# The cockroach

Marianne C. Dominguez

Writer's Comment: Every animal has a fascinating life story. So when I got the chance to write about a chosen group of insects in Dr. Peter Cranston and Dr. Penny Gullan's ENT 100 (General Entomology) class, I decided that, for a change, one of the most reviled insects deserved a spotlight (rather than a crunch from a shoe). Little did I know how challenging the writing would be when different hypotheses seemed to contradict each other, leaving me to decipher a mass of confusing scientific literature, while trying to appreciate the reasoning behind each hypothesis. Let's just say that at the same time roaches were roaming during a horrendously late hour of the night, I was up reading about how they were doing it! Nevertheless, I felt an affinity with these scientific authors. Each article of research helped elucidate a tiny fraction of what makes this insect just as interesting and charming—if I dare assert—as any given animal. I'm no insect expert; I can only retell the "stories," tidbits of research that may challenge you to view your friendly neighborhood cockroach a little differently than before. The cockroach's story certainly changed my perception.

*—Marianne C. Dominguez*

Instructors' Comment: Marianne Dominguez enrolled in the General Entomology course taught by myself and Penny Gullan, having already taken a Freshman seminar in Conserving Australia's Biodiversity, and a lower level course in Biodiversity with us. Last year, Marianne's term paper for the Biodiversity course, "Australia's Terrestrial Vertebrate Biodiversity: The Survival Challenge," was selected for the 2003–2004 *Prized Writing*. Thus we had some prior intimations that a term paper on a topic concerning insects would be a well-researched and exciting read, and so it has proved. In this class students choose their own insect group, about which they are asked to write some 2500 words to provide both breadth and detail. Popular choices are those insects that impact on our life styles—and certainly cockroaches rank highly in this regard. However, the trick here is to understand that the "roaches" are much more diverse than the few anthropophilic species that share our kitchens (and even students' refrigerators). Marianne balanced this extremely well in exploring the love-hate relationships we have with these familiar insects. In a class in which many term papers were excellent for their scholarship, this stood out for its erudition, wit, and even empathy with its subjects. Whether Marianne chooses to study entomology in greater depth or not, this piece of writing will serve as a model for subsequent students in our classes.

*—Peter Cranston and Penny Gullan, Entomology*

Unless you have a penchant for entomology, the thought of a scurrying, antennae-waving cockroach is enough to make you cringe, especially if you have had an unwelcome encounter with a roach in your home, food, or God forbid, in any body orifice. People from all walks of life—including the observant Charles Darwin in his voyage in the Beagle, an annoyed Mark Twain writing about roaches in his hair, and humble African slaves being shipped to America—have shared space with these creatures. You wonder, why devote a simple paper to these animals (unless its purpose is to find effective ways of eliminating them)? But, as I hope you will come to realize, the cockroach world is far more intricate than you can imagine. With an open and curious mind, set aside the pesticide and allow yourself to be intrigued by what makes the cockroach not just a pest, but an amazing creature worthy of respect in the tree of life.

**Origins**

Cockroaches were around at least 200 million years before the first modern humans roamed the earth. The origin of the cockroach is interesting and complicated when one studies extant species relative to the fossil record. Cladistic analyses, anatomical studies, the presence of oothecae (egg sack), external ovipositors (egg-laying tube), and endosymbionts provide answers to how long ago roaches roamed the ancient Earth (Labandeira, 2005; Lo *et al.*, 2003). The time scale in Fig. 1 shows three eras important to cockroach evolution: the Paleozoic (from the Cambrian to the Carboniferous and Permian periods), the Mesozoic (Triassic, Jurassic, and Cretaceous periods), and the Cenozoic (Tertiary period to present). There is a range of theories as to when cockroaches originated. The best evidence is the fossil record, which shows cockroach-like insects as early as the Paleozoic some 300 million years ago (mya). These primitive Paleozoic roaches, called the Paleoblattaria in McKittrick's classification, have primitive wings with the distinctive cockroach form (a "sweeping cubitus vein," *see also Fig. 7*) as well as cockroach body features such as shield-like pronotum, cerci, and hypognathous mouthparts (Labandeira, 2005).

