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Genetic and biological aspects of teats in Suidae – a review

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The objective of the study was to show the breeding and production importance of the number of teats, their growth and development, morphology and function in pigs Domestication gave rise to efforts to improve performance traits, including a moderate heritable number of teats. This polygenic trait can be improved using both classical methodology (the BLUP under an animal model) and a molecular approach. It was shown that the main QTL affecting teat number in pigs is found on chromosome 7. This trait is also influenced by the dam, fetal number and the sex ratio. The present study characterises the trait of teat quality and its determinants, indicating that some abnormalities may be genetically determined. A normally developing and functioning mammary gland provides piglets with colostrum and milk, which offer immune protection, provide nutrients and maintain the dam-offspring bond. No definitive relationships were observed between teat number and fertility. From the genetic point of view the relationship between teat number and weight of weaned piglets appears low, but position along the milk line and fostering of piglets may well contribute to rearing performance. The use of teats by piglets depends on teat position in the upper and lower rows. Their accessibility is determined by teat pair distance (TPD), a trait that is still not being selected for. It should be stated that at present morphological characteristics (including TPD) appear to be of equal importance in breeding programmes as the number of functional teats.

KEY WORDS: heritability / mammary gland / piglet / teat pair distance

It has been suggested, although inconclusively, that teat number is a phenotypic measure of the sow's reproductive capacity [Zhishko and Samson 1975 citing Gronek *et al*. 1996, Buczyński *et al*. 1996a, Zmudzińska-Pietrzak 2015]. A sufficient number of teats is necessary for a female to rear its offspring. In wild species of *Suidae*, fertility

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and teat number have remained low [Komosińska and Podsiadło 2002]. In contrast, genetic improvement programs applied to various breeds of *Sus domestica* have considerably increased fertility and the number of teats when compared to the wild ancestor [Hume *et al.* 2011, Chalkias 2013, Ocepek *et al.* 2016, Report on pig breeding 2017]. In pigs raised today, teat number varies from 8 to 18 depending on the breed [Chalkias 2013]. As reported by Pumfrey *et al.* [1980] and Borchers *et al.* [2002], the coefficient of heritability (h^2) confirms that teat number is a moderately heritable trait.

The aim of the study is to show the breeding and production importance of the number of teats, their growth and development, morphology and function in the the domestic pig and to account for genetic and environmental determinants.

Teats in wild suids

The class *Mammalia* (mammals), the subclasss *Eutheria* (placentals), the order *Artiodactyla* (even-toed ungulates) and the suborder *Suiformes* (non-ruminants – pigs and related species) include three families, among them *Suidae* (suids). The largest subfamily comprises true pigs (*Suinae*), which include 8 genus. These are wild boars (ancestors of domestic pigs), as well as warthogs, forest hogs, river hogs, pygmy hogs, bearded pigs, warty pigs and Sulawesi pigs.

In many species of the subfamily *Suinae*, teat number is lower than in domestic pigs. Babirusa (*Babyrousa celebensis*) is characterized by a relatively small reproductive system, which is consistent with its small litter size [Macdonald and Leus 1995]. After a 158-159 day pregnancy the female most often gives birth to one or two (sometimes three) piglets per litter and it has one teat pair [Macdonald and Leus 1995, Animal Lexicon. Mammals 2002]. European wild boar (*Sus scrofa*) females an average produce 4-12 piglets per litter. This species has 5-6 teat pairs [Fruziński 1992]. The giant forest hog (*Hylochoerus – Hylochoerus meinertzhageni*), which inhabits Uganda, gives birth to 2-4 piglets per litter and has only two teat pairs [Pigs, Peccaries and Hippos 1993]. Females of the warthog (*Phacochoerus africanus*), a species common to South, East and Central Africa, most often produce 3 offspring (from 1 to 7) after a 172-day gestation and can easily nurse its offspring using two teat pairs [Pigs, Peccaries and Hippos 1993]. Africa is also inhabited by the bushpig (*Potamochoerus larvatus*), which is a member of the *Suidae* family. After a 120-day gestation the female gives birth to an average of 1-4 piglets, although sometimes the litters are larger (6 piglets). The sow can rear 4 piglets, because animals of this species have 4 teats. The red river hog (*Potamochoerus porcus*), which lives in some regions of Africa and in Madagascar, birth 3 to 6 piglets [Great Encyclopedia of Nature 1997]. Red river hog sows have three teat pairs [Komosińska and Podsiadło 2002]. Females of the bearded pig (*Sus barbatus*), a species found in Sumatra, Borneo, the Malay Peninsula and the Philippines, gives birth and rears 2-3 young per litter. Larger litters of 4-8 animals sometimes occur [Kilpatrik and Hard 1990]. The bearded pig has five teat pairs [Illustrated Encyclopedia of Wild Animals 1997], which means that it is naturally predisposed to nurse fairly large litters. The pygmy hog (*Sus salvanius*), which inhabits south Himalayas, India and Nepal, produces litters of three to five [www.ultimateungulate.com]. The female can rear the entire litter, because it has 3 teat pairs [Gaisler and Zejda 1997]. The warty pig (*Sus verrucosus*) is found in Java and in surrounding smaller islands [www.encyklopedia.pwn.pl]. The sow produces litters of 1-4 piglets [Komosińska and Podsiadło 2002]. According to Reichholf [1996], the animals have five teat pairs, which suggests a potentially higher fertility and predisposition to nurse a large number of offspring.

