The Genetics of the Pig, 2nd Edition

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The Genetics of the Pig, 2nd Edition

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Preface

The first edition of *The Genetics of the Pig* was published more than 12 years ago. During the past several years a deep transformation has occurred in all of the biological sciences. Beginning in 2001, several mammalian genomes were sequenced. The latest addition to this list is the pig genome, whose first draft sequence was obtained at the end of 2009. While the annotation of the pig genome is still an ongoing process one can confidently expect that in the near future this process will be significantly advanced. These developments in the biological sciences have led to the practical implementation of powerful laboratory methods which, together with the emergence of advanced bioinformatics, have caused dramatic accumulations of new data in diverse databases.

Genetic theory and practice have also evolved considerably over the last 12 years. The previously separate fields of classical and quantitative genetics have now been joined with genomics, molecular genetics and immunogenetics, creating new methods and insights into understanding numerous biological processes. Today, more than in the past, genetics serves as a key pillar of modern agricultural sciences, medicine and the biotechnological industry. Animal breeders and geneticists, more widely than ever before, are using knowledge from the different fields of genetics for development and improvement of their livestock. Given these dramatic changes in current genetic applications and theory it seems an appropriate time to publish the second edition of books devoted to genetics of domestic livestock species. *The Genetics of the Pig* opens this series of books.

Domestication of the pig occurred some 9000 years ago, and the consequences of this process have been tremendously important for the food supply in different civilizations. Today, the pig continues to be a valued source of food worldwide. Modern biological discoveries and technological improvements in management practices have revolutionized pork production. Approximately one billion pigs are raised annually worldwide and pork remains the dominant meat source, representing over 40% of all the red meat eaten. Owing to its physiological and genetic similarities with man, the pig serves as an excellent animal model for biomedical research, and as an important source for xenotransplantation and other potential medical applications. Numerous animal scientists, geneticists, veterinarians, livestock producers, medical researchers and students are interested in the biology and genetics of the pig. This new edition of the book brings a wealth of knowledge that we hope will be useful for this diverse group of scientists and practitioners around the world.

The purpose of this book is to present in one location a complete, comprehensive and updated description of the modern genetics of the pig. It is our intention to combine essential knowledge from the various fields of genetics and biology of the pig, integrated with livestock management aspects, in order to provide an updated and informative reference book. The genetic improvements in the pig industry over the past couple of decades have been very impressive, with growth rates increasing, feed efficiency improving and a continued rise in overall

leanness. These successes have in great part been due to the incredible progress in the understanding and application of genetics to pig production. As recently as 1990, only about 50 genes and markers were mapped or assigned to individual porcine chromosomes. Now the genome draft sequence has been obtained and the completion of very detailed genetic and genomic maps has been accomplished. Furthermore, genetic improvement within the pig industry that rests on the introduction of gene tests and on genomic selection based on thousands of genes is coming.

This book is addressed to a diverse audience, including students, researchers, veterinarians and pig breeders. The initial two chapters are devoted to the taxonomy and domestication of the pig. This area has advanced significantly over the last decade. Chapters 3 and 4 extensively cover the genetics of coat colour, morphological characteristics and inherited disorders. Molecular genetics and immunogenetics are described in Chapters 5 and 6. Cytogenetics, chromosome maps and genomics are presented in Chapters 7 and 8. Chapter 9 concentrates on the genetics of behaviour, while the next three chapters are relevant to the biology and genetics of reproduction, modern reproductive technologies and the genetics of development.

Chapter 13 addresses genetic diversity and concerns for maintaining exotic and rare local breeds. The genetics of performance traits and carcass and meat quality traits are discussed in Chapters 14 and 15. Chapter 16 is devoted to overall genetic improvement. Chapter 17 examines the pig's contribution and future potential as an important model for biomedical sciences and a key species for possible organ donation. Chapters 18 and 19 cover pig breeds and genetic nomenclature.

A significant effort was made to consistently implement the current genetic nomenclature. Unfortunately, there are a few shortcomings that seem to be unavoidable. The genetic nomenclature requires that not only genes and alleles, but also traits, should be spelled according to the American style. Essentially, just a few words like colour (color), behaviour (behavior) and flavour (flavor) cause some difficulties. It is not always absolutely clear whether a word like the above describes a trait from the formal point of view and as such the American style should be used. As this book is published in the UK the British spelling rules should apply in all other cases. More on this nomenclature matter can be found in Chapter 19.

The considerable and never-ending progress in genetics research makes it impossible to cover all new and relevant literature. Therefore, it is inevitable that some publications will not be cited. We hope that any errors or omissions will be noted and brought to our attention. Also, during the time when this book was being written there were incremental changes in genetic nomenclature. Despite the consistent attempts to introduce all these changes into the book, we probably cannot claim to have been completely successful. Finally, in no way is this book meant to replace the many fine textbooks devoted to the theory of animal breeding.