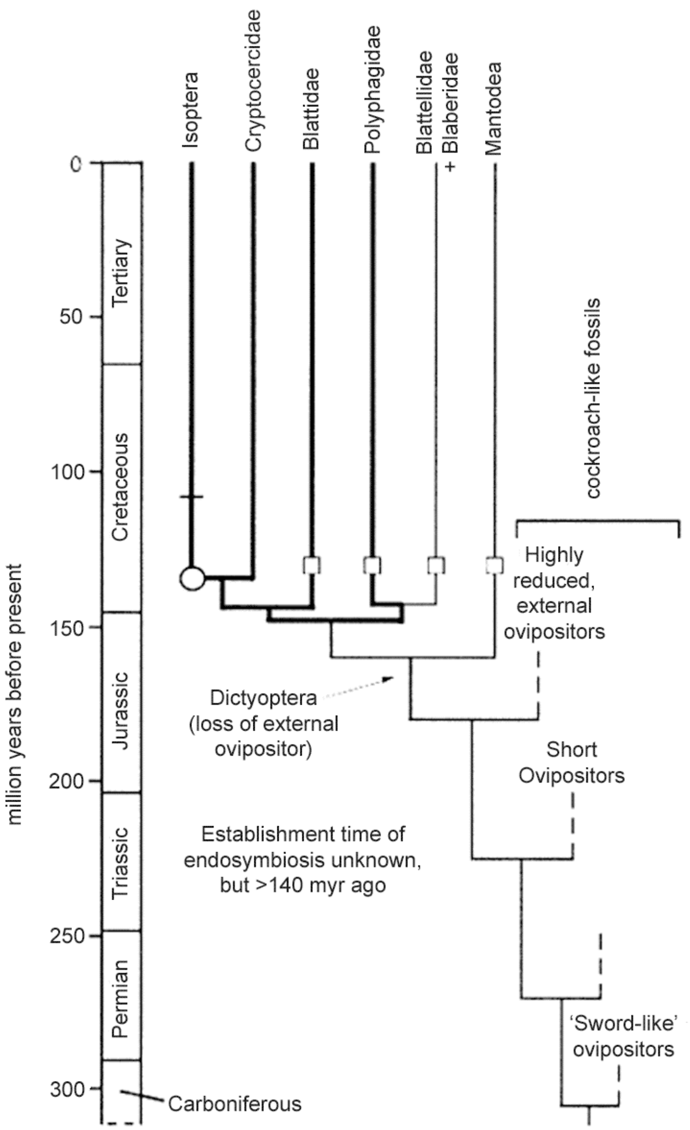


**Fig. 1:** Timescale for the evolution of Dictyoptera. Ovipositor length of cockroach-like fossils decrease through time. The lack of endosymbionts in the Mantodea lineage precludes an estimation of its divergence time, and the time shown is based on Grimaldi (1997). The bar on the termite lineage represents the loss of Blattabacterium from all other linages other than that leading to M. darwiniensis. (Figure and caption from Lo, et al., 2003)

In *Cockroach*, Marion Copeland gives particular emphasis to the Carboniferous Period, labeling it the Age of the Cockroach for the high species diversity of cockroach-like insect fossils—an estimated 800 different kinds (Copeland, 2003). The fossil record also indicates a trend in decreasing ovipositor length from long, sword-like ovipositors in Carboniferous specimens to highly reduced ones in late Jurassic specimens (Lo *et al.*, 2003). Interestingly, Labandeira (2005) points out that some modern lineages show rudiments of an external ovipositor located within the female genitalic assembly, an indication of this evolutionary retraction. He goes on to say that while some presume that roaches with long ovipositors laid eggs in the substrate, oothecae are found no earlier than the Cenozoic. Contrary to the fossil record, the loss of fat body endosymbionts in all other termite lineages (bar on Isoptera lineage in Fig. 1) except those that lead to *Mastotermes darwiniensis* indicate a closer relationship between termites and the wood-feeding cockroach *Cryptocercus*, placing the radiation of cockroach stem groups earlier—sometime between the late Jurassic and early Cretaceous, not the fossil-rich Carboniferous (Lo *et al.*, 2003).

In general, cockroach origin dates that are earlier than the Mesozoic reflect more encompassing taxa and Dictyopteran relationships. As Labandeira (2005) notes, a problem with paleoentomology is the difference in the "temporal and spatial taxonomic scope of the definition of taxa." For instance, Gullan and Cranston (2005) exclude the cockroach-like early blattoid forms from the Mesozoic and Paleozoic eras, dating the modern cockroach lineages from the Jurassic (~210 mya), corresponding to the loss of the external ovipositor. Others, such as Labandeira (2005) and Lo *et al.* (2003), prefer to include the basal forms when discussing taxa origins. Even so, a few entomologists even believe that cockroach-like insects originated as early as the Silurian period (~400 mya) before fossils could tell their story (Copeland, 2003).

**Classification and Phylogeny**

Cockroaches (Blattodea), termites (Isoptera), and mantids (Mantodea) are typically classified in the order Dictyoptera (shaded in Fig. 2).

