

maximum power conversion point in the available current-voltage ( $I$ - $V$ ) output plane exists for any photovoltaic device operating in a given photon flux. Device efficiency is defined as this maximum power output divided by the incident radiative power. The maximum power is usually expressed as the product of  $V_{oc}$ ,  $J_{sc}$ , and FF, the fill factor, which is the ratio of the area in the  $I$ - $V$  plane defined by the maximum power output divided by the area defined by the product of  $V_{oc}$  and  $J_{sc}$ .

**Alternative materials.** While this explanation of the photovoltaic effect has been given in terms of the familiar crystalline silicon  $pn$  photovoltaic device, many alternative materials and device structures have been explored since the discovery of the photovoltaic effect in the nineteenth century. In fact, the first all-solid-state photovoltaic device appears to have used a semiconducting layer of glassy selenium illuminated through a semitransparent gold electrode in what would now be considered a metal-semiconductor Schottky barrier configuration.

Amorphous materials tend to have low carrier mobilities and, therefore, short diffusion lengths of minority carriers prior to recombination. Thus, devices utilizing amorphous materials tend to require internal electric field-induced carrier drift in order to achieve efficient carrier separation. Fortunately, the optical absorption of amorphous films can be matched so well to the incident solar radiation that devices as thin as 0.5 micrometer can be utilized, thus permitting the presence of electric fields throughout most of the absorbing layer thickness. See AMORPHOUS SOLID.

**Multiple-layered devices.** Various multiple-layered device configurations based on doped and undoped alloys of amorphous silicon have been developed for photovoltaic devices used in applications ranging from solar watches and calculators to remote power generators. The photovoltaic effect in these devices is particularly intriguing since it is possible to build up so-called tandem devices by stacking one device electrically and optically in series above another. In addition to the increased voltage and concomitant reduction in the required current-carrying capability of electrode grid structures, such devices permit, in principle, an increased efficiency of solar photovoltaic energy conversion. This is achieved by matching the band gap in the upper device with the higher-photon-energy portion of the solar spectrum, thereby achieving a higher voltage, while matching the lower device with the lower-photon-energy portion, thereby utilizing a higher portion of these lower-energy photons than could be efficiently achieved in a single device.

**Other configurations and phenomena.** The junction in photovoltaic devices, normally configured to lie in the plane normal to the incident radiation, can be contoured to promote significant lateral drift of carriers to point-source contacts on the back surface of the device, where they do not occlude any of the incident radiation. Such device structures, when they also include surface texturing to enhance trapping of incident photons, can increase solar conver-

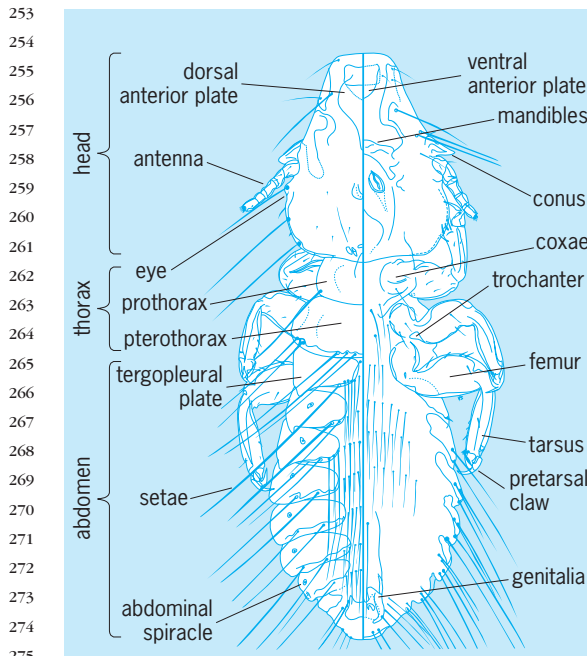
sion efficiency. Finally, while band bending and internal fields are implicitly combined to create rectifying junctions in a single material (homojunctions), these two charge-separating mechanisms can be utilized independently, in principle, in heterojunctions, which are junctions created between two dissimilar semiconductor materials. Extension of the thin-film deposition techniques used to create tandem amorphous devices appears to have the potential for creating structures, including epitaxial structures, in which the Fermi level and the conduction and valence band energies are independently controllable throughout the device thickness. Such control could permit the consideration of practical photovoltaic device structures which today exist only as theoretical possibilities. See SEMICONDUCTOR HETEROSTRUCTURES; SOLAR CELL.

