different numbers of toes on each of its front feet.

The hind feet are rarely affected and are only ever affected if the front feet are also affected. I have received a report of a Maine Coon with hind foot polydactyly and apparently normal fore paws; it seems likely that it was genetically polydactyl for all four paws, but that the extra toes had not been visibly expressed in the fore paws for some reason. I also received the following report about a random-bred hind-foot polydactyl with normal front paws.



Rufus (Photo Karen Kohl)



TOES BETWEEN THUMB AND PAW



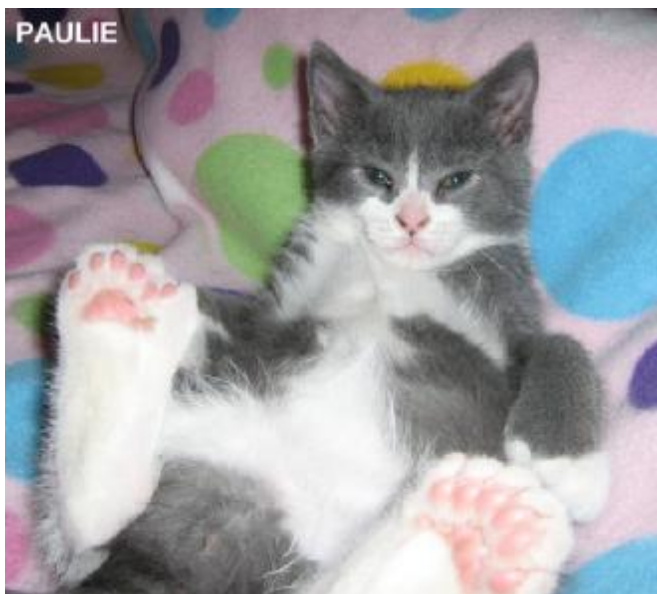
HIND DEW CLAWS
Photos copyright Lizzie Ellis

Karen Kohl's orange tabby kitten (Rufus, pictured) has no thumbs on his front paws and apparently normal front dew claws (described as a short splinter of a nail on the inside of his left front paw), but has 6 toes on each of his hind paws. The inside toes of each hind paw are thumb-like and have both a toe pad and an extra palm pad. One of them is retractile like his other toes and one isn't. Rufus was born in Boston in June, 2003. He and two normal-toed brothers were rescued feral kittens and probably inbred. Rufus was the only healthy one of the three. They were taken to a local cat shelter which had seen one or two cats with more toes on the back paws than on the front so Rufus isn't the only one and this form of polydactyly may be present in the local feral population. One explanation is that the polydactyly of the front paw has been suppressed by other genes. An alternative is that Rufus and other cats in that area have a mutation which affects only the hind paws - a form of polydactyly previously only seen in leopards. Boston has a high incidence of polydactyly; either due to mutations occurring there or due to "lucky" polydactylous ships' cats being taken there with early settlers.

The normal cat's front paw has 4 toes and one dewclaw (rudimentary toe or thumb which does not touch the ground) while the back paw has 4 toes. A polydactyl will usually have one or two extra toes on each foot. Most polydactyl cats have a form of pre-axial (i.e. situated in front of the axis of a limb) polydactyly with the extra toes appearing on the thumb side of the foot. The gene for Polydactyly can give rise to either extra toes or extra dewclaws. Each extra toe has its own terminal pad (fingertip) and normally an additional palmar pad and additional plantar pad. When extra toes occur on the hind paws, these are not generally dewclaws. Some owners report their cats have five toes on the hind paws, however by definition a dewclaw does not touch the ground. Possession of a hind dewclaw or extra digit is considered a throwback in cats, but is relatively common in dogs (a photo is shown below for comparison).

In August 2002, Dominic emailed about the appearance of "thumbs" on the back feet of a polydactyl cat. Both of his polydactyl kittens appeared to have rear thumbs with claws (which were not fully retractile, probably due to the kittens' young age). The photo above is one of Zelda Annabelle's hind feet. On closer examination, the extra hind toe is not really a thumb. To be a thumb it needs to have not only a terminal pad (the "fingertip") but also a palm

pad (like the palm of a person's hand or the ball of a person's thumb). A feline "thumb" sticks out at a different angle



to the other toes, like the thumb of a mitten. It can be wiggled independently of the rest of the foot. Zelda Annabelle's additional hind toes are typical of polydactyl back feet - they do not have the palm-pads and they follow the curve of the foot. Because the hind paws are constructed differently to the fore paws, there are rarely true "thumbs" on the back feet (only one or two reported cases of opposable hind thumbs, but no photographic evidence). Robert O'Rourke's "Paulie" (Paulie-dactyl!!) also has extra palm pads on the back feet.

In reviewing the various reports of polydactyly, Robinson noted that many indicate a dominant gene, but that not all cases need be due to the same mutant gene. It is possible for the exact same gene to have arisen by mutation in different localities at different times which could account for the similar heredity. Some gene loci (areas of chromosome) are more prone to mutation than are others. However, Robinson cautioned his reader that other cases of polydactyly might prove to be inherited differently.

During the 1990s, other researchers reported forms of polydactyly which they believed to be recessive. One researcher into feline curiosities suggested two different dominant forms and one recessive form all of which had subtly different effects on the structure of the paw. This was based on the sudden appearance of polydactyl cats in a population of normal-toed cats. This could only have occurred through a gene mutation or through recessive genes. Apparently the evidence among a number of random-breeding cats suggested a recessive gene for polydactyly.

Dan Williams contacted me in July 2006 about a localised population of cats with about 5-10% polydactyls in Syracuse, Central New York. The "7-toed cats" that are consistent in conformation: 4 regular toes, with an extra toe just outside the innermost digit, but the foot sits flat, including the innermost digit. The 7th toe comes from counting the vestigial toe (dew claw) on the outside, up from the actual paw. There is a digit-less claw between the opposable "thumb" and the wrist. The paw-pads resemble a human hand-print with no separate pad for the dew-claw toe. An analogy is a human with a tiny duplicate unjointed thumb (with nail) growing from the first joint of the normal thumb and which moves with the thumb. Dan thought the gene might be recessive as it only appeared in 5-10% of these random-breeding cats. He also thought it was a mainly male trait. If verified, this would be different from Danforth's classical polydactyly which is a non-sex-linked dominant trait.

Leanne Falkingham, Shelter Manager at an animal shelter in Elmira NY, 2 hours north of Syracuse, confirmed this pocket of polydactyly in March 2008. In a South Carolina shelter she saw around 3 polydactyls per year. In New York, polydactyly is common enough (more than 10% of the shelter's cats) that it is not remarked upon.