This book is the result of international efforts. These efforts are dedicated to our families, to supportive colleagues and to the pig industry that employs and feeds hundreds of millions of people worldwide. The editors offer a special thank you to each of the authors who contributed chapters so graciously and without reservation. Previous authors are also thanked for providing materials useful to this second edition. Publication of colour plates was generously supported by PIC (part of Genus plc), Hendersonville, Tennessee, USA, and the USDA/CSREES Pig Genome Coordination program. Finally, the editors also acknowledge with appreciation all the efforts of CABI to help in producing the book. It is our hope that this text will serve as a useful resource for all those people who study or work with pigs.

Max F. Rothschild
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November 2010

1 Systematics and Evolution of the Pig

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Introduction

According to the current classification, pigs belong to order Cetartiodactyla, which includes even-toed ungulates (the former order Artiodactyla), and whales and dolphins, which are representatives of the former order Cetacea (Murphy *et al*., 2001; Novacek, 2001). Cetartiodactyla diverged from placental mammals approximately 87.2 million years ago (mya) (Murphy and Eizirik, 2009). There are three well-established suborders: (i) Tylopoda – camels and llamas; (ii) Suiformes (also known as Suina) – pigs and peccaries (and formerly hippos); and (iii) Ruminantia.

The fourth and more recently created suborder – called Cetancodonta – includes hippos, dolphins and whales (Price *et al*., 2005; O'Leary and Gatesy, 2008; Huffman, 2009). Phylogenetic analyses of the cytochrome b sequences from 264 of the 290 extant Cetartiodactyla show that the Suiformes and Ruminantia cluster together as a sister clade of Cetancodonta, while the Tylopoda cluster in a separate clade (Agnarsson and May-Collado, 2008). Molecular genetic studies of the Cetartiodactyla have shown good agreement with the basic structure of their phylogeny as supported by morphological data (Novacek, 1992), but the position of hippos and camels

remains contentious (Thewissen *et al.*, 2007; O'Leary and Gatesy, 2008; Spaulding *et al.*, 2009).

Suborder Suiformes

The Suiformes consist of two living families: Tayassuidae (peccaries) and Suidae (pigs). Currently Tayassuidae has three genera, each with a single species, and all these species live in the Americas. The modern Suidae family is more diverse and consists of six genera with 18 or 19 recognized species depending on the source of information. Many of these species live in South-east Asia, others broadly in Eurasia and several species are found only in Africa.

Family Tayassuidae

The family Tayassuidae (peccaries) diverged from pigs in South-east Asia somewhere in the late Eocene, or possibly later, and then migrated to Eurasia, Africa and North America, finally colonizing South America (Ducrocq, 1994). However, the modern species live only in the Americas. The peccaries, like pigs, have a snout disc, but the differences between the two families are significant. The stomach in peccaries is subdivided into three compartments. In several features of the digestive system, peccaries resemble ruminants; it is not known whether these features developed independently. Peccaries have three hooves on their back legs. In addition, their upper canine teeth are pointed down and the total number of teeth is 38. A scent-producing gland located on their backs is another specific feature. Peccaries are significantly smaller than pigs, with an average body size of approximately 30 kg.

There are three recognized extant peccary species that are distributed on the American continent: *Catagonus wagneri* (Chacoan peccary), *Tayassu pecari* (white-lipped peccary) and *Pecari tajacu* (collared peccary) (Grubb, 1993a). The collared peccary spread across South and Central America and the southern part of North America. It is a very common species, reproducing well and widely hunted because of its good meat and leather quality. The white-lipped

peccary is bigger than the collared peccary. This species is spread from southern Mexico to the south of Central America. Hybridization between the white-lipped peccary and the collared peccary has been observed in captivity (Sowls, 1997) and in the wild (Andrea *et al.*, 2001), with the wild hybrid being sterile. The Chacoan peccary was known only through fossil records until it was discovered on the Paraguay–Bolivia–Argentina border about three decades ago (Wetzel, 1977a). This species has been shown to differ significantly from the two other peccaries in chromosome number ($2n = 20$) (Benirschke *et al.*, 1985; Benirschke and Kumamoto, 1989).

There are conflicting hypotheses about the evolution and relationships of modern peccary species. Based on osteological and dental traits, collared and Chacoan peccaries were considered to be more closely related, while the white-lipped peccary was considered to be a member of a separate clade, along with other extinct species (Wright, 1998). However, other morphological studies (Wetzel, 1977b) suggested that collared and white-lipped peccaries are more closely related to each other than to the Chacoan peccary. In contrast, phylogenetic studies using mitochondrial and nuclear DNA sequences show that white-lipped and Chacoan peccary species are more closely related to each other than to the collared peccary (see Fig. 1.1) (Theimer and Keim, 1998; Gongora and Moran, 2005). Additional DNA studies have suggested that the geographically widespread and phenotypically diverse collared peccary may consist of at least two separate lineages deserving specific status, which are as genetically distinct as white-lipped and Chacoan peccaries (Gongora *et al.*, 2006).

