Contents

1 The Dog and Its Relatives

This text is based on anatomic studies of many dogs of diverse and usually unknown ancestry commonly referred to as *mongrels*. Domestic dogs are probably the most polymorphic mammals referred to as a single species, *Canis familiaris*, and some workers have suggested that no domestic animal be given species designation (Groves, 1971). The alternatives are the use of subspecific names or breed designations. Because all members of the family Canidae are interfertile and human interaction has affected their hybridization and distribution throughout the world, it appears simplest to adopt one term for all purebreds, mongrels, and feral dogs. While the complete genome of the domestic dog was published in 2005 (Lindblad-Toh et al., 2005), subsequent analyses have revealed the importance of feral dogs, or the "village dogs" around the world, in developing an understanding of the origins of the domestic breeds (Boyko, 2011). The village dogs are descendants of ancient village-dog populations with little inflow of genes from modern breeds of dog (Boyko et al., 2009) and provided the genetic foundation for modern domesticated breeds (Boyko, 2011). Domestication may have preceded human agricultural practices (Clutton-Brock, 1995) and may have had several origins, one in Europe and another in central Asia (Shannon et al., 2015; Frantz et al., 2016). While Shannon et al. (2015) placed the domestication of dogs at least 15,00 years before present, others suggest a single domestication path starting between 20,000 to 40,000 years before present (Botigué et al., 2017). Parker et al. (2017) investigated the relationships of breeds within functional groups (herding dogs, for example) and elucidated how some physical traits may have arisen in separate breed lineages. For historical considerations of the world's wild and domestic dogs, see Smith (1845–1846) *Mammalia: Dogs*, vols. I and II (with color plates), in *The Naturalist's Library*, vol. 18, by W. Jardine; Darwin (1868); *Animals and Plants under Domestication*, Ash (1972); Fiennes and Fiennes (1968); Titcomb (1969); Epstein (1971); American Kennel Club (AKC) *The Complete Dog Book* (2006) and *The New Complete Dog Book* (2017); and Fogle and Morgan (2009) *Encyclopedia of the Dog*, which covers 420 breeds.

The Order Carnivora

The domestic dog, gray wolf, red wolf, coyote, dingo, jackals, dhole, and others are interfertile and frequently cross in their native habitats all over the world. They have been assigned to various genera over the years depending on the criteria used and will probably continue to be a problem for systematists for many years to come. It is not possible to assign the domestic dog with certainty to any one progenitor, but it is clear that the dog and the wolf are closely related and evolved together.

Order Carnivora
Family Canidae
  Genus *Canis*
    Species familiaris

The order Carnivora is worldwide in distribution and is an assemblage of intelligent, mostly flesh-eating mammals with prominent canine teeth; molars adapted for crushing, cutting, and grinding; and a relatively short alimentary canal. Members of the order have digits provided with claws and sometimes with interdigital webs. Behavioral characteristics identify most of them as predators with strong family ties and devoted to the care of their young. Many of the species adapt readily to domestication (Clutton-Brock & Jewell, 1993; Ewer, 1973).

Since the time of Linnaeus the levels of classification have become more accurate and useful, and we can now also consider genomic evidence for relationships between animals.

Wayne and Ostrander (2007) have investigated the dog genome sequence and associated genomic resources and declared that these studies "will revolutionize the study of dog evolution, population structure and genetics." They presented a chart of canid relationships that shows the major groupings of species. A more accurate phylogeny of the Dog family, Canidae, is in the making, and molecular markers that identify gene pools now allow the assignment of mixed "breeds" to specific gene pools. The WISDOM Panel MX of Mars Veterinary, Inc., has a DNA-based test that is said to identify 134 breeds registered by the American Kennel Club (AKC) that may be present in a mixed-breed dog (Giger et al., 2007). A newer entry in the pool for consumer genomics—or, in this case, canine genetic testing—is EMBARK (www.embarkvet.com), whose testing platform aims to provide information related to a dog's risk for inherited diseases, as one example.

