**Physical properties of palladium**

| Property | Value |
|---|---|
| Atomic weight | 106.4 |
| Naturally occurring isotopes (percent abundance) | 102 (0.96) |
| | 104 (10.97) |
| | 105 (22.23) |
| | 106 (27.33) |
| | 108 (26.71) |
| | 110 (11.81) |
| Crystal structure | Face-centered cubic |
| Thermal neutron capture cross section, barns | 8.0 |
| Density at 25°C (77°F), g/cm$^3$ | 12.01 |
| Melting point, °C (°F) | 1554 (2829) |
| Boiling point, °C (°F) | 2900 (5300) |
| Specific heat at 0°C (32°F), cal/g | 0.0584 |
| Thermal conductivity, (cal·cm)(cm$^2$·s·°C) | 0.18 |
| Linear coefficient of thermal expansion, ($\mu$in./in./)/°C | 11.6 |
| Electrical resistivity at 0°C (32°F), $\mu\Omega$-cm | 9.93 |
| Young's modulus, lb/in.$^2$, static, at 20°C (68°F) | $16.7 \times 10^6$ |
| Atomic radius in metal, nm | 0.1375 |
| Ionization potential, eV | 8.33 |
| Binding energy, eV | 3.91 |
| Pauling electronegativity | 2.2 |
| Oxidation potential, V | −0.92 |

gold. Other consumer applications are in automobile exhaust catalysts and jewelry. *See* INTEGRATED CIRCUITS.

Palladium supported on carbon or alumina is used as a catalyst for hydrogenation and dehydrogenation in both liquid- and gas-phase reactions. Palladium finds widespread use in catalysis because it is frequently very active under ambient conditions, and it can yield very high selectivities. Palladium catalyzes the reaction of hydrogen with oxygen to give water. Palladium also catalyzes isomerization and fragmentation reactions. *See* CATALYSIS.

Halides of divalent palladium can be used as homogeneous catalysts for the oxidation of olefins (Wacker process). This requires water for the oxygen transfer step, and a copper salt to reoxidize the palladium back to its divalent state to complete the catalytic cycle. *See* HOMOGENEOUS CATALYSIS; TRANSITION ELEMENTS. D. Max Roundhill

Bibliography. G. W. Gribble and J. J. Li, *Palladium in Heterocyclic Chemistry*, Pergamon, 2000; F. R. Hartley, *Chemistry of Platinum and Palladium*, 1973; J. Tsuji (ed.), *Palladium in Organic Synthesis (Topics in Organometallic Chemistry)*, Springer, 2005; J. Tsuji, *Palladium Reagents and Catalysts: New Perspectives for the 21st Century*, Wiley, 2d ed., 2004.

## Palpigradi

An order of rare arachnids comprising 21 known species from tropical and warm temperate regions. American species occur in Texas and California. All are minute, whitish, eyeless animals, varying from 0.03 to 0.11 in. (0.7 to 3 mm) in length, that live under stones, in caves, and in other moist, dark places. The elongate body terminates in a slender multisegmented flagellum set with setae. In a curious reversal of function, the pedipalps, the second pair of head appendages, serve as walking legs. The first pair of true legs, longer than the others and set with sensory setae, has been converted to tactile appendages which are vibrated constantly to test the substratum. *See* ARACHNIDA. Willis J. Gertsch

## Palynology

The study of pollen grains and spores, both extant and extinct, as well as other organic microfossils. Although the origin of the discipline dates back to the seventeenth century, when modern pollen was first examined microscopically, the term palynology was not coined until 1944.

The term palynology is used by both geologists and biologists. Consequently, the educational background of professional palynologists may be either geologically or biologically based. Considerable overlap exists between some areas of the fields, however, and many palynologists have interdisciplinary training in both the earth and life sciences. Palynologists use a range of sophisticated methodologies and instruments in studying both paleopalynological and neopalynological problems, but the utilization of modern microscopy is fundamental in both subdisciplines.

Palynologists study microscopic bodies generally known as palynomorphs. These include an array of organic structures, each consisting of a highly resistant wall component. Examples include acritarchs and chitinozoans (microfossils with unknown affinities), foraminiferans (protists), scolecodonts (tooth and mouth parts of marine annelid worms), fungal spores, dinoflagellates, algal spores, and spores and pollen grains of land plants. This discussion will focus on the palynomorphs produced by land plants, beginning with a general description of pollen grains and spores and then providing an overview of the primary areas of investigation within neo- and paleopalynological subdisciplines. *See* MICROPALEONTOLOGY.