Taxonomy and Phylogeny of the Suidae Family

Systematics

The Suidae family includes the most widely spread species of non-ruminant even-toed ungulates, commonly known as pigs and hogs. All of them have an elongated muzzle with a snout disc and four-toe extremities with well-developed

side toes. The canine teeth are large and the upper ones are curved. The stomach is simple with an additional sac. The Suidae are omnivorous. This family traces back to the upper Eocene of Thailand (~35–40 mya), or possibly later (Ducrocq *et al.*, 1998; Liu, 2003). During the Neogene, suids greatly diversified into over 30 genera, and colonized different parts of Eurasia and Africa, where they radiated further (Pickford, 1993, 2006). The extant family Suidae comprises 15 species grouped into several genera: *Sus* (domestic and wild pigs) from Eurasia; *Porcula* (pygmy hogs) from northern India (the separation of *Porcula* from *Sus* is not finally resolved); *Babyrousa* (babirusa) from the island of Sulawesi and its satellite islands; and *Potamochoerus* (bush pig and red river hog), *Phacochoerus* (common and desert warthogs) and *Hylochoerus* (forest hog) from sub-Saharan Africa (Grubb, 1993a,b). The origin, evolutionary relationships and dispersal patterns of Suidae remain contentious. For instance, it has been suggested that some modern suids from sub-Saharan Africa are more closely related to species from Eurasia than to their African congeners on the basis of cranial and dental similarities (Thenius 1970; Cooke, 1978) and cytochrome b sequence (Agnarsson and May-Collado, 2008). In contrast, other morphological analyses suggest that the modern African Suidae could be sister lineages (Harris and White, 1979; Bender, 1992; Geraads, 2004). This lack of consensus extends to the Asian congeners of the Suidae. For instance, it has been suggested (on the basis of mitochondrial DNA) that *Sus salvanius* (pygmy hog) deserves a separate status from the genus *Sus*, and no one has conclusively demonstrated whether *Babyrousa* from South-east Asia or *Phacochoerus* from Africa occupies a basal position within the Suidae (Pickford, 1993; Funk *et al.*, 2007). Some DNA studies have contributed to understanding the relationships within *Phacochoerus* and *Sus* (Randi *et al.*, 1996, 2002). Recently, a concatenated mitochondrial and nuclear DNA study by Gongora *et al.* (submitted) has provided new insights into the evolutionary relationships of Suidae as a way to resolve conflicting and unresolved Suidae topologies generated by individual sequences. This study shows that all sub-Saharan African genera cluster in a monophyletic clade separate from the Eurasian *Sus* species, and confirms that *Babyrousa* is the sister taxon to the other extant species of Suidae, when Tayassuidae is used as the out-group (Fig. 1.1). Accordingly, Gongora *et al.* (submitted) propose that the five extant genera of Suidae should be grouped into the subfamilies Babyrousinae and Suinae, with the latter consisting of three tribes, the so-called 'true' pigs (Suini), warthogs and the forest hog (Phacochoerini) and the bush pig and red river hog (Potamochoerini).

Subfamily Babyrousinae
    Genus *Babyrousa*
        Species *Babyrousa babyrussa* (babirusas on the Sula Islands and Buru Island)
        Species *Babyrousa celebensis* (babirusas from the northern arm of Sulawesi)
        Species *Babyrousa togeanensis* (babirusas restricted to the Sulawesi Togean islands)
Subfamily Suinae
    Tribe Phacochoerini
        Genus *Phacochoerus*
            Species *Phacochoerus africanus* (common warthog)
            Species *Phacochoerus aethiopicus* (Cape and Somali warthog)
        Genus *Hylochoerus*
            Species *Hylochoerus meinertzhageni* (forest hog)
    Tribe Potamochoerini
        Genus *Potamochoerus*
            Species *Potamochoerus porcus* (red river hog)
            Species *Potamochoerus larvatus* (bush pig)
    Tribe Suini
        Genus *Sus*
            Species *Sus scrofa* (Eurasian wild boar)
            Species *Sus verrucosus* (Javan warty pig)
            Species *Sus barbatus* (bearded pig)
            Species *Sus celebensis* (Sulawesi warty pig)
            Species *Sus philippensis* (Philippine warty pig)
            Species *Sus cebifrons* (Visayan warty pig)
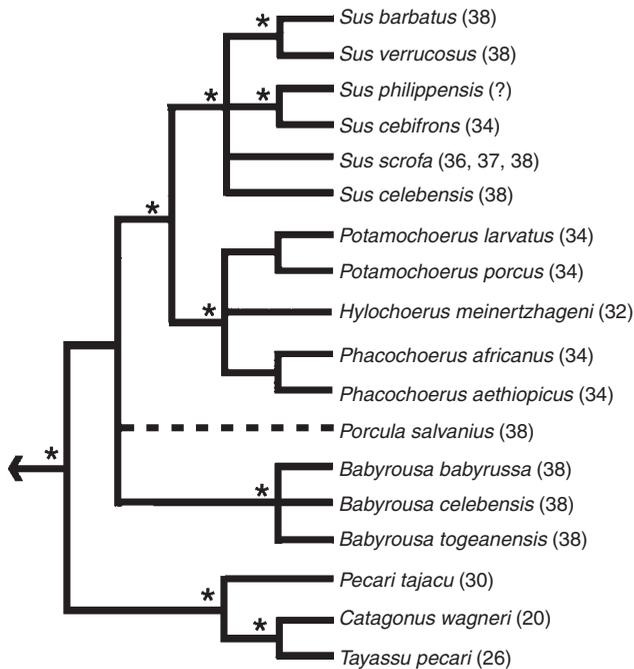   Species *Sus salvanius* or *Porcula salvanius*? (pygmy hog)