Since polydactyly is seen more commonly in cats compared to other mammalian species, what is it about the cat genome (or kitten developmental processes) that makes polydactyly this common? It could simply be the location of certain gene(s) on the chromosome(s). Because of the way chromosomes are duplicated and shared out in cell division when eggs and sperm are made, some areas of chromosomes are more prone to mutation than others. These are known as mutational hot-spots. During cell division, chromosomes duplicate and the chromosome pairs are physically joined together; these are pulled apart and during separation genes can cross over from one copy to the other. Genes adjacent to the join might be affected by the separation process, resulting in small changes. This hot-spot effect could account for the spontaneous appearance of unrelated polydactyl cats in widely separated areas.

Some polydactyls (mitten cats) have double or triple dewclaws because the genes seem to give the instruction "add another digit to what is already present" rather than saying "produce 5 toes instead of 4" or "produce 6 toes instead of 4". Back in the 1960s, a cat lover in an English village reported a high incidence of polydactyl cats, mostly fathered by a local tomcat. Each generation of cats had more toes than the mother - as if the genes simply said

"add another toe". Presumably there was either a limit to how many toes could be added or the tomcat left the area as the phenomenon was not reported again.

There is a similar report from the USA. Each successive generation of a colony of barn cats had more toes than the previous one. Eventually this led to crippling. The colony was severely inbred with each generation being fathered by the same polydactyl tomcat. When he disappeared, a non-polydactyl cat took his place and no further crippled kittens occurred. I also received a first hand account of crippling in later generations of polydactyl barn cats (relating to the writer's grandmother's farm). This may be the same case. Although the latter report of inbred polydactyl farm cats claimed up to 12 toes per paw, this extreme number is unlikely; 8 or 9 is generally the upper limit. The gene is variable in expression so in these colonies, paws range from mitten-paws (with a "thumb") through to double paws.

So far, veterinary literature has not confirmed the "add another toe" gene. Even in the homozygous state (which would occur in inbred colonies), the most common form of polydactyly does not appear to be detrimental to health. However, there is another gene, which resembles polydactyly, which causes severe crippling. Radial hypoplasia (also called radial hemimelia) (RH) is discussed later in this article.

Polydactyly is probably an incomplete dominant. With a normal dominant trait, a cat either has the trait or doesn't have it. With an incomplete dominant there are different "levels" of the trait depending on whether the cat is homozygous or heterozygous for the trait. A homozygous cat shows the trait more fully than a heterozygous cat. This may have been the explanation for the apparent "add another toe" form of the gene in the English village cats. Observation suggests that the incomplete dominant is expressed only 40%-50% of the time when inherited - this concurs nicely with the 50/50 split of polydactyl/non-polydactyl in Hemingway's colony.

The suggested recessive form may also be due to incomplete dominance. The apparently "normal footed" cats would have been polydactyls with barely discernible extra toes, but whose offspring had more prominent extra toes - giving the appearance of either spontaneous mutation or recessive genes.

Because several different genotypes (genetic make-up) produced a similar or identical phenotype (physical appearance) it could be difficult to identify which cat carried which mutation. As it turns out, there are several forms of polydactyly due to several genes which produce a similar-looking trait and in the 2000s, the need to identify and isolate the various forms became crucial due to fears of a link with radial hypoplasia (Twisty Cat mutation). There was evidence for a second dominant form of polydactyly which resulted in a different form and structure to the familiar "mitten cat" form and which affects not only the paw, but the whole leg.

The form of polydactyly most commonly seen in cats is a simple autosomal (i.e. not linked to gender) dominant trait which does not affect the cat adversely and is not associated with other abnormalities. Despite suggestions of "natural snowshoes" there is no real evidence that polydactyly has any significant natural selective advantage or disadvantage. If it was disadvantageous, polydactyl cats would quickly have died out. It is simply an endearing anomaly.

It has been said that if the parent has extra toes, the kittens inherit extra toes in the same configuration as the polydactyl parent. So, if the parent has double dewclaws, the kittens have double dew claws and if the parent has an extra toe, so will the kittens. This may not be 100% true because there are undoubtedly numerous gene mutations causing polydactyly. This may be true in polydactyl breeding programs where cats are carefully matched, but in the random-breeding population, the incomplete dominance of polydactyly means the configuration is variable - and it also depends on what genes the kitten inherits from the other parent!

It is reported that in Maine Coons (where there is work to restore the polydactyl form of the breed), non-polydactyl kittens born to a polydactyl parent appear to have heavier boning in the legs and chest than kittens born to two non-polydactyl parents. In random-breeding cats, polydactyls often appear robust, but this may be due to the overall impression caused by big feet.

THE "BAD" FORM OF POLYDACTYLY



Most expressions of polydactyly are not a handicap to the cat (such as the polydactyl kitten pictured here). The exception is the gene which causes a whole spectrum of effects ranging from extra toes through to radial hypoplasia/radial hemimelia/radial agenesis (the "thalidomide" or "twisty" mutation). This is the gene which causes a condition known as triphalangeal pollex-radial hypoplasia. In mice, there are several gene mutations known to cause this form of polydactylism; unlike conventional "thumb cat" polydactyly, the mutations seem to cause more general disruption of limb formation in an embryo.

In the 1990's an American breeder of "Poly-Bob" cats bred kittens with disabling twisting of the forelimbs. Though originally breeding for polydactyl bobtails (possibly cashing in on the new Pixie-bob) she viewed the twisty trait as creating a cat less likely to run away and become wild. This trait is variously called radial hypoplasia, radial hemimelia or radial agenesis. According to Towle & Breur the most common form of feline hemimelia preaxial longitudinal intercalary radial hemimelia. They found

radial hemimelia (absence of all or part of the distal half of the limb) in Siamese and domestic shorthair cats to possibly be a hereditary trait.

This is the "second dominant form of polydactyly" mentioned earlier. With this trait the pollex (thumb) has an extra joint, making it look more like a human finger than the usual rudimentary feline dewclaw. This triphalangeal (three-boned) thumb may be duplicated and sometimes the next digit is also duplicated. A cat with triphalangeal pollices (three-boned thumbs) may produce kittens with hypoplasia (underdevelopment) or aplasia (absence) of the radius, one of the two bones that make up the forearm. Hypoplasia, according to the Cornell Book of Cats, 1997, is "underdevelopment of a given tissue." So in cats with radial hypoplasia (RH) the radius in the front leg will be underdeveloped or missing. Though the scientific data is still scanty regarding triphalangeal pollex being strongly linked to radial hypoplasia, rather than a coincidence, it remains good practice to avoid breeding from these cats based on studies by Solveig Pflueger and on reports from owners of patty-foot cats whose offspring have show radial hypoplasia.