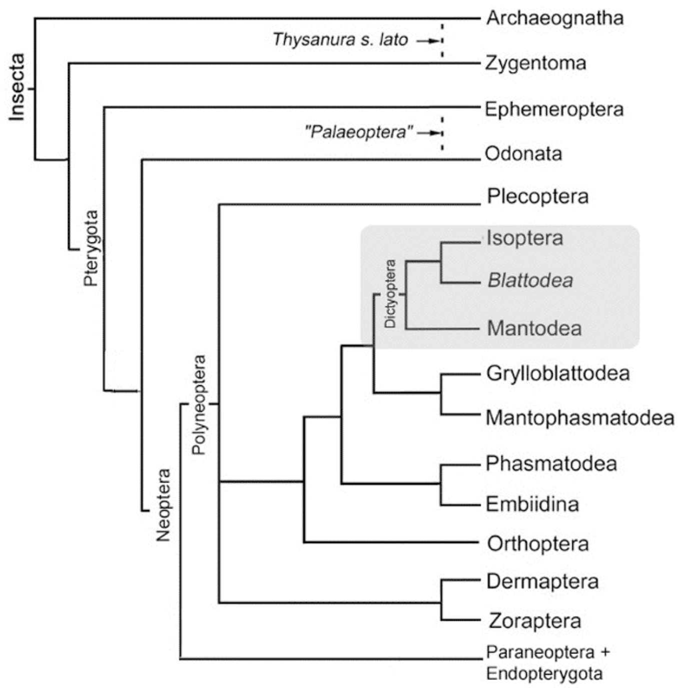


**Fig. 2:** Insect phylogeny (simplified from Cranston & Gullan, 2005)

Stemming from the placement of the subsocial wood cockroach *Cryptocercus,* there are two controversial hypotheses (see Fig. 3) regarding the relationship of cockroaches within the Dictyoptera (Gullan & Cranston, 2005; Cranston & Gullan, 2003; Maddison, 2002). First, many studies, such as those by McKittrick (1964), Lo *et al.* (2002), Henning (1981), and Klass (1998) argue for a sister group relationship between termites (Isoptera) and cockroaches, particularly on the basis of termite-like features of the subsocial wood cockroach *Cryptocercus*. Previously thought to be a result of convergent evolution, termite similarities such as sociality and the transfer of cellulose-digesting protists between generations now appear to support the hypothesis that termites arose from within the cockroaches, thus arguing for the paraphyly of Blattaria with respect to the Isoptera (Cranston & Gullan, 2005). Even so, studies by Boudreaux (1979), Thorne & Carpenter (1992), DeSalle *et al.* (1992), Kambhampati (1995), and Wheeler *et al.* (2001) argue the sister grouping of mantids (Mantodea) and cockroaches on the basis of synapomorphies involving morphological modifications associated with predation (Cranston & Gullan, 2003; Maddison, 2002). To determine for certain whether termites or mantids is the sister group of cockroaches thus requires further research on both the morphological and molecular level.

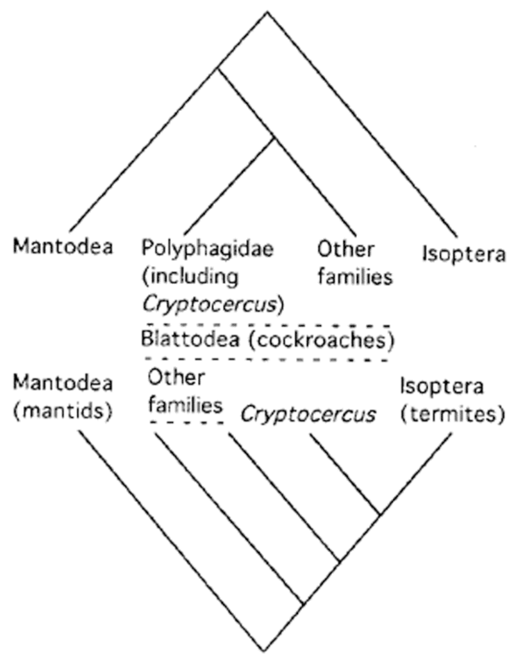


**Fig. 3**: Cladogram depicting alternate relationships among Dictyoptera. Dashed lines indicate paraphyly in classification (from Cranston & Gullan, 2003).

When we delve into the cockroach lineage, the higher classification of cockroaches gets even more complicated. Cockroaches make up at least 3500 species in 8 families worldwide, though there are still many more to discover (Gullan & Cranston, 2005).