The most complete treatment of fossil and living families and genera of mammals can be found in *Classification of*

Mammals above the Species Level, by Malcolm McKenna and Susan Bell (1997) with contributions from George G. Simpson. This classification project was begun by Simpson (1945) in 1927, at the American Museum of Natural History in New York City. Many people cooperated in assembling this tome, which includes all mammals of the world. The number of extinct taxa is much greater than living forms, and many fossil animals are known only from a few bones or teeth.

Wozencraft (2005) revised the order Carnivora in Wilson and Reeder's (2005) *Mammalian Species of the World.* He raised the Giant Panda, the Madagascan Carnivores, the African Palm Civet, the Skunks, and the Walrus each to family rank. While Wozencraft recognized 273 species, Nyakatura and Bininda-Emonds (2012) proposed recognition of 286 species based on changes in taxonomic opinion and new discoveries.

This pictorial family tree (Fig. 1.1A) is an approximation of how animals in the order Carnivora are related to each other according to prior classifications. The major divisions are the Feliformia (cats) and the Caniformia (dogs), which may have arisen from Miacid stock between the Eocene and the Paleocene approximately 40 to 60 million years ago. This time frame witnessed the evolution of modern mammals and birds. Every year new fossils are found (as well as extant forms), and we are able to improve our understanding of animal phylogeny. For photographs of various mammals see Nowak (1991).

Cat Families

Felidae

Lion, Leopard, Snow Leopard, Cheetah, Tiger, Lynx, Bobcat, Domestic Cat, Marble Cat, Flat-Headed Cat, Golden Cat, Black-Footed Cat, Roaring Cats, Caracal, Ocelot, Puma, Jaguarundi, Serval, Jaguar, Eyra

Herpestidae

Mongooses, Ichneumon, Cusimanses

Hyaenidae

Hyaena, Aardwolf

Viverridae

Oriental Civet, Genets, African Civet, Palm Civets, Water Civet, Linsangs, Binturong, Bornean Mongoose, Suricate, Meerkat

Eupleridae

Fanaloka, Fossa (Madagascan Carnivores)

Nandinidae

African Palm Civet

Dog Families

Canidae

Dogs, Wolves, Coyote, Foxes, Dhole, African Hunting Dog, Culpeo, Guara, Crab-Eating Fox, Raccoon Dog, Dingo, Bush Dog, Jackals, Dire Wolf

Ursidae

Bears

Ailuridae

Giant Panda

Otariidae

Eared Seals, Fur Seals, Sea Lions

Odobenidae

Walrus

Phocidae

Harbor Seal, Ringed Seal, Ribbon Seal, Harp Seal, Hair Seals, Earless Seal, Bearded Seal, Gray Seal, Hooded Seal, Elephant Seal, Monk Seal, Ross Seal, Leopard Seal, Weddell Seal

Mustelidae

Minks, Otters, Stink Badger, Marten, Sable, Fisher, Pine Marten, Weasels, Stoat, Ferret, Polecat, Badgers, Grison, Zorille, Taira, Ratel, Wolverine