### Pollen Grains and Spores: An Overview

Spores and pollen grains are reproductive structures and play a paramount role in the life history of land plants. The sporophyte generation of nonseed-bearing plants (ferns, for example) produces single-celled spores that ultimately germinate to grow into the haploid gametophyte generation. Homosporous species produce a single type of spore, whereas heterosporous species produce two spore types. Microspores germinate and grow into "male" sperm-producing microgametophytes, and megaspores develop into "female" egg-producing megagametophytes. The gametophytes of most nonseed plants are multicellular and proliferate outside the spore wall during development. All seed-bearing plants

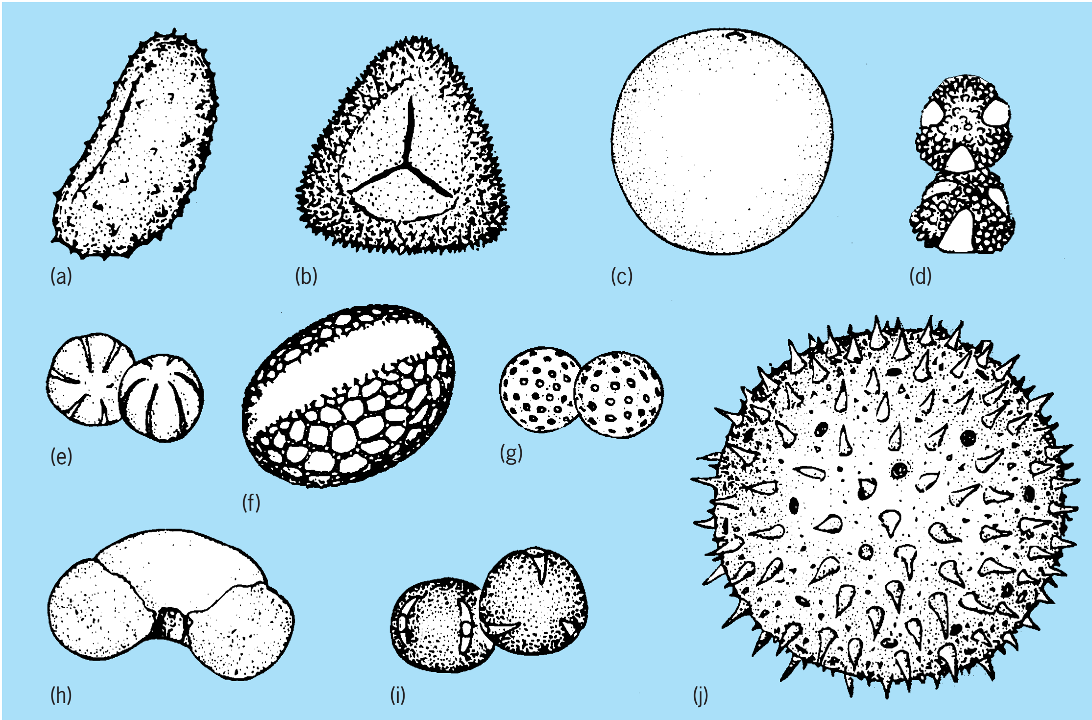


**Fig. 1. Pollen and spore morphology, (*a*, *b*) Spores. (*c–j*) Pollen grains. (*After Y. Iwanami, T. Sasakuma, and Y. Yamada, Pollen: Illustrations and Scanning Electron Micrographs, Kodansha and Springer, 1988*)**

(gymnosperms and angiosperms) are heterosporous, and their pollen represents the microgametophyte generation. Pollen grains consist of just three to a few cells, and these remain within the microspore wall, where they originally developed. *See* REPRODUCTION (PLANT).

Spores and pollen grains are formed in multiples of fours following meiotic divisions. During development, the four are united into a tetrad that, in most plants, subsequently dissociates into the four individual propagules. In nonseed plants, each spore commonly bears a mark on its proximal surface indicating where it made contact with the others at the center of the tetrad. In most spores this external mark is either straight or Y-shaped (**Fig. 1**), and it is typically characterized by a suture that spans the spore wall and is the site through which germination occurs. In contrast, most pollen grains lack sutures and germinate through thin areas in the wall, or apertures. Apertures are typically located in either a distal or an equatorial position. Common aperture types include elongate furrows, pores, and furrows with a central pore. Aperture type, number, and position are important systematic characters by which fossil and modern taxa can be compared. Other descriptively and systematically relevant characters include size, shape, presence and structure of air bladders, surface ornamentation, and wall ultrastructure. *See* POLLEN.