Domestication of the wild ancestors gave rise to improvement of performance traits in domestic pigs, including reproductive traits such as teat number.

Heritability of teat number

Pumfrey *et al.* [1980] and Rząsa [2007], who analysed their own results and those of many other researchers, concluded that coefficients of heritability (h^2) for teat number in the Large White, Landrace, Duroc, Lacombe × Yorkshire, Czech Large White and Yorkshire pigs ranges from 0.07 to 0.79. McKay and Rahnefeld [1990] and Lewczuk *et al.* [1993] obtained heritability estimates ranging from 0.2 to 0.4. Similarly, Lewczuk *et al.* [1991] reported that the coefficient of heritability for teat number in the Polish Landrace (PL) and Polish Large White (PLW) breeds is 0.255. Subsequent studies estimated the coefficient of heritability for PL, PLW, PL × PLW, Hampshire and Złotnicka Spotted (ZS) pigs [Lewczuk *et al.* 1993, Buczyński *et al.* 1996a] and the h^2 value for the number of teats varied depending on the breed (purebred or crossbreds) and position (anterior or posterior). Lechowska and Ruda [2000] reported very low coefficients of heritability for teat number in a population of PL pigs. The analysis spanned a 30-year period and the h^2 value for this breed was only 0.02 – 0.06. For the ZS breed this coefficient was higher (0.334). McKay and Rahnefeld [1990] estimated the coefficients of heritability for the total number of teats and found the h^2 during the study period to increase from 0.23 to 0.39 in Lacombe, from 0.32 to 0.44 in Yorkshire, and from 0.20 to 0.27 in F1 Lacombe × Yorkshire pigs. The same authors also observed that heritability of posterior teat numbers was higher than that of anterior teat numbers. In the Pietrain breed, Borchers *et al.* [2002] determined the heritability of teat number to be 0.20 on the left body side and 0.18 on the right body side.

Pomykoł and Chojnowski [1976] consider that intensive selection for teat number may succeed despite the fairly low heritability of this trait. In a 10-year selection programme those authors increased the number of teats by 0.11-0.13 in PL sows and by 0.65-0.83 in PLW sows. Selection performed on the ZS pig population produced a similar effect [Lewczuk *et al.* 1993]. For PL sows Lechowska and Ruda [2000] found a phenotypic increase in this trait by 0.56. When comparing teat number in the breeds of pigs raised in Poland in 2016 in relation to 2008 [Report on pig breeding 2009, 2017], teat number in sows of maternal breeds was found to increase by 0.33 in PLW, by 0.40 in PL, by 0.02 in Puławska, by 0.20 in Złotnicka White, and by 0.19 in ZS.

Except for the Puławska breed, these results are promising, since they indicate that offspring can be reared despite a progressive increase in the number of piglets born per litter in the analyzed breeds of pigs.

The trait number of teat exhibits low genetic variation as a result of long-term selection. Nevertheless, studies showed considerable variation in the h^2 value of this trait [Pumfrey 1980, McKay and Rahnefeld 1990, Lewczuk *et al.* 1991, Lewczuk *et al.* 1993, Buczyński *et al.* 1996a, Lechowska and Ruda 2000, Borchers *et al.* 2002].