Mephitidae

Skunks

Procyonidae

Ring-Tailed Cat, Olingo, Kinkajou, Coatis, Raccoon, Lesser Red Panda

The Family Canidae

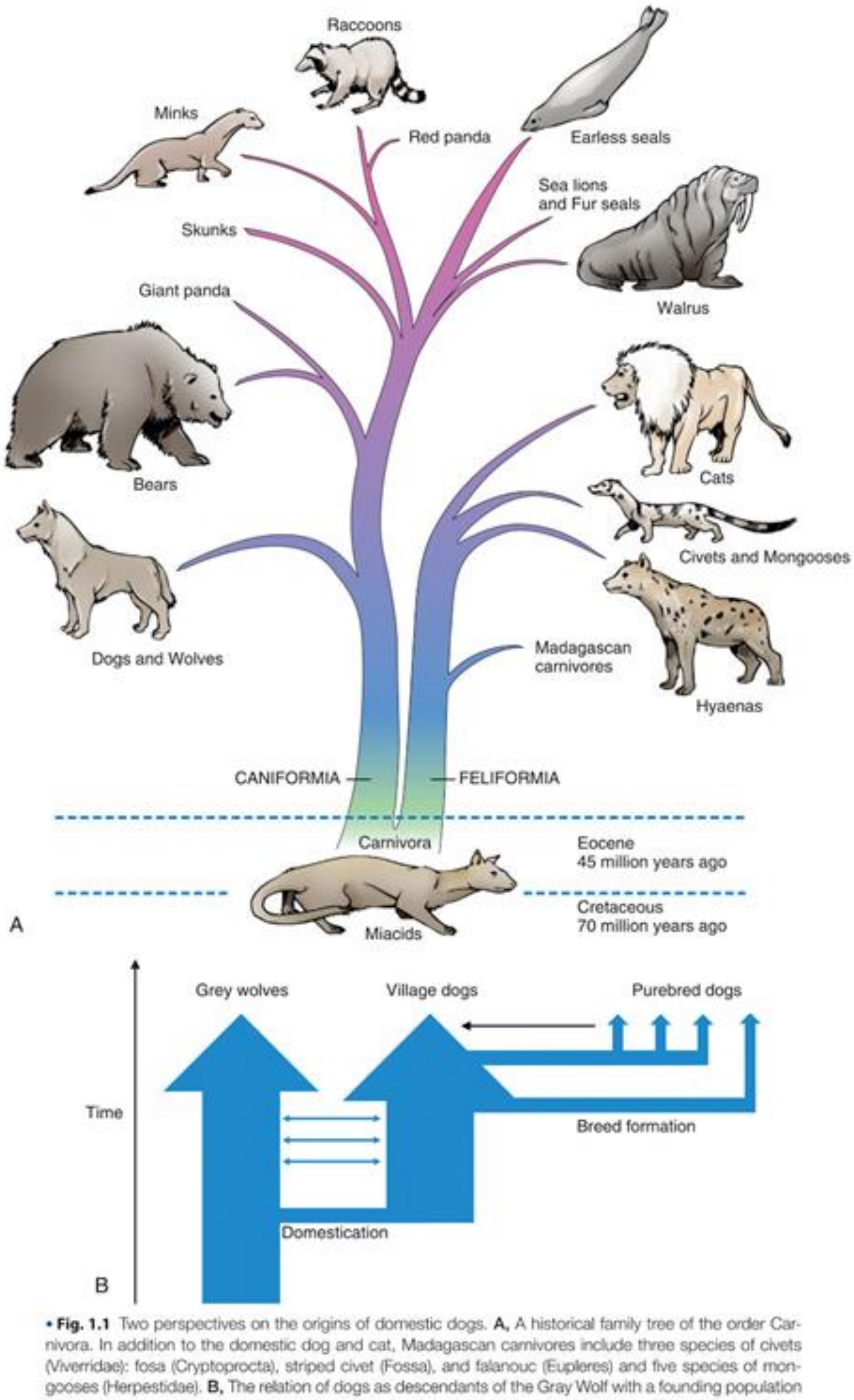
The family Canidae is a distinct group of dog- and foxlike animals distributed throughout the world (Gittleman, 1989; Mivart, 1890; Sheldon, 1992). Although there is general agreement about which genera are included in the family, there has been disagreement about the generic status of several species and their groupings into subfamilies. Clutton-Brock et al. (1976) reviewed the family Canidae using numeric methods and suggested a classification at the generic level based on 90 characters of the skeleton, pelage, internal anatomy, and behavior. Their results indicated that the three largest genera—*Canis* (dog, wolf, coyote, jackal), *Vulpes* (foxes), and *Dusicyon* (South American foxes and foxlike animals)—all are closely related but merit the separate designations they now have.