The wall of spores and pollen grains is known collectively as the sporoderm (or "skin of the spore") and actually consists of two distinct walls (**Fig. 2**). The inner wall, or intine, is primarily composed of cellulose and pectin; as such, it is similar to most other plant cell walls. The outer wall, or exine, is principally composed of sporopollenin, a chemically enigmatic macromolecule that is resistant to biological decay and geological degradation. The exine is further characterized by several ultrastructural layers and an array of sculptural elements. It is the very presence of the exine that allows for the spectacular preservation of pollen and spores in the fossil record.

### Neopalynology

This discussion focuses on several subdisciplines of neopalynology, including taxonomy, genetics, and evolution; development, functional morphology, and pollination; aeropalynology; and melissopalynology.

**Taxonomy, genetics, and evolution.** Taxonomy and systematics are concerned with classifying organisms into hierarchical ranks that reflect evolutionary, or phylogenetic, relationships. Pollen and spore morphology is important systematically, with particular features characteristic of different taxonomic ranks. For example, distinguishing characters may include aperture type for a family, different ornamentation patterns for its subordinate genera, and variation in exine ultrastructure for its congeneric species. Palynological characters are especially useful systematically when evaluated in conjunction with other characters (for example, plant morphological and molecular characters). Cladistics is one technique that has employed such an integrated approach. Cladistic analyses are based on numerical algorithms

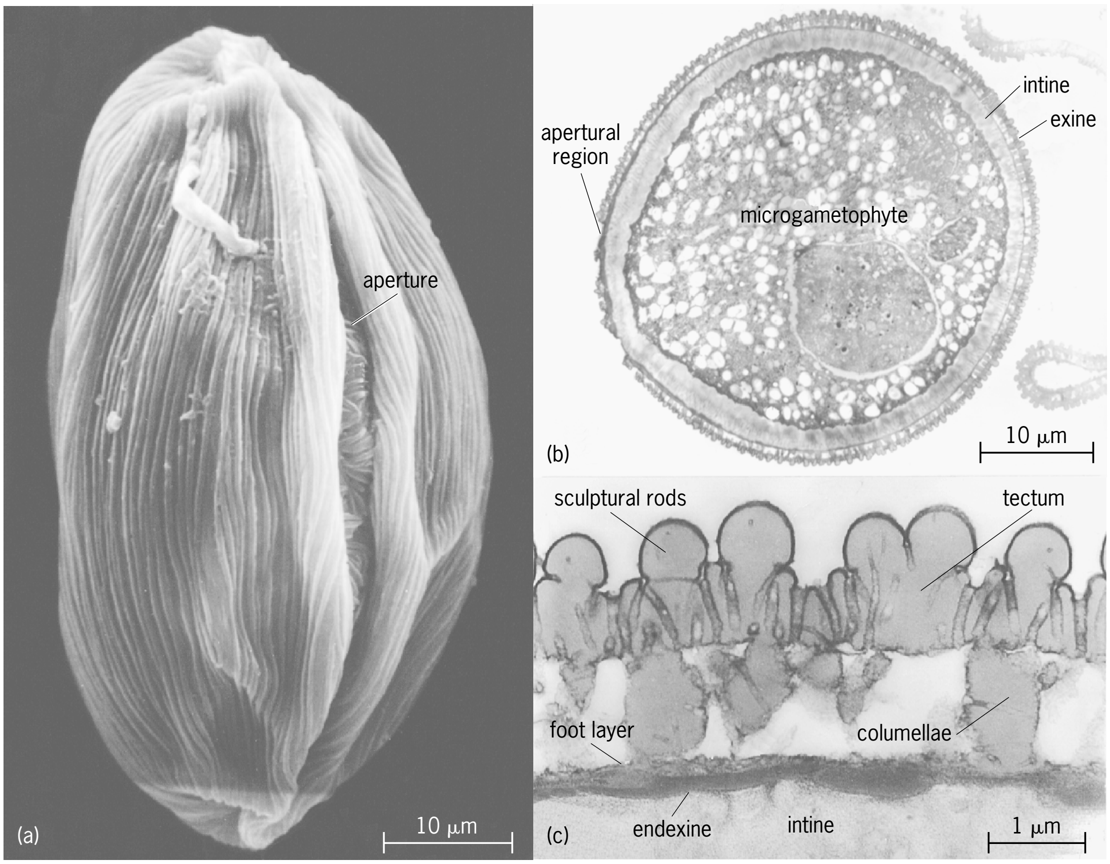


**Fig. 2. Pollen morphology and sporoderm ultrastructure of *Cabomba caroliniana* (Cabombaceae), a modern water lily and primitive flowering plant. (*a*) Distal view of grain. (*b*) Cross section through the entire grain. (*c*) Cross section through the sporoderm.**

