Osborn, J. M. 1997. Palynology. *In: McGraw-Hill Encyclopedia of Science and Technology*, 8th Edition, Volume 13, pages 70-74. McGraw-Hill, New York.

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 secton, 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, (μin./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)	16.7×10^6
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

are being used by organic chemists to develop new strategies in organic synthesis. *See* CARBONYL; DELOCALIZATION; METAL CARBONYL; ORGANOMETALLIC COMPOUND.

Extraction. Palladium occurs with the other platinum metals, and the concentrate is dissolved in a mixture of nitric acid and hydrochloric acid. The concentrate is obtained either by a series of operations based on selective precipitation or by solvent extraction methods. Addition of ammonium chloride leaves salts of tetrachloropalladate ($PdCl_4^{2-}$) in solution, while causing any platinum to precipitate as ammonium hexachloroplatinate [$(NH_4)_2PtCl_6$]. Precipitation of dichlorodiammine palladium [$PdCl_2(NH_3)_2$] followed by ignition gives the metal as palladium sponge.

Uses. The major applications of palladium are in the electronics industry, where it is used as an alloy with silver for electrical contacts or in pastes in miniature solid-state devices and in integrated circuits. Palladium is widely used in dentistry as a substitute for gold. Other consumer applications are in automobile exhaust catalysts and jewelry. *See* INTEGRATED CIRCUITS.

Some palladium-silver alloys are used for electrical contacts. Those containing above 60% palladium are strongly resistant to tarnishing when exposed to sulfur. The palladium-silver-gold alloys offer a series of noble brazing materials covering a wide range of melting temperatures. A palladium-silver alloy can be used as a diffusion septum for the separation of hydrogen from gas mixtures. *See* BRAZING.

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

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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.

Palynology can be classified into two broad fields, paleopalynology and neopalynology. Consequently, the educational background of professional palynologists may be either geologically or biologically based. However, considerable overlap exists between some areas of the fields, and many palynologists have interdisciplinary training in both the earth and life sciences. Although a range of methodologies and instruments are employed in both subdisciplines, the utilization of contemporary microscopy is fundamental.

Palynologists study microscopic bodies generally known as palynomorphs. These include an array of organic entities, 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. Focusing on land plant–produced pollen grains and spores, this discussion will begin with a consideration of these palynomorphs and then provide an overview of the primary areas of investigation within respective palynological subdisciplines. *See* MICROPALEONTOLOGY.

Spores and pollen grains are reproductive propagules and play a paramount role in the life history of land plants. The sporophyte generation of nonseed plants (for example, ferns) produces single-celled spores that give rise to the haploid gametophyte generation. Homosporous plants produce a single type of spore, whereas heterosporous plants produce two spore types. Microspores give rise to microgametophytes, and megaspores develop into megagametophytes. The gametophytes of most nonseed plants are multicellular and proliferate outside the spore wall during development. By comparison, all seed plants (gymnosperms and angiosperms) are heterosporous, and pollen represents the microgametophyte. Pollen grains consist of only three to several cells, and these remain contained within the microspore wall, within which they have 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 individual propagules. Each propagule commonly bears a mark on its proximal surface indicating where it made contact with the others within the center of the tetrad. In spores, the external mark is typically characterized by a suture that spans the spore wall and is the site through which germination occurs. Most spores have either a straight or a Y-shaped mark (**Fig. 1**). In contrast, most pollen grains lack sutures and germinate through thin areas, or apertures, in the wall. Apertures are typically located in either a distal or an equatorial position. Common types include elongate furrows, pores, and furrows with a central pore. Aperture type, number, and position are important systematic characters regarding both extant and fossil pollen. Other descriptively and systematically relevant characters include size, shape, presence and structure of air bladders, surface ornamentation,