Because the usual form of polydactyly is so variable in expression, X-rays are needed in order to distinguish between the harmless usual form of polydactyly and the form associated with RH. Some polydactyl cats without dewclaws have 5 or 6 toes all the same length (called "patty" feet). This trait is the one most often associated with RH. However, not all cats with additional same-length toes have the gene for RH. In cats without dew claws or visible thumbs, an X-ray is required to determine whether the radius is deformed in any way - if it is, the cat carries the gene for RH. The gene for RH is variable in expression (possible due to incomplete dominance/heterozygous vs homozygous state), ranging from extra toes to crippling leg deformities, hence the need to determine which non-mitten polydactyls may carry the gene for RH and which carry the more usual form of polydactyly.

In a physical examination, the best way to tell the difference is to check for dewclaws. Polydactyl cats without dewclaws are disqualified from shows but may safely produce normal-footed show-quality offspring which can be used in breeding. The cats should be bred with non-polydactyl cats to keep the trait heterozygous as it appears to be the homozygous cats which are affected by RH. A number of genes in cats are less harmful in the heterozygous form, but are either crippling or lethal in the homozygous form e.g. the Manx mutation, the Scottish Fold mutation.

HIND PAWS ONLY POLYDACTYLY

According to Danforth and to Chapman & Zeiner; polydactyly is never observed in the hind feet except when it is also present in the front feet. Since polydactyly has variable expression, the extra digits on the front feet might not be evident, or they could even be suppressed by other genes. A hind-foot only polydactyl may have extra digits on the front feet that are not readily discernible or can only be found by x-ray.

The following photos show Aurora, a hind-paws-only polydactyl Maine Coon kitten bred from non-polydactyl bloodlines by Paul and Natasja in The Netherlands. There are no poly cats within the first six generations and parents, grandparents, about 30 relatives and also related lines are non-polydactyl. Aurora's 3 brothers have no signs of anything similar.



Aurora has true dewclaws on both her paws. They form a normal thumb and are complete: footbed, nail and muscles. Usually extra toes only occur on the back feet if the front feet are also polydactyl. Aurora does not have polydactyl front paws. Also unusually, the extra toes on the back paws are true dew claws, placed higher up than ordinary toes. According to Paul "We only discovered it last Friday, when Natasja thought her headache was playing tricks with her. She checked four times if the tail was still at the back, and it still was."



A similar case has apparently occurred in a Norwegian Forest Cat but there is no further information. Another has turned up in a Manx out of British bloodlines and has not been inherited by any of his offspring (ruling out a dominant gene). Current thoughts are that it is a random mutation, the result of polygenes meeting up or a non-genetic developmental trait. A recessive gene would have shown up in other cats. Aurora will later be test-mated to see if the trait is hereditary.

Stacey Bliss also has a hind paw polydactyl which had an extra toe on the right hind paw and lacked front dew claws. She had previously produced mitten cats, including Stacey's silver tabby cat Mia, and recently gave birth to a male orange kitten with no front dew-claws, but with extra toes on the hind paws. The kitten's front feet were at first at an odd angle, being bent down more like a human's wrist, but as he began to crawl and eventually walk, his feet flattened out. Stacey believes it may have been due to some lack of bones in the feet, but sadly the kitten vanished at the age of 10 weeks before this could be investigated. Mitten-pawed Mia is due to have a planned litter in Spring 2005, after which she will be spayed, and it will be interesting to see what form of polydactyly she passes on.

Pamela Alley's "Beaker" also had front paws bent at the wrist. He was an orange-and-white male one of 5 kittens born in 1984 to a random-bred female in a barn in Yreka, California, USA. Both of Beaker's front feet were firmly bent at the 'wrist'. He was significantly polydactyl with 7 toes on the front and 6 on the back. Pamela gently stretched the feet to normal positioning, and after about 2 weeks he was able to use his feet normally. He had to have the dewclaws removed as there was a danger of the boneless claws catching and ripping off the pad and attached skin; this still left him with 6 toes on each front paw. Beaker reached the grand old age of 17.5 years.

MINOR PROBLEMS WITH POLYDACTYLY

In general, polydactyly causes no ill-effects in cats. It is certainly not a handicap and is an anomaly (deviation from the norm) rather than a deformity. Although some owners like to have the extra toe removed for cosmetic or safety reasons, cats rarely catch the extra toe(s) on furnishings. In rare cases, nail growth can be affected, but only if the extra toe is incompletely formed and the nail bed is deformed. This can lead to a number of claw problems such as ingrowing claws, overgrown claws or "superclaw syndrome".

Sometimes a claw develops between the thumb and the rest of the paw as Brian Tinker describes regarding his grey cat "Buddy". Buddy's back paws have 5 toes each, 4 normal ones and 1 dew claw. His front paws have between 5 and 7 toes each. The left front paw has 4 normal toes and an opposable thumb that remains underneath the paw and cannot lay in line with the rest of the toes. Between the opposable thumb and the regular toes (i.e. in the angle or crevice) was an additional claw. This was not associated with a toe and simply stuck out from the skin, unfortunately tearing the surrounding skin. Above the thumb is a vestigial toe that is only discernible through handling. On the right front paw, a similar vestigial toe has a segment of extra, jointed bone that can be felt and seen, but has no muscles or tendons controlling it (it can be freely wiggled up and down by the owner). On the right front paw, the thumb lies in line with the rest of the toes, but can also wrap downwards as an opposable digit. One of the claws on the right thumb became deformed and curled around on itself. The claw had died and snapped off easily. The nail-bed has since been removed.

Overgrown claws are not restricted to polydactyl cats, but are more common in polydactyls because the extra toe is often shorter than the regular toes or it points in a slightly different directions. This means that the cat is unable to strop the extra claws on a scratching post. Unless clipped regularly, the claw can become overgrown and embed themselves in the paw pad.

Ingrowing claws grow twisted or crooked instead of growing straight with a smooth downward curve. Ingrown claws can grow into the paw pad and need either more frequent clipping or surgical removal. In the UK, such problem claws are the only time when declawing (of the affected toes only) is permitted. Ingrowing dewclaws can also occur in non-polydactyl cats where the claw grows into side of the foot.

If the claw is set in such a way that it snags on furnishings etc, it can tear and infection can set in. Nail-bed infections or nail bed damage can lead to abnormal claw growth e.g. thickening or twisting. Where the toes are cramped together, the skin between them should be checked for infection as it provides a handy undisturbed crevice for bacteria. In general, the cat's own cleaning routine should prevent this, but if the toes cannot be spread then its tongue cannot easily clean between them.