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Bibliography. B. K. Das and S. N. Singh (eds.), *Photovoltaic Materials and Devices*, 1985; A. L. Fahrenbruch and R. H. Bube, *Fundamentals of Solar Cells*, 1983; H. J. Moller, *Semiconductors for Solar Cells*, 1993; L. D. Partain (ed.), *Solar Cells and Their Applications*, 1995; S. M. Sze, *Physics of Semiconducting Devices*, 2d ed., 1981; R. J. Van Overstraeten and R. P. Mertens, *Physics, Technology and Use of Photovoltaics*, 1986; K. Zweibel, *Harnessing Solar Power: The Photovoltaics Challenge*, 1990.

## Phthiraptera

An order of small wingless insects, permanently parasitic on mammals and birds. The Phthiraptera are one of approximately 30 major groups of insects and can be divided into four suborders, three of which (the Amblycera, Ischnocera, and Rhynchophthirina) are known as chewing or biting lice, and the fourth (the Anoplura) as sucking lice. Amblycera and Ischnocera are found on both mammals and birds, whereas species of Rhynchophthirina and Anoplura are confined to mammals. In total there are approximately 5000 known species, of which just under 70% are recorded from a single host species. See ANOPLURA; INSECTA; PARASITOLOGY.

**Characteristics.** Lice spend their entire life cycle in the microhabitat provided by the hosts' skin, fur, or feathers, and are highly adapted to this environment. The louse body (see **illustration**) is dorsoventrally flattened, and their legs are modified for clinging to feathers or fur. Their adult size ranges from 3 to 11 mm (0.1 to 0.4 in.) and frequently correlates with the size of the host species on which they are normally found. Coloration varies from pale white through shades of yellow and brown to black. Patterns are evident on some species, and cryptic coloration is often employed to match the coloration of the host. Chewing lice have mandibles that have been variously modified in each of the suborders. The mandibles are involved in cutting up the hair or feather material before it is digested, and play a vital secondary role in anchoring the louse to the host. The mandibles of Rhynchophthirina (the elephant and warthog lice) are present at the end on



(a) (b)  
**Ischnoceran bird louse *Strigiphilus vapidus*, a male from an owl (*Ninox novaeseelandiae*), shown in (a) dorsal view and (b) ventral view.**

a long rostrum and, unlike most chewing lice, articulate outward rather than oppose each other. This enables them to tear at the hosts' thick skin and feed from the pool of blood that forms. In most species of sucking lice, the mandibles have been completely lost. Instead, sharp stylets protrude from the head and are used to pierce small vessels located close to the skin surface. Anoplura draw up blood using these stylets—hence their name sucking lice.

**Phylogeny.** Parasitic lice are closely related to their nonparasitic free-living ancestors, the Psocoptera (book- or barklice). Just one louse is known from the fossil record—a spectacularly preserved specimen that has been dated at approximately 44 million years old. The evolutionary position of this fossil louse in a relatively contemporary group of living lice suggests that the origin of parasitic lice significantly predates the age of this fossil. Based on the latest molecular evidence, the data suggest that lice diversified from their psocopteran ancestors at least 100 million years ago, long before the extinction of the dinosaurs. Given the common ancestry between birds and dinosaurs, and the more recent diversification of mammal lice compared to those infesting birds, it has been suggested that the first hosts for parasitic lice might have been the feathered theropod dinosaurs known from this period. The close association between hosts and lice may parallel similar patterns of evolutionary relationship, with particular events in the evolutionary history of lice being matched to events in the evolutionary history of their hosts. In some cases, these patterns have been used to resolve controversies in host evolutionary history, such as those surrounding the affinities of modern and archaic humans, and the relationships of flamin-

gos with storks and ducks. See ORGANIC EVOLUTION; PSOCOPTERA.

**Distribution.** The present distribution of lice essentially mirrors that of their hosts, although true geographic distributions of lice are known to occur within the range of certain host species. Consequently lice are found worldwide on every continent and in virtually every habitat occupied by mammals and birds. All bird orders and most bird families have records of host-specific lice. Likewise, most mammals have lice with the exception of species belonging to the orders Chiroptera (bats), Edentata (anteaters, tree sloths, and armadillos), Pholidota (pangolins), Cetacea (whales and dolphins), and Sirenia (dugongs and manatees). The host specificity of most louse species can be attributed to the infrequency of contact between different host species; however, some lice have physical adaptations to particular host species and are not capable of living on another species. Because lice are unable to survive for more than short periods off the hosts' body, behavioral adaptations in the lice reinforce host specificity. For example, lice are attracted by body heat and repelled by light, preventing them from leaving the warmth and darkness of the hosts' plumage or pelage. Most birds and some mammals are typically infected with more than a single species of louse, with many having three to five species. These usually inhabit different parts of the hosts' body, and are adapted to the particular microhabitat of the host in which they normally live.