Determinants of teat number

Genetic

Teat number is a polygenic trait and results from the intra- and inter-locus interaction. Only some genes responsible for quantitative traits have been identified at the molecular level in pigs. The search continues to find genes with a considerable effect on quantitative traits (QTL).

Conventional methods to improve reproductive traits in pigs are not very effective [Haley *et al.* 1988]. Beneficial changes most often appear after a long time and to a very small extent. BLUP Animal Model is considered the best method to predict a breeding value for lowly heritable traits such as teat number [Orzechowska *et al.* 2010]. This model accounts for traits subject to improvement, e.g. maternal traits in dam lines (Pen Ar Lan and Norsvin), the maternal index, including teat number and quality in PIC, and teat quality in Large White and Landrace pigs in France (weight of trait 12%) [EPSPA 2007].

In order to increase breeding progress for lowly heritable traits (e.g. reproductive traits) it is necessary to use elements of molecular genetics [Dekkers 2004, Korwin-Kossakowska 2007]. The focus of research is on DNA polymorphism and genome mapping, associated with economically important quantitative trait (QTL) loci. It has been scientifically demonstrated that QTLs for teat number are located on chromosomes 1, 2, 3, 6, 7, 8, 10, 11, 12 and 16 [Cassady *et al.* 2001, Hirooka *et al.* 2001]. Studies to identify QTL encompass components of the trait defined as "fertility", anatomical features of the reproductive tract and the number of active teats [Bidanel and Rothschild 2002]. The studies concerning the presence of QTLs for the number of active teats show that this region is found on chromosome 2 [Hirooka *et al.* 2001], chromosomes 1, 6, 7, 8, 11 [Cassady *et al.* 2001], and on chromosomes 16 and 17 [Bidanel and Rothschild 2002]. Genes that determine the number of teats on the right side of the udder, are located on autosomal chromosomes 3, 4, 5, 7 and 12, while those that determine the number of teats on the left side of the udder are found on chromosomes 1, 3, 4, 5, 6, 7, 8 and 12. The most important QTLs, which determine the total teat number of the right and left sides, are those on chromosome 7 [Nengshui *et al.* 2009].

Maternal effect

The number of teats is maternally and paternally inherited by the offspring [Allen *et al.* 1959, Drickamer *et al.* 1999]. A greater number of teats was reported in sows from litters with more females [Saal *et al.* 1999, Górecki 2003]. In addition to genetic and environmental variation, reproductive traits are hormonally affected by the intrauterine position effect [Ryan and Vandenbergh 2002, Rekiel *et al.* 2010]. In multifetal and multiparous species, including pigs, a female fetus may be positioned next to a male fetus, between two male fetuses, or between two female fetuses. With a unidirectional blood flow in the uterus, this results in the interaction of the hormones produced by adjacent fetuses [Vandenbergh and Huggett 1995, Ryan and Vandenbergh 2002]. Androgens produced by male fetuses may cause phenotypic modifications by giving male characteristics (masculinization) and inhibiting teat growth [Drickamer *et al.* 1999, Hotchkiss *et al.* 2007]. In addition to the dam effect, the number of teats is also influenced by the number of fetuses and the sex ratio [Vandenbergh and Huggett 1995, Drickamer *et al.* 1997].

Teat quality and its determinants

In terms of nursing neonates it is not only teat number, but also teat quality, shape and distribution that are important [Lewczuk *et al.* 1991, Chalkias 2013]. Teats with a single canal were found in cows and sheep, while those with multiple canals in humans and dogs. Two milk canals are most often found in the pig and horse teats [Chalkias 2013]. Rząsa [2007] confirmed that pigs have 1-, 2- and 3-canal teats. The studied group was dominated by sows with 2-canal teats (over 90%). Two- and 3-canal teats were found in all zones of the mammary gland, whereas 1-canal teats only in the caudal part. Single-canal teats were the least attractive for piglets, while 2-canal teats were the most frequent choice.

Breeding sows, especially those of maternal breeds, should have as many teats as possible and the teats should be of normal conformation/quality, because these parameters determine if the sows will be able to nurse and rear neonates. Gronek *et al.* [1996] reported after Zhishko and Samson [1975] that the coefficient of phenotypic correlation between teat number and sow prolificacy is $r = +0.334$, which shows the practical importance of this trait in rearing the offspring.