If two extra toes are fused together, the nail bed will also be fused. The claw that grows from this dual nail bed can also be fused, leading to something known colloquially as "superclaw syndrome". The fused claw or "superclaw" is thicker than a regular claw and may twist abnormally. A non-twisting superclaw is not normally painful for the cat, but because the claw is thicker and stronger than usual, it can gouge wood - and flesh - more deeply than a regular claw. If the superclaw grows twisted, there is a danger that it will become ingrown.

Where the extra toe causes repeated problems, it can be removed in a straightforward operation, but this is rarely necessary.



Left: Queenie, domestic shorthair.

Above: Close up of Queenie's forepaws; she has two extra toes where the dew claw should be. These were used as opposable thumbs to pick up small objects or hold on to fingers!

POLYDACTYLY AND THE CAT FANCY

Historically, the polydactyl made up 40% of the original unregistered Maine Coon population. There are claims that the extra toes acted as snowshoes, helping these rugged cats negotiate snowy New England winters. Local folk tales claimed that these cats were fierce hunters who used their oversized paws to catch live fish, even taking fresh fish home to feed their owners! However, breed standards made no allowance for polydactyl Maine Coons and stipulated a normal foot configuration. Because polydactyly in the Maine Coon is due to the autosomal dominant gene, the trait could easily be eliminated by breeding only from non-polydactyl Maine Coons. The trait was deliberately bred out of Maine Coons and only recently have there been attempts to reinstate it.

Selection against polydactyly means the trait seems to have become associated with the term "harmful deformity" in many minds and there have even been postings on Usenet stating, quite erroneously, that "polydactyl cats almost always have some other sort of abnormality". Many cat registries happily recognise breeds defined by mutations which can have lethal or crippling effects such as spina bifida in the Manx, but refuse to permit polydactyl cats as either breeds or breed variants. Some cat enthusiasts feel that registries are right in refusing to accept polydactyl cats, fearing that breeders would try to produce cats with excessive and disabling numbers of toes on each paw. Since polydactyly doesn't work in this way and the number of toes appears to be limited, those fears are largely unfounded. In addition, breed standards could be written to define the maximum number of toes in polydactyl breeds to discourage such attempts.

Polydactyly is one of the traits of the PixieBob breed. Early write-ups on this breed suggested that only normal-footed PixieBobs would be accepted for shows. What one registry would not accept, another embraced and as well as the American Polydactyl, PixieBob and Polydactyl Maine Coons there are other polydactyl breeds being developed including the Hemingway Sphynx (a hairless polydactyl cat) now called the Dossow Cat and of developing polydactyl Munchkins a (short-legged polydactyl). The Mojave Spotted (formerly Hemingway Spotted) is being developed from Bengal x Polydactyl crosses. Several breeders in Illinois are working with a curl-eared polydactyl cat called Impians (previously called Tulips). Impians were originally developed in the 1990s by crossing American Curls with polydactyls, creating a harlequin patterned semi-longhaired breed. The markings, which can be any colour, are restricted to the head, down the spine, shoulders, hips and tail.



*Mojave Spotted
(formerly Hemingway Spotted): Developed
from Bengal x Polydactyl crosses.*

In New Zealand, a polydactyl breed called the Clippercat is under development. These are descended from domestic cats that are themselves descended from polydactyls that reached the country on the Clipper Ships between 1850 and 1900.

In Britain, polydactyly is still considered a serious breed fault or defect. According to one breeder, polydactyls can be shown but cannot receive certificates or a first prize in the GCCF. Other sources state that the GCCF absolutely prohibits the showing of polydactyl pedigree cats and that they would be turned away during vetting in (with exceptions for those shown as household pets). A complete bar on the showing of polydactyl cats would be especially unfortunate for owners who wish to show polydactyl household pets and in some registries (FIFe), the prejudice is so great that polydactyl cats were banned from Cat Association shows. They feel that encouraging such abnormalities encourages inbreeding. The blunt statement is that polydactyly is a fault and cats with such defects are not allowed to be shown. This is a totally inconsistent approach since taillessness is also a fault, yet the Manx breed is perpetuated and shown. There are far fewer detrimental side-effects associated with polydactyly than there are with the Manx. The usual argument in these cases is that the Manx is a historical breed even though the polydactyly trait is equally historical. Not to mention that such bodies recognise ultra-typed or extreme Persians whose faces are so compressed that their tear ducts are distorted and their breathing may be compromised. It has to be noted that cat fancies are consistently inconsistent in their approach in such matters!

The GCCF is an extremely restrictive and conservative cat fancy. Its "Standard list of withholding faults - all breeds" (dated 13/10/95) states that certificates and first prizes be withheld for a number of defects considered undesirable in breeding stock and detrimental to individual cats. This includes "Abnormal number of toes - anything other than four toes on each foot and one dew-claw on each foreleg." This applies only to pedigree breeds; non-pedigrees do not have standards of points. This withholding is usually academic, because cats with "defects" (according to the GCCF definition of defect) should not pass the vetting-in stage. The "Rules, section 5, veterinary surgeons" (effective 1 June 1997) has Rule 10 which bars "Exhibits which have been declawed should be rejected (see Section 4 Rule 14) together with polydactyls and cats with folded ears, curly tails or any other abnormality. With the exception of declawing, this does not apply to unregistered non-pedigree exhibits." In spite of its stance on abnormalities, the GCCF's double standards means it has not prevented the increasingly abnormal ultra-typing of Persians or Siamese. Even though non-pedigrees are not covered by the GCCF ban on showing polydactyls, it is possible that some judges mark down a polydactyl in the non-pedigree classes because of ingrained views that it is a defect.

The British prejudice against polydactyly may have to change following the importation of PixieBobs into Britain in 2004. In The Netherlands and Belgium, there is a move to restore the polydactyl lines of Maine Coon and the attitudes of the European registries, particularly FIFe, may also have to change. However, in Germany, the prejudice has legal backing as it is forbidden to breed cats (and dogs) that have genetic defects. "Defects" encompasses the harmless anomalies as well as the more harmful mutations. During 2009 the Governing Council of the Cat Fancy (GCCF) strengthened its anti-polydactyl stance (this primarily affects the Maine Coon Polydactyl and Pixie-Bob). While other World Cat Congress member registries accept polydactyly as a harmless trait in these breeds, the GCCF remained close-minded and insistent that polydactyly is a genetic defect. At the April 2009 World Cat Congress meeting in Arnhem, The Netherlands, the GCCF delegate responded "Never!" when asked if and when the GCCF would accept polydactyly. In spite of discussions by scientists at the meeting, the GCCF's position is that polydactyls are at "greatly increased risk of deleterious impact" and therefore should not be recognized nor accepted in the (Maine Coon) breed. The GCCF disregarded a British report into polydactyly known as the "Edinburgh Study". The GCCF have also produce a draft rewrite to the Breeding Policy which will refuse recognition to any new breed based upon structural anomalies and specifically includes polydactyl feet. With such closed minds and with other cat associations active in the UK, the GCCF is likely to become extinct long before the traits it

condemns (I'm noticing increasingly poor attendance at its shows) while other, more enlightened, registries active in Britain will benefit.