Fig. 1.1. A cladogram depicting the relationships in the suborder Suiformes. This tree amalgamates information from several recent publications that have generated mitochondrial and nuclear DNA sequences. Polytomies indicate a lack of resolution with respect to branching order, and the dashed line leading to the pygmy hog represents the current uncertainty with regard to its position within the tree. Well-supported nodes are marked by asterisks, and diploid chromosome numbers are placed within parentheses following the species name. This tree will be revised as newly elevated species are included and new genetic and morphological data resolve the branching order.

The general taxonomy of the family seems reasonably justified, although the taxonomy of some genera, *Sus* and *Babyrousa* in particular, is likely to be the subject of future reconsiderations. There are indications concerning the existence of at least two more species: *Sus bucculentus* and *Sus heureni*, which have been purported to inhabit South Vietnam and the Flores Islands (Indonesia), respectively. A recent paper based upon mitochondrial signatures, however, demonstrated that *Sus bucculentus* is not sufficiently different from *Sus scrofa* to deserve full species recognition (Robins *et al.*, 2006).

Subfamily Babyrousinae

Genus Babyrousa

Until recently, there was only one species of babirusa ('babi-rusa', Indonesian, babi = pig,

rusa = deer): *B. babyrussa*. Based upon a reconsideration of morphological characters, Meijaard and Groves (2002) proposed that this single species be split into three extant species, *B. babyrussa, B. celebensis, B. togeanensis,* and a fourth extinct species from the southwest arm of Sulawesi which they call *Babyrousa bolabatuensis*. These designations are likely to be altered again when DNA evidence is brought to bear on the question.

The members of this genus differ significantly from Suinae in that they have long legs, relatively small heads and bodies mostly free of hair. The morphology of the stomach is complex. Grass comprises the main source of food and the typical digging or rooting behaviour of pigs is not known. The canine teeth in males are considerably more developed and are very large and curved, sometimes creating a spiral. The most unusual feature is that the mandibular canine and the maxillary canine teeth

are both pointed upwards, which is uncommon for mammals. Females usually deliver two offspring and the adults are large in size. Babirusas are spread across Sulawesi and nearby islands, and, because they can swim well, whether they arrived on nearby islands by themselves or were ferried by humans remains an open question.

Eleven of the autosome pairs and the X chromosome in this genus look very similar to the chromosomes of the domestic pig (Bosma *et al*., 1991a; see also Table 7.4). Future molecular phylogenetic investigations may give a clearer answer concerning the origin of the babirusa. A morphological study of the placenta and heart anatomy indicates that the babirusa has a significant number of traits in common with pigs (MacDonald, 1994).

Subfamily Suinae

Tribe Phacochoerini

GENUS *PHACOCHOERUS*. The common warthog (*P. africanus*), is widespread in many African countries. The name is derived from the large warts that are located on the muzzle, whose function is not known. The shape of the skull of the warthog differs essentially from that of other pigs and the number of teeth is greatly reduced. The canines are large, sharp and represented in both sexes. Adults are approximately 145–190 cm in length, 65–85 cm in height and weigh 50–150 kg. Average litter size is about three to four piglets. The offspring are susceptible to the cold immediately after birth and therefore do not leave their burrow, where the temperature is around 30°C constantly. Their main food is grass and the animals graze on their knees, which causes callus development. Adults, in contrast, to their offspring, enter the burrow backwards. The species is spread widely in sub-Saharan Africa, but not in the rainforests of Western Africa. In Southern Africa, this species has been reintroduced for hunting. The diploid chromosome number of the common warthog is 34 (Melander and Hansen-Melander, 1980).