According to Roach and Rentz (1997) of CSIRO Entomology, three "modern" classifications arose from the works of McKittrick (1964) and Princis (1960), the latter integrating his observations into Handlirsch's (1926–1930) system (Table 1). McKittrick's classification served as a starting point for studies that support (Roth, 1970), modify (Grandcolas, 1993; Roth, 1988), or contradict (Maekawa & Matsumoto, 2002) his proposed phylogeny.

**Table 1: Cockroach classification systems**

| Author | Type of Data | Conclusion |
|---|---|---|
| Princis (1960) | Morphological<br>• wing venation and folding<br>• patterns of spines on legs<br>• shape of male subgenital plate | 4 suborders<br>28 families<br>21 subfamilies |
| McKittrick (1964) | Reproductive morphology & behavior<br>• female ovipositional behavior<br>• morphology of genitalia and proventriculus | 2 superfamilies<br>5 families<br>20 subfamilies |

(data from Roach & Rentz, 1997)

Authors also disagree in their discussions of phylogenetic relationships between cockroach families. For instance, although all morphological studies and some molecular studies support the derived sister grouping of Blaberidae and Blattelidae, others including Klass (1997) and Grandcolas (1996) suggest paraphyly of Blattelidae based on reproductive behaviour (Maekawa & Matsumoto, 2002). Fig. 4. illustrates four different proposed lineages.

Roach and Rentz (1997) speculate that the lack of consensus over cockroach classification stems from several reasons: the first problem is the extensive use of cockroach names, both in early and modern literature, with inadequate accompanying life history and taxonomic details. The second problem is identifying taxa based on external characters that may or may not have resulted from convergent or parallel evolution. Internal characteristics such as the

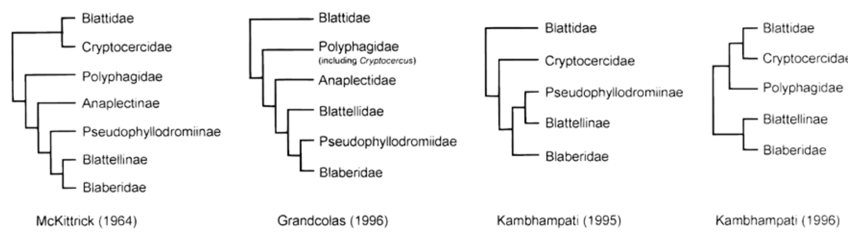


**Fig. 4:** Four hypotheses on phylogenetic relationships among cockroach families (-idae) and subfamilies (-inae) (from Grandcolas & D'Haese, 2001)

proventriculus, the genitalia of both sexes, and the ovipositional behaviour of the female have made cockroach higher classification more stable, recently elucidating many incorrect generic taxonomic placements (Roach & Rentz, 1997).

## Biology

The cockroach's body consists of three bilaterally symmetrical segments (from anterior to posterior: head, thorax, and abdomen) that are ovoid and dorsoventrally flattened, an advantage for fitting in the smallest cracks and fissures (Gullan & Cranston, 2005; Copeland, 2003). Concealed by the enlarged prothoracic shield-like pronotum, the head is hypognathous, directed vertically with mandibulate mouthparts directed ventrally and used for eating a generalized diet (Gullan & Cranston, 2005). If present, the compound eyes occupy the head's lateral wall, while the multisegmented filiform antennae, articulated at a rigid (ventral) and flexible (lateral) point, occupy the eye's antero-medial indentation (Guthrie & Tindall, 1968). The meso- and metathorax are rectangular and subequal, with the former holding the leathery sclerotized forewings called tegmina (singular: tegmen) that protect the membranous metathoracic hind wings folded beneath (Gullan & Cranston, 2005). Not all cockroaches have wings; those that do may have absent or reduced hind wings with the characteristic large anal lobe (Gullan & Cranston, 2005). Forewings lack the anal lobe and are dominated by the branching radius (R) vein and the cubitus anterior (CuA) vein (Fig. 5) (Gullan & Cranston, 2005). The many branches in cockroach wings are part of what gives the *Dictyoptera* (Greek for 'net-wing') its name (Copeland, 2003). Nymphs of winged species have wing pads and gradually develop wings with subsequent molts (Ebeling, 2002).