that produce trees, or cladograms, demonstrating phylogenetic lineages among the organisms examined. *See* PLANT EVOLUTION; PLANT TAXONOMY.

Assessing pollen flow is another approach used to study evolutionary questions. Because pollen is the sperm-producing generation, the patterns and rates of pollen transfer are important factors in determining the spread of genes throughout a population. Competition can occur among reproductive organs, and pollen flow may be influenced by the correlation of pollen characters with those of reproductive organs. For example, the ovulate, or female, cones of some gymnosperms, such as pines, are aerodynamically adapted for entraining airborne pollen grains that themselves have particular aerodynamic characters, such as extended air bladders. Furthermore, competition may exist among individual pollen grains. Following pollination in some flowering plants, intraspecific variation can result in the grains of a more reproductively fit plant producing faster-growing pollen tubes than others of the same species. *See* POPULATION GENETICS.

**Development, functional morphology, and pollination.** In most seed plants, a layer of callose, a carbohydrate, surrounds the entire tetrad and separates each immature pollen grain during development. Formation of the pollen wall and positioning of the aperture begin while each grain is encased within the callose layer. Both the internal ultrastructure and the sculptural surface ornamentation of the outer pollen wall, the exine, are dependent upon the depositional pattern of the chemical that makes up the exine, sporopollenin. Sporopollenin is primarily derived from the developing pollen grain, but can also be released from a specialized layer of cells known as the tapetum, which surrounds the developing pollen grains. The inner pollen wall, or intine, is synthesized last.

When the tapetum breaks down, or undergoes programmed cell death (apoptosis), it also releases several proteins, lipids, and other substances that become isolated within the spaces and on the surface of the developing pollen wall. In flowering plants, many tapetum-derived proteins function as recognition molecules in pollination systems and are important in determining the extent of compatibility of a particular pollen grain on a floral stigma. Other pollen-derived proteins become stored within the intine and may also be involved in compatibility-incompatibility reactions. Several tapetal lipids also play important roles in pollination. Pollenkitt, for example, functions in pollen adhesion and acts as a visual and olfactory attractant. Additionally, pollen morphology and exine architecture may be correlated with pollination systems. For example, the pollen of wind-pollinated plants is typically smooth, has a thin exine, lacks pollenkitt, and may have air bladders, whereas that of animal-pollinated plants is commonly highly ornamented and bears pollenkitt. *See* FERTILIZATION.

**Aeropalynology.** Aeropalynology is the study of pollen grains and spores that are dispersed into the atmosphere. Wind-pollinated plants typically produce copious amounts of pollen, thereby enhancing successful pollinations. The abundance of airborne pollen commonly causes allergic reactions in a large proportion of the human population. Pollinosis, allergen rhinitis or hay fever, is elicited when allergen-containing pollen makes contact with the mucous membranes lining the nose, trachea, or bronchi, and the cornea of the eye. Allergens leach out of the pollen and bind to immunoglobulin E antibodies. The antibodies are linked to mast cells that release histamine and other inflammatory chemicals, producing allergy symptoms. Ironically, the allergens that induce pollinosis include many of the same compatibility-incompatibility, recognition proteins involved in pollination.

Knowledge of the temporal, seasonal, and environmental aspects of pollen dispersal is also important in understanding and avoiding hay fever. Flowering time and season vary widely for different plants, and the release of airborne pollen is typically inhibited by high humidity or rain. To monitor risks of pollinosis, the diversity and quantity of various pollen types are assessed by filtering the air throughout the year. *See* ALLERGY; ANTIBODY.