In Germany, the Federal Government erroneously decided polydactyly was a semi-lethal (deferred-lethal) defect and have banned the deliberate breeding of polydactyl cats under their Animal Protection Law. They based the decision on a paper by S & H Willer ("Gene Sites and Alleles of Domestic Cat with Pathological Effects or Side Effects") which stated, erroneously, that polydactyly is an "autosomal dominant semi-lethal error with modifier effect." V Schmidt und M. CH Horzinek refer to S & H Willer's mistake that polydactyly is semi-lethal in the German book "Krankheiten der Katze" (Diseases of the cat). As well as this error, an unsubstantiated fact (or propaganda) states that polydactyl kittens suffer a 50% mortality rate during the first 6 months and that polydactyl cats live in pain. In fact the kitten mortality rate in polydactyls is no different to that in normal-foot cats (the possible exception being those caused by the distinct and disabling radial hypoplasia condition).

Having persuaded the American cat fancy that polydactyly was not a deformity, the trait was soon back in the feline geneticists' spotlight due to its unfortunate association with the Twisty Cat. Twisty Cats have a crippling deformity of the forelegs. They arose spontaneously when a horse-breeder began to breed Poly-Bobs, a type of cat sometimes confused with the PixieBob. Some Poly-Bob litters contained kittens with flipper-like forelegs. The mutation is occasionally found at random in the cat population, but was occurring with greater frequency in Poly-Bob litters. This was the second form of polydactyly and its effects ranged from the Poly-Bob's simple extra toes through to the Twisty Cat's vestigial or missing long bones of the leg.

Some breeders and cat lovers have become concerned that the Twisty trait was the hidden downside of polydactyly and that "all polydactyly was bad" despite the fact that perfectly healthy extra-toed cats have been around for hundreds of years. Most forms of polydactyly are no more than a harmless and attractive quirk. In polydactyl cats, it has become important to work out which ones have which gene, so that breeders working with polydactyls do not inadvertently breed crippled kittens.

In 2006, TICA proposed to clamp down on certain breeding trends, including the creation of new polydactyl breeds created through crossing to other breeds. Their Genetics Committee report stated: *"The Committee proposes that TICA does not accept any proposed breeds for Registration Only status that do not exhibit novel mutations. The current mutations would be reserved for currently recognized breeds exclusively. This would end the seemingly endless applications for "munchkinized" new breeds, and then deter the inevitable introduction of "rexed", "Bob-tailed" and Poly-ed" everything else."*

POLYDACTYLY IN BIG CATS

Polydactyly is not limited to domestic cats. It is also found in big cats, though this is less widely reported for the obvious reason that we do not (normally) share our homes with big cats!

In 1925, The Journal of the Bombay Natural History Society published a photograph of a polydactyl leopard. It had an extra claw-bearing toe on each hind paw. Several years earlier it had published a letter regarding a leopard shot by S Eardley-Wilmot - this creature had an extra claw-bearing toe on each hind paw. In 1946, the same journal published a letter from another big game hunter who had also shot a leopard with extra toes (again fully functional with claws) on the hind feet.

Probably the most interesting fact is that the leopards had the extra toes on the hind feet and not the front feet whereas in domestic cats, the hind feet are only affected if the forepaws are affected. This means that a different gene was responsible for hind-foot polydactyly in leopards ... and what can occur in a big cat might possibly one day appear in domestic cats.

There are unverified reports of polydactyl tigers in China. The tale of a race of unusually large tigers with "thumbs" would appear to be exaggeration, but it is conceivably based on polydactyl individuals. None have been captured or photographed.

Part 2

POLYDACTYL RECORDS

The greatest number of toes EVER found on a cat is 32 (eight on each paw) reported in October 1974. This was male cat called "Mickey Mouse" owned by Mrs Renee Delgade of Westlake Village, California, USA. It is possible he had a condition known as double-paws where each paw is actually 2 fused mirror image paws; this is a different condition to polydactyly. The condition is seen in humans where there is a central thumb with four fingers either side of it (making a natural baseball catcher's glove!). There have been reports of a cat where all 4 paws are doubled. When the cat "sat to attention" it had eight paws in a row. Double-paws is a developmental defect - during early development, the tip of the limb-buds fork to produce 2 mirror-image paws which may be set at right angles to each other.

A pure-bred Siamese named "Big Foot" owned by Miss Joan Conerly of Wauchula, Florida, USA in 1978, had 26 toes (seven on each front paw, six on each back paw). His mother had 22 toes, his sister had 22 toes and a brother had 24 toes.

A female cat named "Triple" owned by Mr and Mrs Bertram Bobnock of Iron River, Michigan, USA in 1976, had 30 toes, but these are arranged on 5 legs and 6 paws! The back left leg had 2 complete lower leg extensions from the hock down, and one of those lower legs had 2 paws. This is probably a developmental defect which caused the growing tip of the limb bud to split into two and each part of the fork continued to develop into a limb. It would have forked twice, once as it got to the hock and one side would have forked again when it began to grow the paw.

In May 2002 Jennifer Beierle wrote to me about a litter of kittens whose total of toes exceeds that of Big Foot and his litter-mates. Her non-polydactyl cat got pregnant by an unknown tomcat and produced 10 kittens. One was stillborn, 9 survived and seven were polydactyls. Two kittens had 26 toes (Peter and Paula,) two had 23 toes (Pollyanna and Penelope,) two with 22 (Phoebe and Peace,) one with 21 (Paprika,) and two with the normal 18 (Ace and Jean). Peter is double-pawed in front, with 7 toes on each front foot and six on the rear but no dewclaws at all. Paprika has a superclaw in front. Phoebe has the appearance of double-dewclaws on back, and Penelope has an under-developed toe with an ingrown nail.