Wayne (1993) Wayne & Ostrander (1999, 2007), and Wayne et al. (1989) have investigated the evolutionary relationships of carnivores using karyologic and molecular procedures. Their techniques, such as DNA hybridization, protein electrophoresis, albumin immunologic distance, and high-resolution G-banding of karyotypes, have helped define relationships. Our current understanding of the taxonomy of carnivores and dogs, in particular, is discussed by Wayne and Ostrander (2007) and Boyko et al. (2010).

Behavior is a feature that is sometimes characteristic of a breed. Takeuchi and Mori (2006) compared the behavior of purebred dogs in Japan with those in the United States and the United Kingdom. Stockard (1941) also took note of behavior in the purebred crosses he was producing.

Hybrids

Because all dogs are interfertile, many intermediate physiognomies are not assignable to any particular breed (Stockard, 1941; Van Gelder, 1977). Even first-generation hybrids of purebred parents may exhibit bizarre combinations of body characteristics (Figs. 1.2 and 1.3).



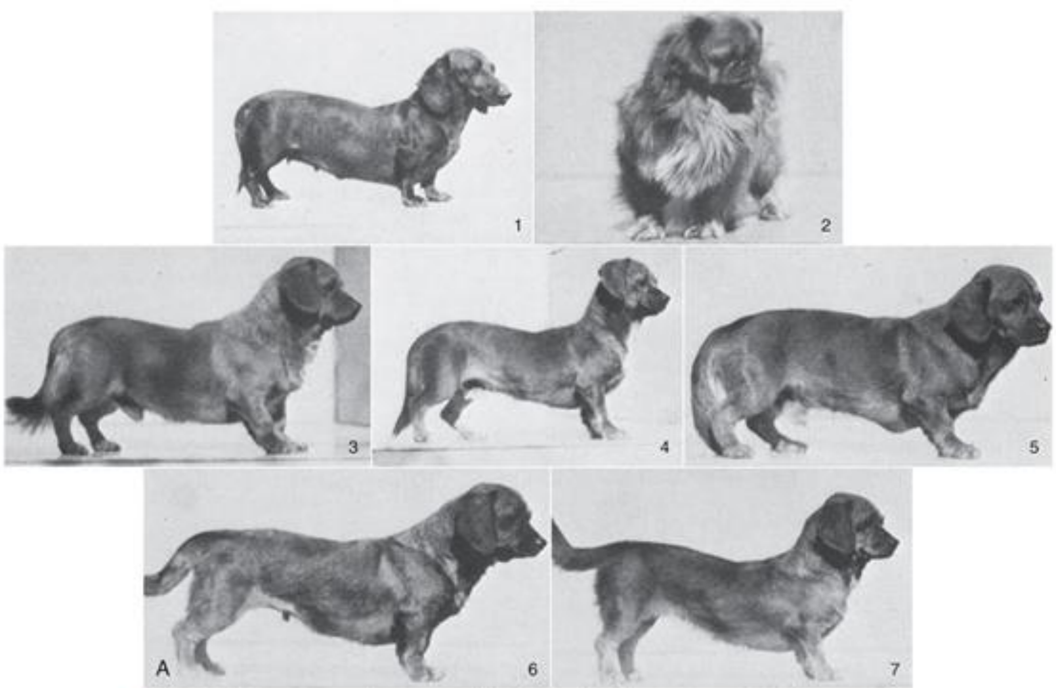
• **Fig. 1.1** Two perspectives on the origins of domestic dogs. **A,** A historical family tree of the order Carnivora. In addition to the domestic dog and cat, Madagascan carnivores include three species of civets (Viverridae): fosa (Cryptoprocta), striped civet (Fossa), and falanouc (Eupleres) and five species of mongooses (Herpestidae). **B,** The relation of dogs as descendants of the Gray Wolf with a founding population of various village dogs giving rise to the multiple breeds of living domestic dogs. (Modified with permission from Boyko, 2011.)

Differences in the conformation of the body or its parts are common and are considered as malformations only when extreme. Susceptibility of the developing embryo or fetus to malformation varies with developmental stage or age, and malformation may affect only one part or organ of the body. Malformations may be due to genetic, endocrine, metabolic, infectious, or mutagenic influences.