The Cape and Somali warthog, *P. aethiopicus*, was recognized by zoologists as a separate species relatively recently (Grubb, 1993b). However, palaeontologists came to a similar conclusion many years ago, mainly because of the lack of functional incisors in *P. aethiopicus*. The common warthog has two incisors in the upper jaw and usually six in the lower jaw.

GENUS *HYLOCHOERUS*. The forest hog (*H. meinertzhageni*) is one of the largest wild pigs (length 155–190 cm, height up to 110 cm and weight up to 250 kg). The forest hogs of East Africa are particularly large (Grubb, 1993b). The head and muzzle are very broad, and the snout is big and well developed for extensive digging. This species and genus is a relatively recent discovery. It was found in Kenya during the early part of the 20th century and is now known to occur throughout the tropical forest region of Africa. The animals are covered with long black hair. The biology of this species is still under investigation.

Tribe Potamochoerini

GENUS *POTAMOCHOERUS*. *P. porcus* (red river hog) is one of the smallest African pigs. This species is widely spread in the central and southern parts of the continent and shows a significant variability in colour and size. The animals that live in West Equatorial Africa, for instance, are usually very bright and red in colour with a white bar on the back, white hairs on the muzzle and brushes of long hairs on the ears. Males from the majority of habitats are characterized by the canine apophyses (located between the ears and the nose), which in older males look like two small horns directed backwards. Length of the body varies from 100 to 150 cm. The height varies from 55 to 80 cm and the weight may reach 80 kg (Bannikov and Flint, 1989). The number of offspring is three to four. The skull of *P. porcus* is very much like that of *Sus*. Groves (1981) considered that the skull structure was an indication that these genera may be more closely related, or both have changed little from their more distant common ancestor. However, an absence of comparative cytogenetic (Bosma *et al*., 1991a) and molecular data makes it difficult to estimate phylogenetic distance from other genera.

The range of the bush pig (*P. larvatus*) is mainly to the east and south of that of the river hog and it occurs not only in East and South Africa, but even in Madagascar. It is also bristly, but bristly pelage extends from the head over

the whole body and gives the live animal a shaggy, crested appearance, which is different from that of the river hog. The two species are for the most part separated territorially, but in some places their areas may overlap (Grubb, 1993b). An introgression between the species is assumed (Kingdon, 1979). The limited amount of information about the biology and evolution of both of these species needs to be rectified.

Taxonomy of the Genus *Sus*

Introductory remarks

Sus most likely originated in Island Southeast Asia and then migrated into East Asia before heading west towards the Near East, North Africa and Europe. (Pickford, 1993; Larson *et al.*, 2005). The earliest fossil evidence of *Sus* (*Sus arvernensis*) is from the Late Miocene (~6–5.3 mya) of Europe, but, as there is no direct known ancestor from this continent, it is considered that this lineage must have arrived by dispersal from Asia (van der Made and Moya-Sola, 1989; van der Made *et al.*, 2006). Groves (1981) presented a comprehensive analysis of the taxonomy and phylogeny of the extant genus *Sus* based on morphological, palaeontological and biogeographical data. Groves and Grubb (1993) revised the systematics of the genus. This basic analysis and newly published data are summarized in the following section. DNA and morphological analyses suggest the existence of three evolutionary groups within *Sus* that could have diverged during the Pliocene – *S. cebifrons/S. celebensis*, *S. barbatus* and *S. verrucosus/S. scrofa*, with *Sus ahoenobarbus* as a new species within the latter group (Lucchini *et al.*, 2005). This contrasts with the three groups (*S. verrucosus*, *S. philippensis* and *S. scrofa*) proposed by Groves (1981), as well as partially with other DNA studies that cluster *S. verrucosus/S. barbatus* as a sister clade of *S. scrofa* (Randi *et al.*, 2002). Morphological studies of extant and extinct forms have divided the genus *Sus* into two groups, the primitive 'scrofic' and the derived 'verrucosi' (van der Made and

Moya-Sola, 1989); other dental studies have also indicated a separation of *S. scrofa* from the rest of *Sus* (Genov, 2004). Several studies (e.g. those of Larson *et al.*, 2005 and Mona *et al.*, 2007) have pointed out that certain DNA sequences widely used to discover the relationships between taxa were not sufficient to discriminate between some species of *Sus*. At present, the genus *Sus* comprises seven species. Investigations of this genus conducted over the past 170 years have taken different approaches, and the number of discriminated species has varied from very few to a total of 37. Future classifications, based on classical and molecular phylogenetic data, are likely to alter the current knowledge concerning *Sus* taxonomy and evolution.