In August 2002, the Canadian Press reported the case of a Manx cat that narrowly escaped death by euthanasia was a contender for the cat polydactyly Guinness world records. Bobbi has 28 toes, one more than the current record holder. Bobbi is owned by Kathy Williams of Stone Creek, near Prince George, British Columbia, Canada. She adopted Bobbi from the Prince George SPCA shelter where he was due to be put to sleep because of a heart condition (this turned out to be minor). His toe count must be authenticated by a vet before the record can be claimed.

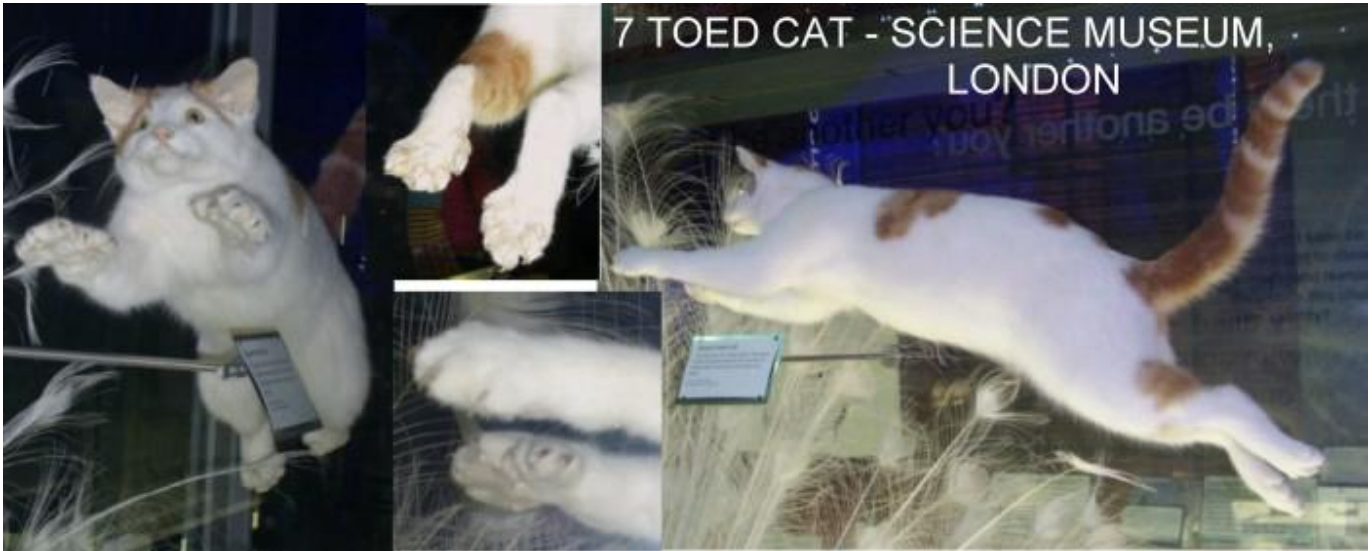


Bobbi is not the first reported 28-toe cat, but he may be the first authenticated one. Saffy, owned by Joan Snoswell, was also reported to have 28 toes. Other cats with 28 toes are Patsy, a Maine Coon adopted from the Boston Animal Rescue League, and Bigfoot, owned by Tanya Welsch. Several others are reported on the internet including 28-toed Clyde from Albuquerque, New Mexico (below), whose details were emailed to me by his owner's sister who describes Clyde's oversized paws as resembling the feet of a snowshoe hare.



LEFT: CLYDE FRONT PAWS
MIDDLE: CLYDE, ALL 4 PAWS
RIGHT: CLYDE BACK PAWS

The current (i.e. verified) record holder (2002) is Tiger who has 27 toes. Tiger is owned by Gareth Ukrainetz of Leduc, Alberta, Canada and has seven toes on each front foot, and seven on her left hind foot, but only six toes on her right hind foot.



POLYDACTYLY AND NATURAL SELECTION

If polydactyls are common and not disadvantaged, why are there no polydactyl cat species or sub-species? There are, after all, localised polydactyl populations e.g. near Hemingway's home, some farm colonies.

Firstly there is the question of genetic isolation. For a distinct variety to be perpetuated, it must be genetically isolated from other cats. Farm colonies breed not only among themselves, but also mate with roaming feral tomcats and with other cats attracted into the colony. Unless the outsiders are polydactyls, this dilutes the genes. There are few cat populations isolated enough to give rise to a sub-species, let alone a species no longer able to interbreed with normal-toed cats. Recent artificial isolation of polydactyl cats (i.e. by establishing and controlling breeding lines) is giving rise to polydactyl breeds. An obvious case of an isolated population is the Manx cat from the Isle of Man. For genetic reasons (discussed later), though the tailless trait came to predominate (outnumber the fully tailed cats), it was never "fixed" i.e. it did not breed 100% true. Manx cats also produce non-Manx kittens.

It is suggested that the lack of a polydactyl sub-species means there is some sort of natural selection against the trait e.g. there may be hidden ill-effects or polydactyls are somehow at a disadvantage compared to normal-toed cats. This is the case in Manx cats where the gene can cause spinal abnormalities and pre-natal death. However, polydactyly is a "neutral" mutation - it is neither advantageous nor disadvantageous to the cat (tales of natural snowshoes notwithstanding). So why has it not become fixed in isolated populations?

The answer is in the mode of inheritance. Polydactyly in cats is due to a dominant gene mutation. This means that many polydactyls also carry the gene for normal toes. Polydactyl cats can produce normal-toed kittens so the trait is never "fixed" (true-breeding). In an isolated population, the trait could become common through inbreeding, but there will still be normal-toed cats because of the hidden recessive gene.

Even if there was some form of natural selection in favour of polydactyly and all normal-toed cats died before breeding age, the mode of inheritance means that the hidden recessive gene for normal toes is still present in the population. Non-poly kittens will still occur i.e. the cats do not breed true for polydactyly. Recessive genes are practically impossible to eradicate in a random-breeding population. In a breeding programme, a polydactyl would have to be test-mated to normal toed cats to see if the polydactyl carried the hidden recessive.

If, however, a recessive gene for polydactyly arose and for some reason the polydactyl cats had an advantage over normal-toed cat, this could give rise to a true-breeding polydactyl population, but only so long as they were isolated from other cats. In this case, polydactyly would not merely predominate, it would become fixed as the cats would be true-breeding.

Because recessive genes breed true, two normal-toed cats almost always produced only normal-toed kittens. "Almost always" because there is a very small chance of a fresh mutation or of one of the cats being genetically polydactyl but not showing the trait.