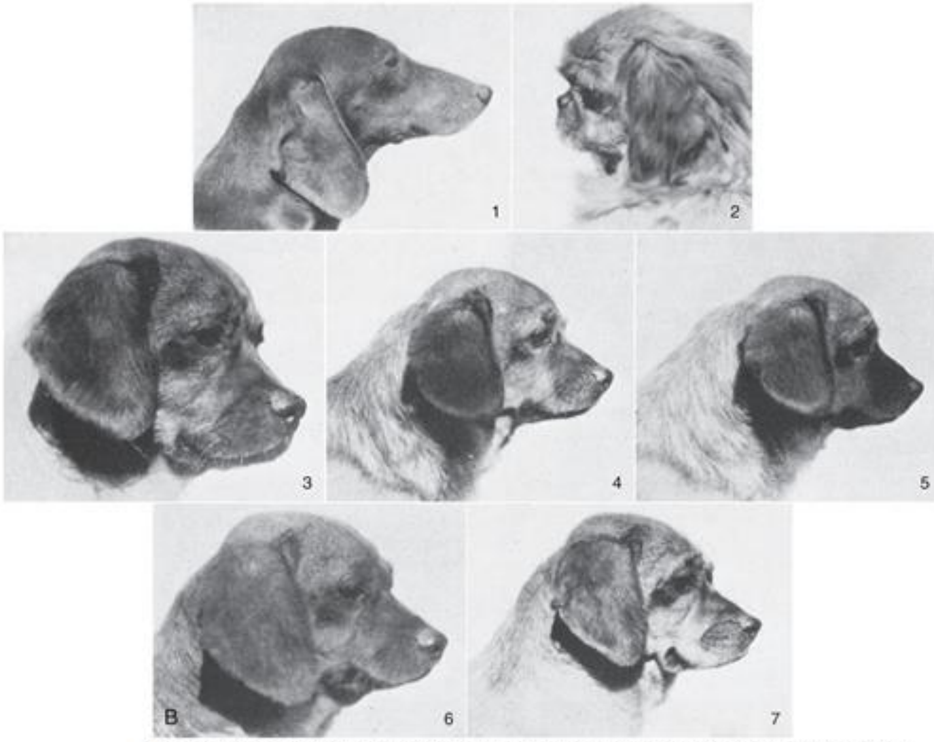
Charles R. Stockard of the Cornell Medical College undertook an investigation, starting about 1926, of the genetic and endocrinic basis for differences in form and behavior in dogs. He made crosses between many purebred dogs of various breeds and their F_1 and F_2 generations to study the physiognomy, skeleton, and endocrine organs of the resulting litters. Unfortunately, like Malcolm E. Miller, who started *Anatomy of the Dog*, Stockard died before his work was completed, but, from his extensive notes, photographs, and specimens, his colleagues were able to publish many of his findings as a monograph of the Wistar Institute (Stockard, 1941). What remains of the records and the extensive skeletal collection is now housed and cataloged in the Museum of Natural History on the campus of the University of Georgia in Athens and can be examined by appointment. Stockard's monumental study has left a legacy of numerical comparisons of body and skeletal parts, documented photographs of parents and hybrids, and many disarticulated skeletons. The purebred crosses he produced raise many questions as to the interactions of a large number of breed factors on external features and deformations of the skeleton.

Cartilage growth distortion (achondroplasia) in the skeleton may be restricted to the appendicular or the axial skeleton, or it may affect both. For example, the lower jaw is developmentally independent of the upper jaw. Thus brachygnathic, prognathic, and normal-muzzled pups may appear in the same litter. Such a disharmony between the superior (upper) and the inferior (lower) jaws usually results in malocclusion, difficulty in eating, uneven wear, and loss of teeth.