Fetal development of the mammary gland is determined by genetic and hormonal factors. The initiation of milk bud development is regulated by embryonic mesenchymal tissue, which is divided into dense tissue and mammary subcutaneous adipose tissue. As pointed out before, androgens produced by male fetuses inhibit the growth of the mammary gland [Krzymowski and Przała 2015]. The increased estrogen content during pregnancy increases the number of receptors in the mammary gland and favours their development. Mainly estrogens are responsible for the development of ducts (ductal mammogenesis), while progesterone accounts for the development of alveoli (lobulo-alveolar mammogenesis). Development of the mammary gland is also promoted by ovarian steroids, the anterior pituitary growth hormone, placental hormones (placental lactogen, placental steroids) and growth factors (MDGF1, TGFα and TGFβ, EGF and insulin-like growth factors IGF-I and IGF-II that stimulate mammary cell proliferation), adrenal cortex hormones (glucocorticosteroids) and prolactin [Krzymowski and Przała 2015]. Prolactin influences mammary growth and development, as well as lactopoiesis and lactogenesis [Colenbrander *et al.* 1988]. In the postnatal period, during the growth and development of gilts, the number of secretory cells in the mammary gland increases [Rekiel 2006]. It may be manipulated through nutrition, because secretory cells are formed in the gland when young females are between 42 and 84 days of age. Dietary provision of unsaturated fatty acids during that time will stimulate pituitary secretion of additional portions of the growth hormone, which by acting synergistically with prolactin stimulates the growth of lobules and lactogenic alveoli in gilts [Barowicz and Pietras 1997]. Overfeeding between 75 and 100 days of pregnancy reduces the number of secretory cells, DNA and RNA in the mammary gland, thus reducing milk production during lactation [Rekiel 2002].

Teat defects, such as inverted, small, blind, flat or telescopic teats are relatively common in sows, affecting up to 20% dams [Chalkias 2013]. Small teats are often located in the posterior part of the mammary gland. Small teats in between two normal teats are called “extra teats” or “blind teats”. They cannot produce milk, because they do not have milk canals. Lundeheim *et al.* [2013] reported that the coefficient of heritability h^2 for the number of inactive teats is 0.09. One of the most common defects are crater teats, recorded at an incidence of 0.24-8.40%. Crater teats in parents were found to be correlated with those in the offspring, which suggests a genetic background of the trait. When there are no receptors in the teat, the milk ejection system and the adjacent tissues fail to develop. A hollow crater surrounded by a fold of skin is formed. QTLs for the number of teats and crater teats were located in the SSC3, SSC5 and SSC11 regions. Rohrer [2000] and Jonas *et al.* [2008] stated that the number of inverted teats may be associated with the total teat number and belive that their QTLs may in part be the same.

Mammary gland development and function

The mammary gland and milk production evolved before viviparity and before the rise of mammals. Most probably, nutriment came into existence through the transformation of antibacterial secretion protecting eggs in the pouch of the *Monotremata* family representing the subclass *Prototheria*. The initial purpose of the gland was to provide antibacterial protection of the offspring. Currently the mammary gland produces milk, which provides food for newborn mammals. Ingestion of nutriment offers immune protection, provides nutrients, and maintains the mother-offspring bond [Engelhardt and Breves 2011].

The mammary growth, development and function (lactation cycle) may be divided into the following stages: mammogenesis, lactogenesis I, lactogenesis II (colostrogenesis, galactopoiesis) and involution. The successive stages are associated with the growth and development of the mammary gland (without milk secretion), which begins during the prenatal period in the mother's womb. It continues during postnatal growth and development. Almost all the accumulation of mammary tissue and DNA occurs in the last trimester of pregnancy [Sorensen *et al.* 2002]. Milk secretion begins before parturition and it is activated during parturition. The lactogenesis-associated supplementary function of the gland is related to the accumulation of immunoglobulins, colostrum production and maintenance of milk secretion [Rekiel 2000, Engelhardt and Breves 2011, Krzymowski and Przała 2015]. Involution of the mammary gland begins with lactation and is associated with apoptosis of lactocytes [Wojewódzka 2000]. Drying off is particularly intense when milk is not drawn and affects mammary glands not occupied by piglets. Several weeks into lactation milk production begins to decrease. Involution, which takes place after weaning of the litter, is a rapid process [Ford *et al.* 2003] and becomes irreversible after 7 days [Theil *et al.* 2005]. It has been scientifically proven that an increased intra-alveolar pressure in the mammary gland and the decreased flow of blood inhibit milk synthesis, filtration and efficient secretion. The pressure of milk on mammary alveolar epithelial cells triggers an apoptotic response. This is accompanied by decreased secretion of prolactin, the growth hormone, estradiol, progesterone and IGF-1 [Motyl *et al.* 2000, Motyl *et al.* 2001, Engelhardt and Breves 2011].