Since polydactyl cats sometimes use their "thumbs" to manipulate or grasp objects, why is the trait not actually advantageous? In spite of the potential usefulness of the opposable thumb, nature does not seem to select in favour of thumbed cats. The best explanation is that although cats have intelligence, it is not the sort of intelligence that makes an opposable thumb an evolutionary advantage over other cats, nor do they walk upright in order to keep their "hands" free for manipulating objects.

PREHISTORIC POLYDACTYLY

Polydactyly is an ancient trait and but for a quirk of evolution, all modern animals would have 7 or 8 digits instead of just 5. The oldest known four-legged animals, Ichthyostega and Acanthostega, had 7 or 8 digits per limb. The "extra" digits were next to the thumb. The extra digits disappeared 350 million years ago, leaving modern animals with just 5 per limb. 100 million years after evolution opted for five digits, throwbacks to ancestral polydactyly occurred, as a fossil of a seven-toed reptile demonstrates. The fossil, an aquatic marine reptile called Nanchangosaurus, was a mutant or evolutionary throwback which lived 100 million years after other seven-toed amphibians had died out.

Nanchangosaurus lived about 242 million years ago in China. The fossil reveals that it had seven complete digits on its forelimbs and six on its hind limbs. Other fossils didn't have well-preserved digits, so we can't be sure whether polydactyly was a trait of the whole species or if it was restricted to a single mutant animals.

SYNDACTYLY (OLIGODACTYLY) & ECTRODACTYLY

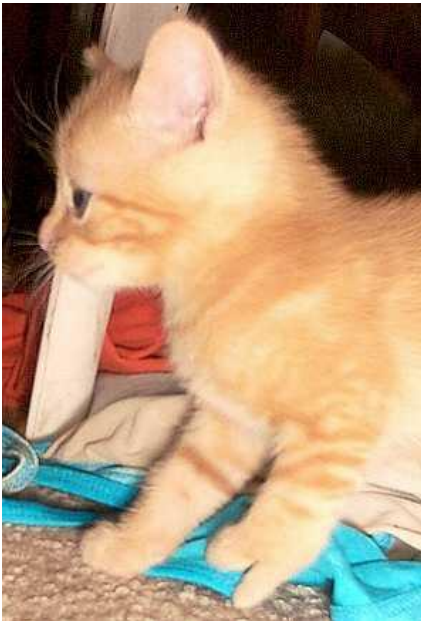


Syndactyly (hypodactyly) or split-foot is the opposite of polydactyly. Instead of having additional toes, the cat's forefeet (rarely the hind feet) have one or more toes fused. In the most familiar form, called Ectrodactyly, there is a central split and two toes giving the appearance of a crab or lobster claw. In humans, the condition is sometimes known as "lobster-hand". The other digits have either been suppressed altogether or each of the cat's toes is made up of two or more fused digits. A paper by A G Searle (in "Annals of Eugenics" Vol. 17, Part 4, pp. 279-283, 1953) discussed the lobster-claw condition in cats; Searle noted that the anomaly was usually inherited as a dominant, and had suggested that the right side was often more severely affected than the left.

Syndactyly and Ectrodactyly are visually similar. Ectrodactyly is the "lobster claw" defect where the paw is split longitudinally, most commonly between the first and second toes. In different mammals there are both dominant and recessive forms of this defect. It often occurs on one side only and there may be other abnormalities: deformed or under-developed toes and partly fused toes. Syndactyly involves the union of bony and/or soft tissue of two or more toes and can be hereditary or congenital (non inherited). Hereditary syndactyly usually occurs on both sides while congenital syndactyly often affects only one side. As the conditions are similar and rarely distinguished from each other in cats, I have used the term syndactyly from hereon.

Syndactyly is rarer than polydactyly so I was interested to receive details of a cat with 4 affected paws. Each paw resembles a crab's pincer (hence the common name of "Lobster Claw Syndrome"), having only 2 toes which are semi-opposable. The cat even uses them as pincers to hold toys and small objects. The toes are apparently oriented one facing upwards and one facing downwards (i.e. a degree of twisting). Syndactyly varies from webbed

toes to fused digits. The fused digits can be simple with the digits connected only by skin, or it can be complicated with the bones, tissues and claws fused. It occurs when the cells between each toe do not die during embryo development and the toes do not separate (these cells are normally programmed to die during digit formation).



Like polydactyly, the condition rarely causes problems so long as the claws are kept clipped. The cat can still run and climb. The only time I have seen a lobster-clawed cat was with a feral cat in a trap-neuter-release program. This may not have caused problems to the cat in the wild (on a farm), but it caused problems in temporary captivity as the claws kept getting caught on the wire mesh. The actual claws were slightly overgrown due to problems with stropping them. In pet cats this can easily be rectified by frequent claw clipping.

Where the two toes are made of fused digits, the claws may form superclaws in the same way as described earlier. There is also the possibility that the cleft between the toes extends further than is normal into the paw itself. Small objects, thorns etc may become trapped between the toes. If the toes splay apart e.g. when the cat has jumped down from a high platform, there is the small chance that the claws will spread apart under its weight and the skin between them may tear. These problems are not common and cats with split foot rarely suffer any real disability.

In May 2005, Stephanie Rubeck of Newark, Ohio, sent this picture of her 4 week old kitten "Faith" who has syndactyly of the left front paw. The vet refused to see the kitten until she reached 6 weeks old on the grounds that a defective kitten would be rejected by the mother and not survive that long. Syndactyly is a minor (cosmetic) defect that does not affect suckling or threaten long-term survival. Faith is one of a litter of two and her brother is solid black with no abnormalities. At 4 weeks, Faith had a few problems walking, mainly when trying to turn around or turn to the left, but should soon learn to compensate. Her climbing abilities are not impaired and the photo shows Faith playing on the couch with her brother.

Jazmin Powell's cat Forest (born August 24th 2007) is another ectrodactyl. He also suffered from horny growths on his "lobster claw" since birth. The claws of the affected paw have had to be removed as they started to grow into his paw pads causing great discomfort to Forest.



Forest

Anastopoulos Thanos of Sparti, Greece provided images and details of a different form of fused toes: "A few months ago I adopted a pair of stray kittens found on the street outside my house. 1female and 1male. They have developed a liking to the indoors. The reason for this email is an anomaly on the hind paws of the female cat

("Zooka", see photos). If I'm right its called syndactyl, a union of the 'toes'. It does not appear on the front legs of the cat. The number of nails is correct but the cushion is united. The bone structure feels to the touch normal. The affected nails seem to have problem retracting. It does not hinder the cat's movement other than a "clicking" sound due to the nails hitting the floor tiles. I am not thinking of seeking medical or surgical treatment because the cat shows no distress over it."