Sus scrofa (Eurasian wild boar)

The earliest known fossil of *S. scrofa* in Europe is from the Early Pleistocene (~780,000 years ago) (van der Made, 1999; Franzen *et al.*, 2000); that from Asia is also from the Early Pleistocene (J. van der Made, personal communication). The modern species exists in four forms: domestic livestock, domestic semi-wild, feral and wild (Genov, 2004). *S. scrofa* spreads naturally through vast territories, and covers most of Europe and Asia. The species was introduced into North and South America, Australia and Oceania. Domestic pigs are very common in the majority of countries worldwide, except for those that have religious restrictions. Several features, including tooth and skull morphology, external proportions, hair and colour patterns, biochemical and molecular polymorphisms, ecology and behaviour, reproductive isolation and natural areas, are used for discrimination of the many species in the genus.

Pigs are one of the most widespread mammalian species and *S. scrofa* is the primary ancestor of domesticated pigs, though other species may also have been involved (see Chapter 2). *S. scrofa* is extremely variable in the majority of traits studied. The number of subspecies is uncertain and depends upon the definition of the subspecies. However, it is possible to discriminate at least 16 more or less

distinct subspecies (Groves, 1981; Groves and Grubb, 1993):

S. s. scrofa	Western, Central and parts of Southern Europe
S. s. attila	East Europe, northern slopes of Caucasus, parts of Western Siberia, Central and Western Asia
S. s. meridionalis	South Spain, Corsica and Sardinia
S. s. algira	North-west Africa
S. s. libica	Asia Minor, Middle East, southern part of Eastern Europe
S. s. nigripes	Southern Siberia, Central Asia
S. s. sibiricus	Eastern Siberia, Mongolia
S. s. ussuricus	Russian Far East, Korea
S. s. moupinensis	Eastern China, South-east Asia
S. s. leucomystax	Japan
S. s. riukiuanus	Ryukyu Islands
S. s. taivanus	Taiwan
S. s. davidi	Western India
S. s. cristatus	Eastern India, western part of Indochina
S. s. affinis	Southern India, Sri Lanka
S. s. vittatus	Malaysia, Southern Indonesian Islands

The areas of these subspecies are close and the level of discriminating differences may be quite small, involving size, colour, proportions, skull characters and, in several cases, chromosome numbers. The variation in chromosome number is a result of two distinct Robertsonian translocations, which were found in the different geographical areas of the species (Tikhonov and Troshina, 1974; Bosma, 1976). The usual number of chromosomes in *S. scrofa* is 38 (Bosma *et al.*, 1995). However, translocation I involving chromosomes 16 and 17 and translocation II involving chromosomes 15 and 17 were found in Kyrgyzstani and European boars (Tikhonov and Troshina, 1978), and reduce the number of chromosomes to 37 in crosses (heterozygotes) and to 36 in homozygotes.

Adaptations of these animals to different food and climatic conditions are dramatic. The flexible behaviour of the wild boar is perhaps one of the important features providing this adaptability. *S. scrofa* is well adapted to Siberian winters, tropical conditions, mountains and semi-deserts. Pigs can tolerate temperatures from −50°C to +50°C due to well-developed thermoregulatory and nest-building behaviour. Despite being under significant human and predator pressure, populations of wild boar and feral pigs are very numerous in many parts of the world (Choquenot *et al.*, 1996).

Variations in body size are significant among subspecies. The largest subspecies are *S. s. ussuricus* (males up to 300 kg) and *S. s. attila* (males up to 275 kg). Generally, mature weight is quite variable depending on age, sex, food availability, season and habitat. Body and head length is about 130–175 cm and height ranges up to 100 cm. The smallest forms of wild boar are from South-east Asia. Detailed descriptions of skulls, and osteometrical studies, have been published (Groves, 1981; Endo *et al.*, 1994).

Current palaeontological knowledge regarding the evolution of *S. scrofa* is still limited, and fragmented data do not create a full-scale picture of the origin and phylogeny of the species. It is known that a fully evolved *S. scrofa* lived in the Biharian fauna in Europe and replaced the previously existing lineages of *Sus strozzii*, a possible descendant of *S. arvernensis* (Hünermann, 1969; van der Made, 1999). The facial shortening that occurred in *S. celebensis* and in *S. scrofa* has been used as a possible argument in favour of their common origin from perhaps the southern or the south-eastern regions of Asia (Groves, 1981). The spread of the two above-mentioned Robertsonian translocations does not contradict this possibility. However, it is obvious that an extensive molecular genetics study of the problem is necessary before any clear conclusions can be drawn. Thus far, an analysis of mitochondrial DNA from an extensive Old World sampling of *Sus* samples generally supported the subspecies listed above, though the resolution of these DNA studies was not sufficient to conclusively demonstrate the existence of all the named subspecies (Larson *et al.*, 2005).