**Melissopalynology.** Honeybees are the primary pollinators of many flowering plants. Honeybees, and other bees, visit flowers to collect nectar and large quantities of pollen (pollen loads), both of which are used as food sources for developing larvae. Melissopalynologists analyze bee pollen loads and the pollen component within honeys. Although bees primarily produce honey from nectar, 1 mL of honey may contain more than 20,000 pollen grains. The foraging behavior of bees can be determined by microscopically examining their pollen loads and taxonomically identifying the pollen constituents. Honey purity can also be assessed by examining the diversity of pollen grains found within the honey.

## Paleopalynology

The main fields of study within paleopalynology are discussed below. The areas addressed involve paleobotany; past vegetation and climate reconstruction; geochronology and biostratigraphy; and petroleum and natural gas exploration.

**Paleobotany.** Fossil pollen and spores typically consist of only fossilization-resistant exine layers. However, these propagules did at one time contain both gametophytic cells and pectocellulosic intines, and functioned in a similar way to that of their extant counterparts. Fossil pollen and spores can be distinguished into two categories based on the general way in which the palynomorphs are preserved. *Sporae dispersae* grains are those occurring within sediments in a dispersed condition; in most cases, information about the parent plants is unavailable. Investigation of dispersed grains is especially important in the fields addressed below. *In situ* grains occur within intact, megafossil reproductive organs (like flower anthers); as such, morphological data from the parent plant are available and provide for better systematic evaluation. Studies of *in situ* pollen or spores also afford the opportunity to evaluate and interpret fossils in a biological context. For example, developmental information can be inferred by examining pollen-containing organs preserved in various ontogenetic stages, and ancient pollination events, such as pollen germination and pollen tube growth, can be assessed when grains are recovered on receptive structures. These types of data allow paleobotanists to better understand and reconstruct the complete life history of fossil plants.

**Past vegetation and climate reconstruction.** A significant focus of palynology involves reconstructing the Earth's vegetational history since the last major glaciation event, within the past 10,000 years, or during the Holocene Epoch. This area of postglacial palynology is known as pollen analysis and primarily includes the study of palynomorphs from lake sediments and peat deposits. Sediments are obtained by several methods (mostly core sampling), and palynomorph diversity, distribution, and abundance are plotted on pollen profiles. Pollen analysis can provide historical information regarding both individual taxa and larger plant communities, including data about vegetational succession. Such analyses must consider all possible sources of palynomorphs and take precaution during sample preparation to avoid contamination with extant pollen because many modern taxa may have also existed in the Holocene. However, because of the excellent preservation potential of key palynological characters, such as those described above, fossil pollen grains yield a high degree of taxonomic resolution.

Because many plants inhabit areas exhibiting particular environmental regimes and have limited geographic distributions, palynological analyses contribute to an understanding of paleoclimatic conditions. For example, a palynoflora may be indicative of source vegetation occupying a polar, temperate, subtropical, or tropical habitat. Therefore, palynological information can also be used in conjunction with other megafossil indicators of climate, such as tree ring data. *See* POSTGLACIAL VEGETATION AND CLIMATE.

**Geochronology and biostratigraphy.** Palynological analyses play a significant role in age determinations of rocks, or geochronology. Dating the geological ages of palynomorph-bearing rocks is dependent upon knowledge of the stratigraphic ranges of extinct plant groups. Because different plant groups are known to have restricted geological time ranges, the pollen and spores produced by their plants are characteristic of particular ages and may serve as index fossils. Comparisons may be made against well-established reference palynomorphs, or index fossils, and palynofloras. Palynological dating techniques are especially useful when correlated with ages of rocks that have been radiometrically dated. *See* FOSSIL; INDEX FOSSIL.

Comparisons of palynomorphs within a given rock section from one site with those of units from other localities are important in documenting stratigraphic similarities among the rock sections, even if the sections exhibit different thicknesses and lithologies. When the occurrence, diversity, and abundance of fossils (palynomorphs, megafossils, or both) are used to correlate geographically separated rock sequences, this is known as biostratigraphy. Historically, biostratigraphic correlation has provided supporting evidence for continental drift theory. For example, some present-day continents, such as Antarctica, Africa, and India, have distinguishing index fossils, of various ages, that are present on these continents and absent from others. These intercontinental correlations are supportive of the previous existence of the single Southern Hemisphere landmass known as Gondwana. *See* PALEOGEOGRAPHY.