Close-up of hind toes

BRACHYDACTYLY

Brachydactyly is not to do with the number of toes, but the length of the toes. Brachydactyly means "short toes". I have only seen one brachydactylous cat - a ginger and white male rescue cat whose toe-pads attached directly to the palm of the paw i.e. he lacked the "finger sections". It was necessary to trim the claws regularly and they grew at irregular angles. The lack of jointed toes resulted in minor mobility problems e.g. in running and on landing when jumping, but he was otherwise not inconvenienced by the condition. Also, he could not knead properly.

This case was believed to be due to a birth defect (developmental abnormality). In humans, brachydactyly is associated with some forms of dwarfism.

OTHER ANOMALIES

Arachnodactyly (spider-digits), a condition causing longer than normal toes, has not been reported in cats to my knowledge. The condition of extra joints/extra bones in one or more of the digits (causing them to be extra-long or extra-flexible) is hyperphalangy.

Uneven Length Toes #1. As well as heritable traits, some individual cats simply have curious toes e.g. uneven length of toes or a twisted toe. These are one-offs caused by early injury or the way the limb has developed in the womb (i.e. not inherited trait). "Bryn" writes "One of our cats has a curious toe on one back foot. It is much smaller than the other four, and is pushed up, so that when the foot is viewed from the bottom, she appears to have three toes. The small toe has a claw. All of her other feet seem to be normal" (photos provided, see below).



Uneven Length Toes #2. Courtney Kahler (2003) provided the following photos and information about her cat Kolohe whose condition is similar to syndactyly, but probably congenital (birth defect) not hereditary. "I have a cat (Kolohe) who either was born with syndactyly in one front paw or she has a congenital defect very similar. She is essentially missing one toe, has a thumb for a dew claw with a non-retractable claw, and the other 3 toes are semi-fused but do have retractable claws. The smallest toe on the outside of the paw is not as fused as the 2 next to it. The paw pads in 2 places on her paw seem to grow and she tends to chew on one of them, but it never bleeds. So that part of her paw pads looks a bit rough. The other paw pad grows out from her foot almost in the shape of a claw, but it's tough paw pad and nothing else. You will be able to see that in the picture. She must occasionally chew that off too 'cause it's not always that long.



Her breeder believed this was a congenital defect not genetic since she has never seen it before in any other kittens. But both parents are spayed/neutered so if it is genetic it won't appear again. Kolohe is also spayed. It has no effect on her whatsoever, she is as active as any other Tonkinese and can play and climb with no problem. I do have to keep the one claw clipped because it can snag on the carpet. When she sits up she sits with that paw out to the side. She's an adorable cat regardless of anything and we often call that foot her lobster claw. "

Another reader reports that her male polydactyl Lynx-point Siamese mix, Tommy, had horny growth similar to those of Kolohe. Tommy's growths grow right up to his claws if left unclipped. In addition, some of his claws are misshapen: one is almost flat, and grows square, but twists like a DNA strand while a double dewclaw on the back looks like 2 claws side by side, fused halfway up and barely fits in the claw clippers.

Off-Centre Claws. Bernice adopted a kitten called Ashley in November 2005. She has long toes (she is a very long cat) and some claws are off-centre as shown by the photo of her back foot (below).



GLOSSARY

- A dominant gene is one which shows up when only one copy of that gene is inherited- one for the mother OR one from the father.
- A recessive gene is one which only shows up if the cat inherits two copies of that gene - one from the mother AND one from the father.
- Heterozygous means that the two genes in a pair are different, the cat will not breed true for that trait as some of the offspring inherit the hidden recessive gene.
- Homozygous means that the two genes in a pair are identical and the cat will breed true for that trait.
- Autosomal means the gene is carried on an ordinary paired chromosome, not on the sex-linked X or Y chromosomes.
- Atavism (and atavistic) means the reappearance of an ancestral characteristic after several generations of absence; caused by chance mutation or by recombination of genes.
- Digit means finger or toe.
- A dewclaw is a vestigial (rudimentary) toe or claw which does not touch the ground, it sometimes resembles a thumb (pollex) which is smaller than the other toes.
- The phalanges are the bones inside the fingers and toes.
- Pre-axial means situated in front of the axis of a limb
- The radius is the long bone of the lower forelimb; in humans it is the forearm (elbow to wrist).
- The pollex (plural: pollices) is the thumb.
- The plantar pad is the heel pad of the paw.
- The palmar pad is the palm-pad of the paw.
- The apical cap is the tip of the limb-bud in a developing embryo.

REFERENCES

- Chapman, VA; Zeiner, FN: The anatomy of polydactylism in cats with observations on genetic control Anatomical Record 141:205-217, 1961
- Danforth CH: Heredity of polydactyly in the cat. Journal of Heredity 38: 107, 1947
- Danforth CH: Morphology of the feet of polydactyl cats. American Journal of Anatomy 80:143, 1947
- Jezyk PF. "Constitutional Disorders of the Skeleton in Dogs and Cats".
- Jude, AC: Cat Genetics, 1955
- Pflueger S. (1998). "Polydactyly and Related Traits". Cat Fanciers Journal, Fall 1998, 5-6.
- Robinson R: Genetics for Cat Breeders, Mar 1977
- Sis, RF; Getty, R: Polydactylism in cats Veterinary Medicine and Small Animal Clinician 63:948-951, 1968

- Todd, NB; Jones, TC: On independent assortment of dominant white and polydactyly in the cat *Journal of Cat Genetics* 1:16-17, 1964
- Towle Heather A.M. DVM & Breur Gert. J. DVM PhD, DACVS "Dysostoses of the Canine and Feline Appendicular Skeleton". *Vet Med Today JAVMA* Vol 225, No. 11, December 1, 2004, 1685-1692.
- Vella, C; Shelton LM; McGonagle J; Stanglein TW: *Robinson's Genetics for Cat Breeders and Veterinarians*, Butterworth-Heinemann Ltd (19 Aug 1999)
- Wenthe, M; Lazarz, B: A case of atavistic polydactyly at the hind limb of a cat [German] *Kleintierpraxis* 40:617-619, 1995
- Winterbotham EJ et al. (1985). "Radial Agenesis in a Cat". *Journal of Small Animal Practice*, 393-398.
- Wittmann, F: Polydactylism in a Cat *Praktische Tierarzt* 73:709, 1992
- Zguricas J, Heutink P, Heredero L, Deurloo J, Oostra BA, Snijders PJ, Lindhout D, Hovius SE Genetic aspects of polydactyly. *Handchir Mikrochir Plast Chir* 1996 Jul;28(4):171-5