In many instances Stockard was able to produce and examine F_2 generations from back-crosses to parent stocks. These back-crosses indicated that reversions were common and that the head and tail ends of the axial skeleton often act independently. For example, the very extreme type of Bulldog head may be present in a dog with a long straight tail, or a dog with a normal long muzzle may have a short screw-tail. All F_1 hybrids of the screw-tailed Bulldog × straight-tailed Basset Hound develop long, straight tails. However, in the F_2 generation, the tail deformity reappears in several different patterns.



• **Fig. 1.2** A, Cross between the long-muzzled Dachshund and the short-muzzled Pekingese to show inheritance of head type. Dachshund female (1), Pekingese male (2), F1 hybrids (3 to 7). This Dachshund bitch was actually larger and heavier than the Pekingese stud.



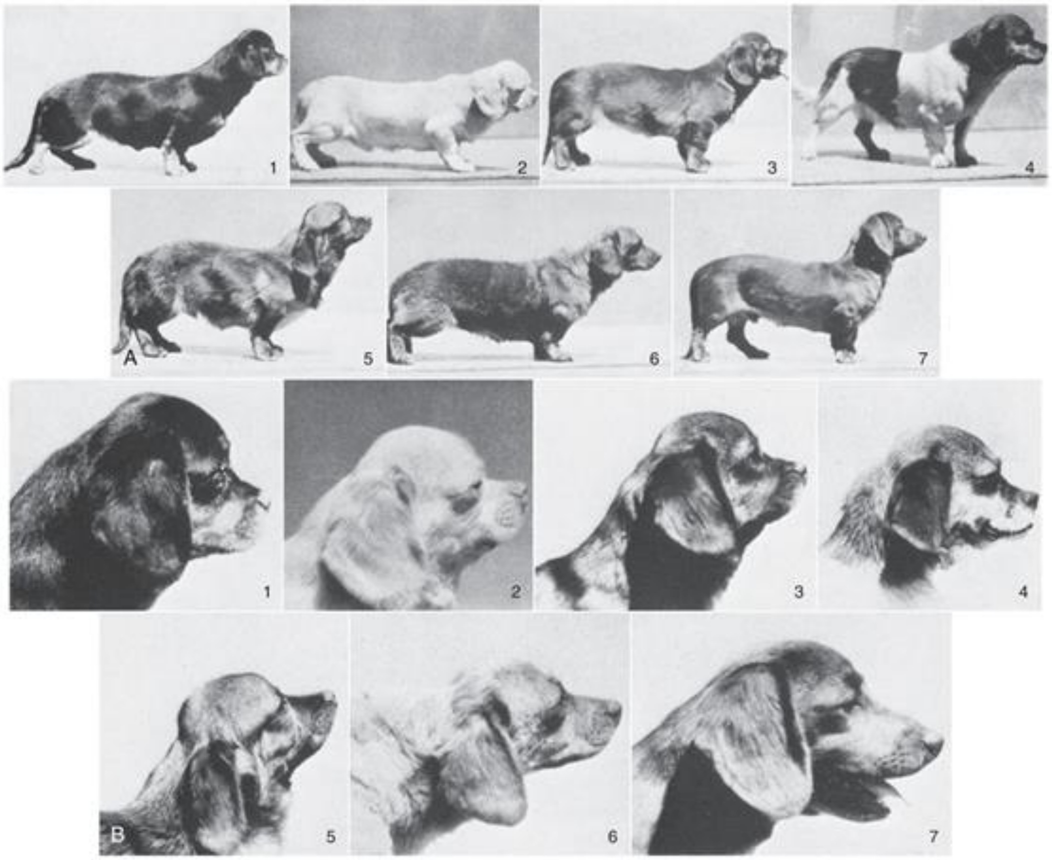
• **Fig. 1.2, cont'd** B, Close-up of the facial features of a Dachshund bitch and a Pekingese stud compared with the same first-generation hybrids as shown in Fig. 1.2A. Of the 22 F1 hybrids produced by several bitches, all were uniform in size and type irrespective of whether they were whelped from Dachshund or Pekingese dams. The hybrids were larger and more vigorous than either parent stock. (From Stockard CR, Johnson AL. The contrasted patterns and modifications of head types and forms in the pure breeds of dogs and their hybrids as the result of genetic and endocrinic reactions. In CR Stockard, editor, *The genetic and endocrinic basis for differences in form and behavior: American anatomical memoirs*, vol. 19, Philadelphia, 1941, Wistar Institute of Anatomy and Biology.)