**Life cycle.** With the exception of the human body louse, all species complete their entire life cycle from egg to adult on the body of their host. Females are typically larger than males and often outnumber them on any one host. In some species, males are rarely found, and reproduction can occur without male fertilization (parthenogenesis). Eggs are laid singularly or in clumps, and in most cases are cemented to the feather or hair shaft. Once hatched, lice pass through three nymphal instars (developmental stages between molts) before reaching adult stage. This typically takes 20–30 days, depending upon temperature and the louse species. Often the life cycles of lice are carefully timed to coincide with the breeding activities of their host.

**Infestation.** Lice are important pests of domesticated mammals and birds. Heavy infestation may cause intense irritation, and scratching may lead to secondary infections. Rubbing and damage to hides and wool may also occur, and meat and egg production can be badly affected. Louse infestations on most animals are usually very low in number, but sick or injured animals, especially those whose ability to preen or groom has been impaired, may have infestations numbering thousands of individual lice. The human body louse (*Pediculus humanus humanus*) is the vector of *Rickettsia prowazekii*, which causes louse-borne typhus. During the seventeenth to early twentieth century, this louse was responsible for the deaths of millions of people during the plagues, famines, and wars that beset people

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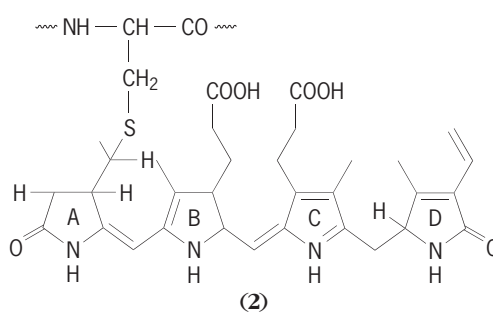
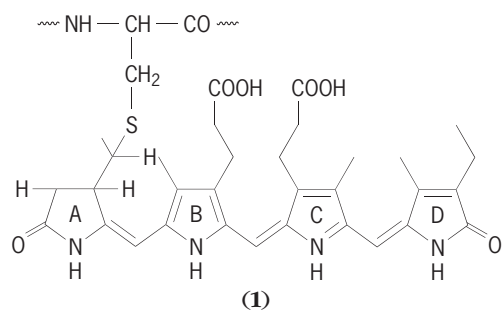
379 living at the time. Today, louse-borne typhus, along  
 380 with louse-borne relapsing fever and trench fever are  
 381 rare occurrences, usually confined to displaced per-  
 382 sons during times of civil or political unrest. How-  
 383 ever, the human head louse (*Pediculus humanus*  
 384 *capitis*) is commonplace in the developed world,  
 385 and infests millions of schoolchildren every year.  
 386 The only other louse known to infect humans is the  
 387 pubic louse (*Phthirus pubis*), which is normally trans-  
 388 mitted through sexual contact. See PEDICULOSIS; RE-  
 389 LAPSING FEVER; RICKETTSIOSES; SEXUALLY TRANSMIT-  
 390 TED DISEASES. Vincent S. Smith

391 Bibliography. L. A. Durden and G. G. Musser, The  
 392 sucking lice (Insecta, Anoplura) of the world: A  
 393 taxonomic checklist with records of mammalian  
 394 hosts and geographic distributions, *Bull. Amer. Mus.*  
 395 *Nat. Hist.*, 218:1-90, 1994; D. Grimaldi and M. S.  
 396 Engel, *Evolution of the Insects*, Cambridge Univer-  
 397 sity Press, 2005; K. C. Kim, H. D. Pratt, and C. J.  
 398 Stojanovich, *The Sucking Lice of North America*,  
 399 Pennsylvania State University, 1986; M. A. Price and  
 400 O. H. Graham, *Chewing and sucking lice as para-  
 401 sites of mammals and birds*, *USDA Agr. Res. Ser. Tech.*  
 402 *Bull.*, no. 1849, 1997; R. D. Price et al., *The Chew-  
 403 ing Lice: World Checklist and Biological Overview*,  
 404 Illinois Natural History Survey, Champaign-Urbana,  
 405 2003; M. Rothschild and T. Clay, *Fleas, Flukes &  
 406 Cuckoos: A Study of Bird Ectoparasites*, Collins,  
 407 London, 1952; H. Zinsser, *Rats, Lice and History*,  
 408 Routledge, London, 1935.