Relationship between teat number and fertility

The results of studies concerning the relationship between the number of piglets per litter and the number of teats on a sow are inconclusive. According to Buczyński *et al.* [1996b] and Zmudzińska-Pietrzak [2015], the number of teats on a sow is one of the more important determinants of litter size. Lewczuk *et al.* [1993] reported that teat number in Złotnicka Spotted sows shows significant, but not very high phenotypic and genetic correlations with the number of piglets born alive, the number of piglets reared and litter weight on day 21. Buczyński *et al.* [1996a] concluded that the number of teats on a sow is positively correlated to the number of piglets born and reared, and to litter weight on day 21 in parities 1-4. However, the coefficients of correlation obtained by the same authors were low ($r<0.104$). A study with Polish Large White sows showed no differences between the number of piglets born and reared depending on the number of teats on a sow ($P>0.05$) [Buczyński *et al.* 1996b]. It follows from a study of Zhishko and Samson [1975] [after Gronek *et al.* 1996] that the coefficient of phenotypic correlation between the number of teats and fertility was $r = +0.334$. However, a study with Polish Large White, Polish Landrace and Złotnicka Spotted pigs failed to confirm that the number of teats is related to the number of piglets on days 1 and 21 and to litter weight on day 21 [Janiszewska *et al.* 1991]. The above-mentioned authors only observed a tendency for these traits to increase in sows with a greater number of teats. Czarnecki *et al.* [1990] did not confirm the relationship between teat number and parameters of potential fertility in gilts.

Relationship between teat number and milk yield

Milk yield has a relatively low heritability and is polygenically determined. It is determined by the number of mammary alveolar cells in early lactation and the number of mammary glands. Of importance is udder occupancy (number of nursed piglets), especially during the first lactation, which depends on realized fertility and the use of equalised litter size (fostering of piglets) [Hoffman 2010, Farmer *et al.* 2012, Devillers *et al.* 2016]. The cells of suckled udders show hyperplasia and increased metabolic activity in successive lactations, thus producing more milk, which helps to increase the growth rate of piglets using the teats. Because unsuckled teats in a previous lactation are less attractive for piglets, neonates fight for previously used teats [Farmer 2013].

Genetic correlations of the total number of teats and functional teats with the mean weaning weight of piglets range from -0.4 to +0.13, which from a genetic point of view indicates that an increased number of teats has little effect on the average weaning weight of piglets [Lundeheim *et al.* 2013]. Zhisho and Samson [1975] citing Gronek *et al.* [1996] reported a correlation coefficient of -0.264 between teat number and milk yield, and -0.238 between teat number and weaning weight of the litter. Sommavilla *et al.* [2015] reported a positive correlation between birth weight and weaning weight, which shows that birth weight determines body weight gains until weaning. However, between farrowing and weaning piglets suckling front teats grew more rapidly, as confirmed by other authors [Pluske *et al.* 2007, Skok *et al.* 2007, Pedersen *et al.* 2011]. This results, among other things, from the differences in milk composition depending on the location of the gland. Studies by Buczyński *et al.* [2001, 2006] show that fat and lactose levels are lowest in the last teat pair. The findings of Skrzypczak *et al.* [2013] are consistent with the results of the authors cited above. After the birth of the litter, piglets that used the anterior (more productive) vs. posterior teats had a high milk consumption and better weight gains. This was additionally determined by a higher nutrient content of the milk from the glands from this location. The losses of piglets suckling the inguinal (posterior) teats were higher than in dominant piglets occupying breast (anterior) teats. The correlation between milk collection and piglet growth up to 3 weeks of lactation is positive [Sommavilla *et al.* 2015]. The results of Rekiel *et al.* [2013] also suggest that teat number may affect rearing performance of piglets up to day 21, but according to the authors access to the teats is not the only determinant of rearing success.