Sus verrucosus (Javan warty pig)

This species now lives mainly in Java. Two subspecies have been described (Groves and Grubb, 1993). The most typical common feature is three warts on a specific location of the muzzle, which are strongly developed in the adult males. Colour varies from overall black to a pale red. Size also varies from relatively large to small. Sexual dimorphism in size is greater than in other species. Despite some differences from *S. s. vittatus* and *S. celebensis* in G-banding and the structure of the Y chromosome, similarity is significant (Bosma *et al.*, 1991b). The closeness of *S. verrucosus* and *S. s. vittatus* is supported by the observation and precise description of interspecies hybrids in nature (Blouch and Groves, 1990). Several morphological features make *S. verrucosus* close to the other South-east Asian species, *S. barbatus*.

Sus barbatus (bearded pig)

The common name of *S. barbatus* – the bearded pig – is due to the elongated whiskers around the muzzle from the mouth to the ears. A few warts on the muzzle are very typical. Mature size varies significantly between several subspecies and is on average close to that of *S. scrofa*. The length ranges from 100 to 160 cm and the weight is approximately 100 kg. Some males are much bigger. The bearded pig inhabits the Malaysian peninsula, Sumatra, Java, Borneo, Palau, Bangka, Palawan and some other islands. *S. barbatus* sometimes migrates, and these migrations involve thousand of animals. Fertile hybrids with *S. scrofa* obtained in captivity are known (Blouch and Groves, 1990).

Sus celebensis (Sulawesi warty pig)

This wild pig from Sulawesi and several other islands, including possibly Timor, has been recognized as a separate species from *S. verrucosus* by Groves (1981). Cytogenetic analysis strongly supported this point, though the structure of the Y chromosome has some differences from that of *S. verrucosus* (Bosma *et al.*,

1991b). Animals are usually black with a few white or yellowish hairs intermixed, and they have crown tufts of hair. Other colour types have been described. The muzzle is short, like the Eurasian wild pig, and is of small size. Legs are also short, and the pig has small short ears with a relatively large head. This species is found on Sulawesi and other offshore islands. There are indications that *S. celebensis* was domesticated during the early Holocene and spread as far as Roti, a medium-sized island south-west of New Guinea, where the pigs are living now (Groves, 1981). In other places, they have probably been replaced by domestic *S. s. vittatus*. Based upon morphological characters, Groves originally claimed that the several forms of wild pigs in New Guinea could be a result of hybridization between *S. s. vittatus* and *S. celebensis* (Groves, 1981).

Recent papers based upon genetic evidence have suggested a different alternative. First, mitochondrial signatures obtained from *S. celebensis* samples on the island of Sulawesi are not monophyletic. Instead, two clades, one made up of samples from the northern arm of the island and one made up of southern samples, cluster within other *S. scrofa*, *S. barbatus* and *S. verrucosus* samples, suggesting not just two species, but that each may have arrived on to the island independently (Larson *et al.*, 2005, 2007). Secondly, pigs from New Guinea possess a completely separate signature known as the Pacific Clade, and, though this does not rule out hybridization with *S. celebensis*, it strongly suggests that the maternal heritage of pigs on New Guinea and throughout the Pacific was derived from an Asian wild boar endemic to Peninsular Southeast Asia (Larson *et al.*, 2007).

Sus philippensis (Philippine warty pig)

According to the latest information, there are sufficient arguments to discriminate *S. philippensis* from *S. celebensis* and *S. barbatus* (Groves, 1981; Groves and Grubb, 1993). The species occurs on several islands of the eastern Philippines. The colour is black, sometimes with a pale snout band and red-brown patches in the mane. This pig is smaller than *S. barbatus*. Further investigations of the species are desirable.

Sus cebifrons (Visayan warty pig)

S. cebifrons is a small pig that occurs allopatrically to *S. philippensis* on the west-central islands of the Philippines (Groves and Grubb, 1993). Data on the biology of this species are very limited.

The pygmy hog: Sus salvanius or Porcula salvanius?

This is the smallest pig. The taxonomy is still controversial as follows from the discussion below. The pygmy hog does not have warts. Body and head length is 66–71 cm in males and 55–62 cm in females. The corresponding shoulder height is 23–30 cm and 20–22 cm, and weight is 9–10 kg and 6–7 kg in males and females, respectively (Mallinson, 1977). The basic colour is dark brown. Structure of the skull differs significantly from that of *S. scrofa*. The number of pairs of teats is three, instead of the six pairs typical of other *Sus* species, and the number of piglets born is usually three to four. Ears are large and rounded. The tail is very short and the inner toes are short compared with other pig species (Groves, 1981). The pygmy hog is currently distributed in quite a narrow part of northern Assam (India) in the long-grass belt. The number of animals in the area is very small. This species is, therefore, considered to be endangered. The diploid chromosome number is 38. Comparative analysis of G-bands shows that the chromosomes of the pygmy hog are very similar to those of the domestic pig and those of wild *S. scrofa,* which possess $2n = 38$ chromosomes (Bosma *et al.*, 1983). Except for the small size of the body there are relatively few characters that may serve as diagnostic for discrimination of this species from *S. scrofa*.