**Petroleum and natural gas exploration.** Economically, palynological biostratigraphy is an important technique used in the exploration for natural gas and petroleum. Biostratigraphic correlations in this context are conducted on a smaller scale, typically within an existing oil field. Besides identifying the locality, it is critical to determine the appropriate level at which to drill. For this endeavor, the palynologist is not necessarily interested in references of depth, but in important palynological indicators of known oil and gas production levels. In addition to the identification of key index fossils, a color evaluation is relevant. Following standard preparations, palynomorphs exhibit a range of colors that indicate their degree of geothermal alteration. Certain palynomorph colors are characteristic of rocks with either oil or gas reservoirs. *See* PALEOBOTANY; STRATIGRAPHY.

Jeffrey M. Osborn

Bibliography. K. Faegri, P. Kaland, and K. Krzywinski, *Textbook of Pollen Analysis*, 4th ed., Wiley, Chichester, 1989; M. M. Harley, C. M. Morton, and S. Blackmore (eds.), *Pollen and Spores: Morphology and Biology*, Royal Botanic Gardens, Kew, 2000; J. Jansonius and D. C. McGregor (eds.), *Palynology: Principles and Applications*, vols. 1–3, American Association of Stratigraphic Palynologists, Salt Lake City, 1996; R. O. Kapp, O. K. Davis, and J. E. King, *Ronald O. Kapp's Pollen and Spores*, 2d ed., American Association of Stratigraphic Palynologists, College Station, 2000; S. Nilsson and J. Praglowski (eds.), *Erdtman's Handbook of Palynology*, 2d ed., Munksgaard, Copenhagen, 1992; A. Traverse, *Paleopalynology*, Unwin Hyman, Boston, 1988.

## Pancreas

A composite gland in most vertebrates, containing both exocrine cells—which produce and secrete enzymes involved in digestion—and endocrine cells, arranged in separate islets which elaborate at least two distinct hormones, insulin and glucagon, both of which play a role in the regulation of metabolism, and particularly of carbohydrate metabolism. This article discusses the anatomy, histology, embryology, physiology, and biochemistry of the vertebrate pancreas. *See* CARBOHYDRATE METABOLISM.

### Anatomy

The pancreas is a more or less developed gland connected with the duodenum. It can be considered as an organ which is characteristic of vertebrates.

**Chordates and lower vertebrates.** In *Branchiostoma* (*Amphioxus*) a pancreatic anlage is found in young stages as a thickening of the gut caudal to the liver. The pancreas of cyclostomes, arising from the gut epithelium or from the liver duct, seems to be purely endocrine; it degenerates in later stages of development.

A true pancreas is found in selachians, with an exocrine portion opening into the intestine and an endocrine portion represented by cellular thickenings of the walls of the ducts.

**Higher vertebrates.** The ganoids (palaeopterygian fishes) show a diffuse pancreas—its principal mass lying between the gut and the liver—in which typical islets of Langerhans are observed. The pancreas of teleosts is either of the massive or dispersed type. Many species, such as the pike, show enormous islets of Langerhans, 10 × 5 mm, from which J. McLeod (1922) extracted insulin. The existence of a pancreas in dipneusts, such as *Protopterus*, is doubtful.

The compact pancreas of the amphibians is located in the gastrohepatic omentum and extends toward the hilus of the liver and along the branches of the portal vein. It develops from three anlagen, one dorsal and two ventral, the evolution of which varies from one species to another. The dorsal anlage would be the only source of endocrine islands. The pancreas of reptiles is very similar to that of amphibians; the number of excretory ducts varies from one to three.

In birds, the massive pancreas always lies in the duodenal loop. It develops from many dorsal and two ventral thickenings of the duodenal epithelium; one (sometimes two) excretory duct persists. The median portion of the dorsal anlage develops into a single mass which subdivides into typical islets of Langerhans. A complete ring of pancreatic tissue surrounds the portal vein.

The pancreas of mammals shows the same variations as in the fishes. The extremes are the unique, massive pancreas of humans, and the richly branched organ of the rabbit. Usually, the main duct, the duct of Wirsung, opens into the duodenum very close to the hepatic duct. Many rodents have this opening of the pancreatic duct as far as 40 cm (15.7 in.) from the hepatic duct. In humans, the pancreas weighs about 70 g (7.5 oz). It can be divided into head, body, and tail. A portion called the uncinate process is more or less completely separated from the head. Accessory pancreases are frequently found anywhere along the small intestine, in the wall of the stomach, and in Meckel's diverticulum. *See* DIGESTIVE SYSTEM.

### Histology

The pancreatic parenchyma is formed by two elements; one is the exocrine tissue of which the