Use of teats, fostering of piglets

It has been scientifically demonstrated that only 46% teats are used by piglets born to primiparous sows and lower row teats are underused, especially in successive lactations, which may increase sibling competition and piglet mortality [Vasdal and Andersen 2012]. Ongoing selection has resulted in a greater litter size, higher growth rate of piglets and an increased number of normal teats [Ocepek *et al.* 2016]. Sows of modern dam lines are heavier and longer, but body development, including mammary size, reaches a peak not earlier than in the 5th-6th reproductive cycle. However, no selection is practiced for such mammary gland parameter as morphology [Ocepek *et al.* 2016]. The studies cited above showed that around 22% of functional, milk-producing teats, were not used on day 1 after birth. It was found that the longer the distance between teat pairs in the middle and posterior positions, the less available the teats become for piglets. Vasdal and Andersen [2012] found that the use of functional teats in the lower teat row was less common for multiparous than primiparous sows. Ocepek *et al.* [2016] demonstrated that teat pair distance (TPD) was greater in multiparous than in primiparous sows. When TPD exceeded 16 cm, teats in the lower teat row in the middle part of the udder were not used and this threshold was 14 cm for the lower posterior teats. The same authors observed that as many as 60% of the studied sows exceeded this limit for the middle teats. This trait appears to be of great practical importance. Increased TPD caused limitation in teat use in the middle and posterior positions because of excessive height above the ground for the upper row and poor exposure of the lower row. Fewer available functional teats during the colostrum period will increase aggressive competition among piglets, especially in large litters. Ocepek *et al.* [2016] underlined the importance of emphasizing udder morphological traits, such as TPD, in the breeding programmes rather than just the numer of functional teats.

Piglets from large litters have a lower potential for growth and development due to fierce competition for teat access. If the number of piglets after farrowing is greater than the number of the dam's teats, weaker piglets will be pushed away by their stronger siblings, the litter will split and piglet mortality will be high. Therefore, one of the important methods is to provide equal nursing opportunity to piglets from large litters or those reared by dams with low milk production. After providing neonatal piglets with colostrum from the biological mother during the first day of life, at the end of the first or during the second day of life the strongest piglets should be moved to nurse sows.

At the beginning of parturition all the mammary glands start to secrete colostrum and those regularly suckled maintain their development and function. Unsuckled udders undergo involution. Fostering of piglets after several days of lactation results in neonate rearing losses [Kim and Easter 2001]. For litters with an uneven distribution in relation to the number and body weight, standardization is essential. Stress due to fostering of piglets is compensated for by higher milk yields of nurse sows [Olsen *et al.* 1998, Rząsa 2007]. The appropriate procedure is to keep at least 12 piglets with a multiparous sow and at least 10 piglets with a primiparous sow [Rząsa 2007]. Keeping a greater number of heavier piglets with the sow will have a positive effect on its milk yield. The best nurse sows are those after the 3rd farrowing, because they have a well-formed udder and are predisposed to extended lactations.

During the first week of life piglets choose sow teats permanently. Competition and group hierarchy formation are associated with the choice of the most productive teats. Larger piglets claim the right to anterior teats, while the other piglets only have access to posterior teats [Kim *et al.* 2000, Drake *et al.* 2008]. However, piglets suckling anterior teats are less motivated to search for other food sources and ignore all-mash feed [Pluske 2007]. The sixth and seventh teat pairs are less attractive and less accessible to piglets. Surdacki and Jóźwiakowska-Rekiel [1988] showed that piglets using anterior teats (1st-3rd pairs) compared to neonates suckling the next teats, had better growth rates and higher body weights at weaning compared to piglets suckling posterior teats throughout rearing. In the group of dominant piglets suckling the anterior teats rearing losses were lowest. A study by Rząsa [2007] demonstrated that piglets suckling 1-canal teats always changed their choice if a more productive teat became accessible.

Conclusions

The number of teats in domestic pigs used for meat production has been considerably increased in relation to their wild ancestors. This was achieved through improvement of this medium heritable trait. The genetic determinants of teat number and the dam effect on this trait have been identified. The practical importance of teat quality and its relationship with rearing performance have been determined. Research determined mammary gland growth, development and function, the association of teat number with fertility and milk yield and the practical, human-controlled use of teats by piglets.

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