The original description of this species by Hodgson in 1847 placed it as the sole species within the genus *Porcula*. This was overturned by Groves (1981), who used a series of morphological markers to assign the species as a member of the genus *Sus*. A recent molecular study of modern and museum specimens of this species, however, demonstrated that pygmy hogs possess a degree of genetic differ-

ence and that phylogenetic inference places them outside the *Sus* genus on a phylogenetic tree (Funk *et al.*, 2007). Even though the tree did not possess enough resolution to confidently ascertain the relationship of *Porcula* to the other genera, its difference from *Sus* was robustly demonstrated. These observations led Funk *et al.* (2007) to suggest that the genus *Porcula* be revived and that Hodgon's original classification was correct, although future reconsiderations using additional data may overturn this designation again.

Interrelationships of the species in genus Sus

A high level of morphological similarities between all species of the genus is an argument in favour of their relatively recent origin from a common ancestor. Their same chromosome number and their high level of homology support this conclusion. However, these close relationships complicate phylogenetic reconstruction. A possible phylogeny of the genus *Sus* is presented in Fig. 1.1 based upon an amalgamation of trees presented in a series of genetics papers.

It follows from the previous species descriptions that, in several cases, different *Sus* species coexist in the same area, yet have maintained significant differences in morphology, ecology and behaviour. This may be reasonably explained by a reproductive isolation that appears to exist between the species which may have contact. This is applicable to *S. scrofa* and the pygmy hog in northern India, and to *S. scrofa* and the 'Indonesian' species: *S. barbatus, S. verrucosus* and *S. celebensis*. None the less, interspecies hybridization with *S. scrofa* can occur, and this probably indicates a limited reproductive isolation (Groves, 1983). The production of fertile hybrids between a European wild boar and *S. barbatus* sows has been reported (Lotsy, 1922). Hybridization between *S. scrofa* and *S. verrucosus* has been recorded fairly recently in Java (Blouch and Groves, 1990). According to Groves (1996, personal communication) in some parts of the Philippines the indigenous wild pigs (especially *S. cebifrons*) are in danger of being hybridized

out of existence by crossing with feral domestic pigs. Groves (1981) assumed that the ancestors of these species were separated at least in the Middle Pleistocene, but this may have happened much longer ago.

A hypothetical scenario of *Sus* evolution has been suggested by Groves (1981). He proposed that the *S. verrucosus–S. barbatus* lineage, which has been present from the beginning of the Pliocene in Europe, entered Indonesia about 2 mya. It appears that these animals cohabited with the older *S. celebensis* lineage. *S. scrofa* may have possibly evolved out of the *S. celebensis* lineages and entered Europe about 700,000 years ago, where it replaced *S. verrucosus*-like pigs. The high level of similarity in chromosome structure of *S. scrofa* and *S. celebensis* does not contradict this hypothesis. Several independent sets of data support a Far East origin of *S. scrofa* and a steady spreading in a westerly direction. The previously mentioned Robertsonian translocations, which are typical for some Siberian, Central Asian and European populations, probably appeared and became fixed in the populations after or during their western movement. Numerous investigations have been devoted to comparing the geographical distribution of alleles for blood group antigens, isoenzymes and other proteins, but have not been directly used as arguments in resolution of the problem of the species origins (Gorelov, 1994). This story, generated from morphological and biological data, has recently been supported by DNA studies. The most likely scenario is that *S. scrofa* originated in Island South-east Asia, and migrated first across the Kra Isthmus into Peninsular East Asia, whereupon *Sus* radiated and diversified across East Asia. From there, the species spread west into Central Asia, the Near East and finally into Europe and North Africa (Larson *et al.*, 2005).

Conclusions

The information presented in this chapter gives a general overview of the systematic position and phylogeny of the wild ancestors of the domestic pig. The family Suidae appeared during the evolution of the early Oligocene, some time after separation of the suborder Suiformes from other Artiodactyla. From a morphological point of view, the Suiformes are more primitive and less specialized.

Members of the Suidae have spread widely across Africa, Europe and Asia. *Sus* itself appeared in the Lower Pliocene at least 3–5 mya in Europe and Indonesia. A distribution of these ancestor species through the Indonesian Islands was possibly essential for speciation within the genus.

One of these species, *S. scrofa*, was tremendously successful and spread through Asia and Europe, replacing previous species. A number of more or less distinctive subspecies emerged, and some of them were independently involved in the domestication process that began over 10,000 years ago.

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