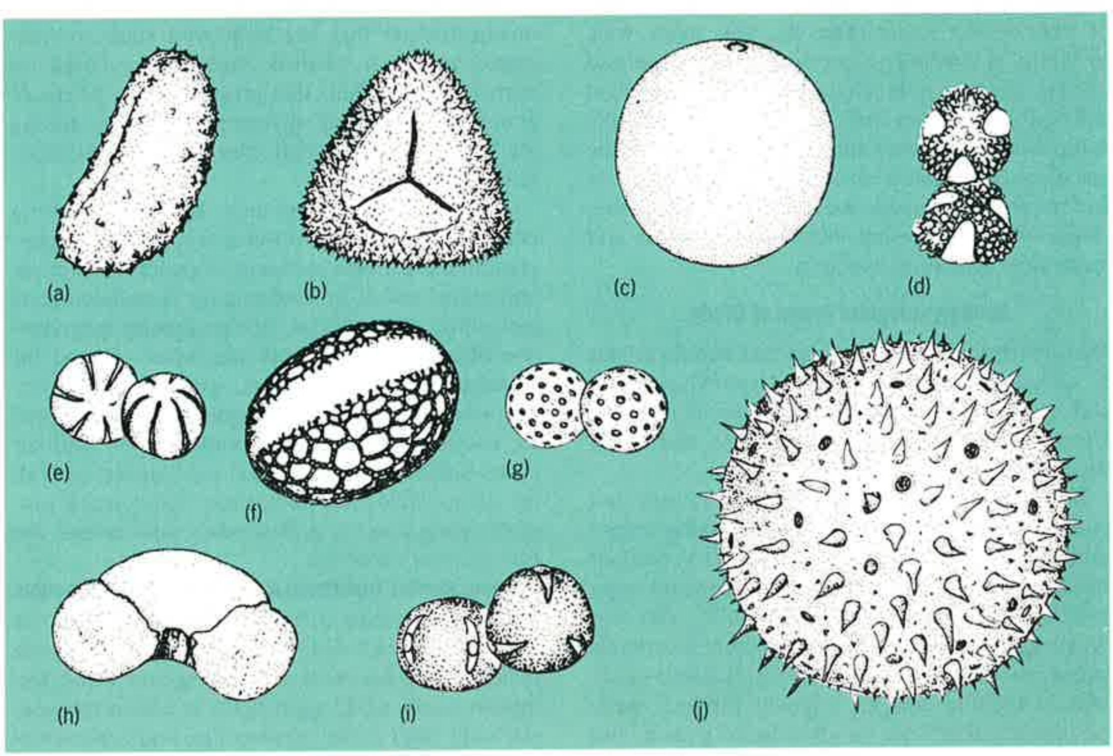

Fig. 1. **Pollen and spore morphology. (*a, b*) Spores. (*c–j*) Pollen grains. (*After Y. Iwanami, T. Sasakuma, and Y. Yamada, Pollen: Illustrations and Scanning Electron Micrographs, Kodansha and Springer, 1988*)**