Dachshund-Pekingese hybrids are good examples of genetic influences on variations in skull form (see Figs. 1.2 and 1.3). The Pekingese dog has a greatly reduced muzzle and a bulging forehead. This is probably a result of achondroplasia of the basicranium and the cartilaginous forerunner of the upper (superior) jaws, a condition similar to that seen in the Bulldog. The Asiatic origin of the Pekingese suggests descent from Chow-Chow ancestors, whereas the Bulldog was developed at a later date from European stock. Thus very different breeds of dog can have very similar mutations in various parts of the world, and, if selected, these mutations can be enhanced.

Because the dominant factor for achondroplasia in the appendicular skeleton results in a more severe shortening of the bones in Bulldog types than in Hounds, Stockard suggested that the "breed quality" of bone may depend on a large number of factors in the genetic constitution of the animal. Thus "Bulldog bone" and "Hound bone" may be more complex entities than we currently imagine.

Breeds of Dogs

The result of human intervention for more than two centuries has established genetic lines that kennel clubs have agreed to recognize as breeds. New breeds will continue to be developed and granted registry according to the rules of national kennel clubs. Not all breeds are granted recognition in all countries, and breed standards are changed from time to time. There were 153 breeds recognized by the American Kennel Club in the 20th edition of *The Complete Dog Book* (2006). This was revised to more than 200 breeds in *The New Complete Dog Book* (2017) and as listed online (akc.org). There are more than 300 breeds of dogs in the world, and each country has some distinctive breeds, as well as introduced breeds.



• Fig. 1.3 **A**, Second-generation Dachshund-Pekingese hybrids. Four F_1 bitches were mated with four F_1 studs and produced 47 pups. The F_2 hybrids varied considerably in size and color. None had a typical Pekingese coat, and none held the tail curled over the rump, which is characteristic of the Pekingese and other Asiatic dogs. All of the F_2 animals had short limbs. The large ears of the Dachshund were dominant. **B**, Close-up of the facial features of the same F_2 Dachshund-Pekingese hybrids as shown in Fig. 1.3A. None of the F_2 hybrids had the very short face of the Pekingese. The dental occlusion of F_2 hybrids varied greatly: a few showed superior and inferior jaws of about the same length with normal occlusion, approximately the same number were slightly undershot (mandibular incisors closing ahead of the superior incisors), and the most frequent condition was prognathism of the superior jaws and malocclusion. The long superior (maxilloincisive) jaw of the Dachshund was inherited independently of the short mandibular jaw of the Pekingese, resulting in a disharmony, which, in the extreme, allowed the tongue to hang out rostral to the chin and made feeding from shallow pans difficult. (From Stockard CR, Johnson AL. The contrasted patterns and modifications of head types and forms in the pure breeds of dogs and their hybrids as the results of genetic and endocrinic reactions. In CR Stockard, editor, *The genetic and endocrinic basis for differences in form and behavior: American anatomical memoirs*, vol. 19, Philadelphia, 1941, Wistar Institute of Anatomy and Biology.)

Australia still has a large population of wild Dingoes in the central and northern regions that often cross with domestic dogs (Corbett, 1995). New Guinea has an unknown number of wild "singing dogs," and, on various isolated Pacific Ocean islands, there are dogs that resemble Dingoes (Titcomb, 1969).

The Chinese were probably the earliest breeders of purebred dogs, several of which are still popular. Often there are several names for the same breed because the name may change when the dog is introduced into another country; thus the Borzoi is also known as the Russian Wolfhound, the German Shepherd Dog as the Alsatian, the Vizsla as the