## 412 Phycobilin

413 Any member of a class of intensely colored pigments  
 414 found in some algae that absorb light for photo-  
 415 synthesis. Phycobilins are open-chain tetrapyrroles  
 416 structurally related to mammalian bile pigments, and  
 417 they are unique among photosynthetic pigments in  
 418 being covalently bound to proteins (phycobilipro-  
 419 teins). In at least two groups of algae, phycobilipro-  
 420 teins are aggregated in a highly ordered protein com-  
 421 plex called a phycobilisome.

422 **Occurrence.** Phycobilins occur only in three  
 423 groups of algae: cyanobacteria (blue-green algae),  
 424 Rhodophyta (red algae), and Cryptophyceae (cryp-  
 425 tophytes), and are largely responsible for their dis-  
 426 tinctive colors, including blue-green, yellow, and  
 427 red. Five different phycobilins have been identi-  
 428 fied to date, but the two most common are phy-  
 429 cocyanobilin [structure (1)], a blue pigment, and  
 430 phycoerythrobilin (2), a red pigment. In the cell,



454 these pigments absorb light maximally in the or-  
 455 ange (620-nanometers) and green (550-nm) por-  
 456 tion of the visible light spectrum, respectively. A blue-  
 457 green light (495-nm) absorbing pigment, phycou-  
 458 robin, is found in some cyanobacteria and red algae.  
 459 A yellow light (575-nm) absorbing pigment, phy-  
 460 cobiliviolin (also called cryptoviolin) is apparently  
 461 found in all cryptophytes but in only a few cyanobac-  
 462 teria. A fifth phycobilin, which absorbs deep-red  
 463 light (697 nm), has been identified spectrally in  
 464 some cryptophytes, but its chemical properties are  
 465 unknown. See CRYPTOPHYCEAE; CYANOPHYCEAE;  
 466 RHODOPHYCEAE.

467 Phycobilins are associated with the photosyn-  
 468 thetic light-harvesting system in chloroplasts of red  
 469 algae and cryptophytes and with the photosynthetic  
 470 membranes of cyanobacteria, which lack chloro-  
 471oplasts. Phycobilins are covalently bound to a water-  
 472 soluble protein that aggregates on the surface of the  
 473 photosynthetic membrane. All other photo-  
 474 synthetic pigments (for example, chlorophylls and  
 475 carotenoids) are bound to photosynthetic mem-  
 476 brane proteins by hydrophobic attraction. Phyc-  
 477obiliprotein can constitute a major fraction of an alga.  
 478 In some cyanobacteria, for example, fresh-water or  
 479 marine *Synechococcus*, phycobiliproteins can ac-  
 480 count for more than 50% of the soluble protein and  
 481 one-quarter of the dry weight of the cell. See CELL  
 482 PLASTIDS.

483 Phycobiliproteins are classified primarily by their  
 484 absorption spectrum (Fig. 1), which depends on the  
 485 protein structure and the number and kind of phy-  
 486 cobilins that are attached. There are three major classes,  
 487 allophycocyanin (APC), phycocyanin (PC), and phy-  
 488 coerythrin (PE) [see table]. All cyanobacteria and  
 489 red algae contain allophycocyanin and phycocyanin,  
 490 while some species of these groups also contain  
 491 phycoerythrin. Cryptophytes possess either phy-  
 492 cocyanin or phycoerythrin, but not both. All three  
 493 biliproteins are composed of at least two polypeptide  
 494 subunits,  $\alpha$  and  $\beta$ , each having a molecular weight  
 495 in the range of 16,000-22,000. The two subunits,  
 496 which are always present in equal amounts, form  
 497 stable aggregates of typically two, three, or six pairs.  
 498 Some phycoerythrins contain a third polypeptide,  
 499 designated  $\gamma$ , which is usually found singly with six  
 500  $\alpha$ - $\beta$  pairs. Each subunit may contain one to four phy-  
 501 cobilin chromophores, depending on the biliprotein.  
 502 Because of the tendency to aggregate to varying de-  
 503 grees, molecular weights of phycobiliproteins range  
 504 widely between 35,000 and 240,000.