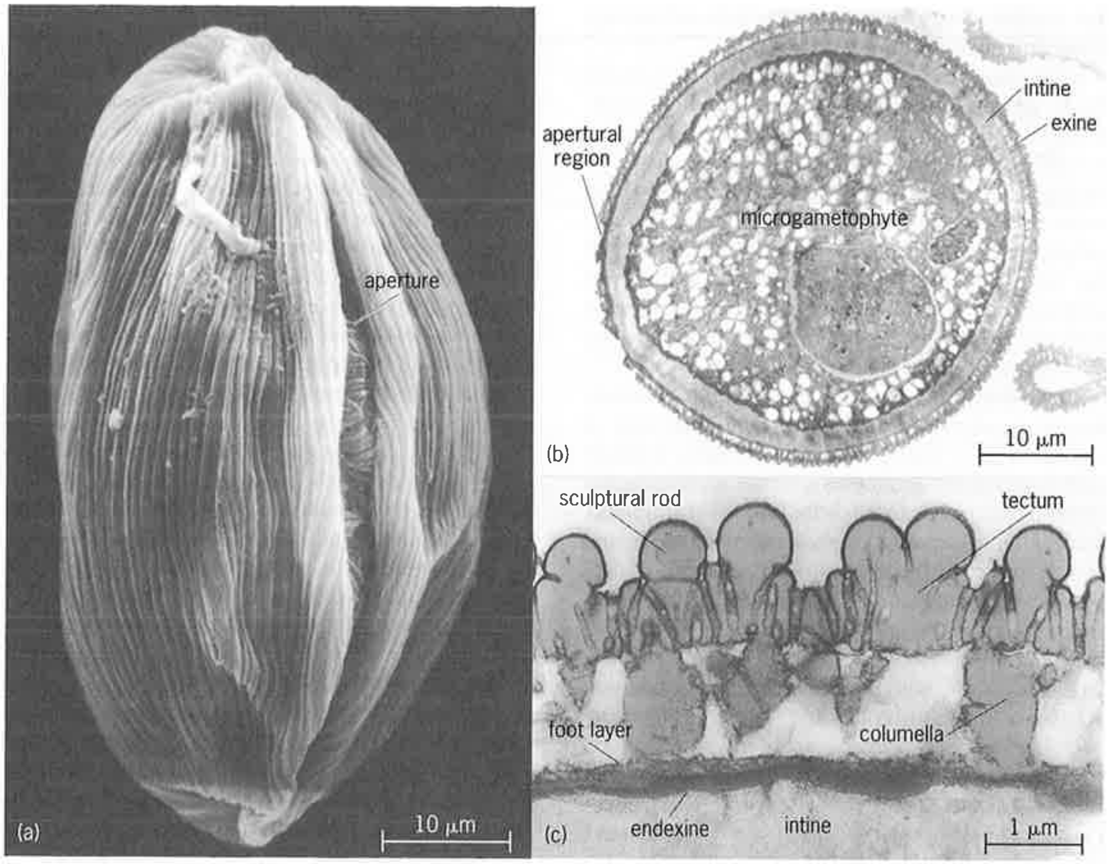

Fig. 2. Pollen morphology and sporoderm ultrastructure of *Cabomba caroliniana* (Cabombaceae). (*a*) Distal view of grain. (*b*) Section through the entire grain. (c) Section through the sporoderm.

and wall ultrastructure. *See* POLLEN.

The wall of spores and pollen grains is known collectively as the sporoderm 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 infrastructural layers and an array of sculptural elements.

Neopalynological Areas of Study

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 infrastructure for its congeneric species. Palynological characters are especially useful systematically when evaluated in conjunction with other characters (for example, gross-plant morphological and molecular characters). Cladistics is one technique that has employed such an integrated approach. Cladistic analyses are based on numerical algorithms that produce trees, or cladograms, demonstrating phylogenetic lineages among the organisms examined. *See* PLANT EVOLUTION; PLANT TAXONOMY.

Another evolutionary area involves assessing pollen flow. As pollen is the sperm-producing generation, the patterns and rates of pollen transfer are important factors in determining population-level gene flow. Competition occurs among reproductive organs; some flowers are better adapted for particular animal pollinators, whereas some gymnosperm cones are aerodynamically well adapted for entraining particular airborne pollen. Furthermore, pollen competition may exist among individual grains; following pollination, some grains produce faster-growing pollen tubes than others. *See* POPULATION GENETICS.

Development, functional morphology, and pollination. In most seed plants, a callose special wall surrounds the entire tetrad and separates each developing pollen grain. Aperture positioning and exine formation begin while each grain is within the special wall. Both exine infrastructure and ornamentation are dependent upon the depositional pattern of sporopollenin. The outer exine layer, or ectexine, is deposited on a glycocalyx template, or primexine. Sporopollenin may be derived either from the developing pollen grain or from orbicules released from the innermost anther wall layer, or tapetum. The inner exine layer, or endexine, is initiated second, with deposition occurring on discrete lamellae. The pectocellulosic intine is synthesized last.

Tapetum degradation also involves liberation of several proteins, lipids, and other substances that become isolated within the spaces and on the surface of the developing exine. Many tapetal-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 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. 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.

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. In addition to enhancing successful pollinations, the abundance of airborne pollen commonly causes allergic reactions in a large proportion of the human population. Such pollinosis, allergin 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 angiosperms. Bees, honeybees, and others 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 milliliter may contain more than 20,000 grains. The foraging behavior of bees can be determined by microscopically examining their pollen loads and taxonomically identifying the pollen constituents.

Paleopalynological Areas of Study

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; as such, concomitant gross morphological data 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 ascertained 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.

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.

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 various groups are known to have restricted time ranges, the pollen and spores produced by their plants are characteristic of particular ages. Although correlative megafossil information is important when it exists, such investigations can also be conducted on nonfossiliferous rocks. 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 SEEDS AND FRUITS; 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. Using fossils and palynomorphs or megafossils (or both) to correlate geographically separated rock sequences 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 characteristic index fossils, of various ages, that are 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 salient palynological indicators of known oil and gas production levels. In addition to the identification of principal 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.

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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