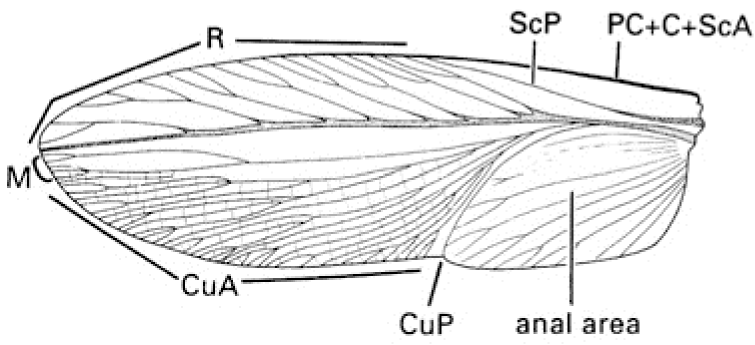


**Fig. 5**: Cockroach forewing (from Gullan & Cranston, 2005)

Also attached to the thorax are six cursorial (adapted for running) legs with many spines, sensory setae, vibration-sensing subgenual organs located in each knee joint, large coxae, and five-segmented tarsi with adhesive pads called pulvilli (Copeland, 2003; Gullan & Cranston, 2005). These features allow the cockroach to detect the slightest environmental stimuli and, if needed, run with amazing flexibility and speed. Among insects, as documented by Guthrie and Tindall (1968), cockroaches have the highest running speeds recorded—130cm/sec (~3 mph!). Additionally, the near horizontal plane orientation of the hind limbs entails very little vertical strut in walking mechanics so that the abdomen is always dragged close to the ground, another adaptation for life in narrow crevices (Guthrie & Tindall, 1968). Behind the thorax is the abdomen with 10 visible segments and typically multisegmented cerci (Gullan & Cranston, 2005). The male abdomen contains asymmetrical genitalia, epiprocts (dorsal relics of segment 11) and cerci like the female, and below the cerci one or two thin appendages called styles that he retains as an adult from those found in the nymphal stages of both sexes; the female abdomen contains the small ovipositor valves concealed beneath tergum 10 (the 10$^{th}$ dorsal segment) inside a genital atrium (Guthrie & Tindall, 1968; Gullan & Cranston, 2005; Ramel, 2005). Throughout the lateral side of the thorax and abdomen are spiracles, external openings of the tracheal system for gas exchange (Gullan & Cranston, 2005). Guthrie & Tindall (1968) provide more extensive and illustrated details of cockroach morphology in *The Biology of the Cockroach.* As Fig. 6 shows, the remarkable cockroach form is worthy of study.

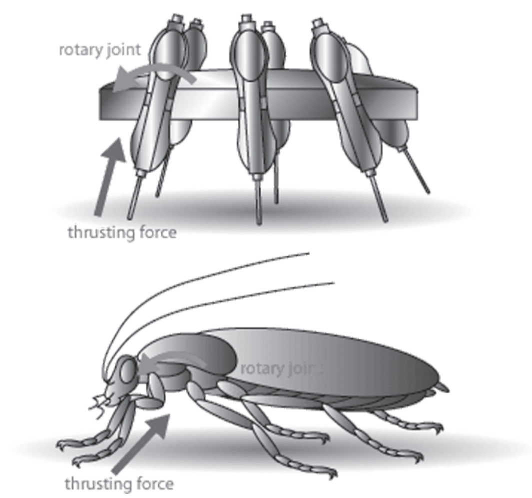


**Fig. 6:** One of many current robotic projects, either as techno-toys or for research purposes, inspired by the cockroach form. Here, researchers from the University of British Colombia have designed and built a robot, noting the cockroach's legs as prime candidates for biomimicry. They explain that "these types of small, fast robots could potentially be used for military reconnaissance, bomb defusion and de-mining expeditions." (from http://bioteach.ubc.ca/Bioengineering/Biomimetics/)

### Life Cycle and Reproduction

Cockroaches are hemimetabolous insects with three stages of development: egg, nymph, and adult (Gullan & Cranston, 2005) (see Fig. 7). Mating generally involves the use of pheromones by both sexes and stridulatory courtship prior to end-to-end copulation (Gullan & Cranston, 2005). In the German cockroach, *B. germanica*, and the American cockroach, *P. americana,* courtship behaviour includes wing-rasing and simultaneous turning of a male, followed by the courtship feeding of a glandular gift (secretions of the exposed male tergal glands) to the female, who is consequently retained in position appropriate for genital contact (Nojima *et al.*, 1999; Ramel, 2005). Courting in populations with male dominance hierarchies, such as in the Madagascar hissing cockroach, *G. portentosa*, involves male-to-male aggression in which the female prefers to mate with the strongest, most dominant male (Bullington, 2003). This sexual selection results in sexual dimorphism. In contrast, when Moore *et al.* (2003) studied female mate choice in the ovoviviparous cockroach *N. cinerea*, they found that females may not prefer dominant males if the males are too costly in their manipulation of the rate of parturition, which is directly related to female lifespan. Sexual signals can indeed have multiple components with contrasting effects, and complex fitness relationships can arise in species with sexual conflict (Moore *et al.*, 2003).

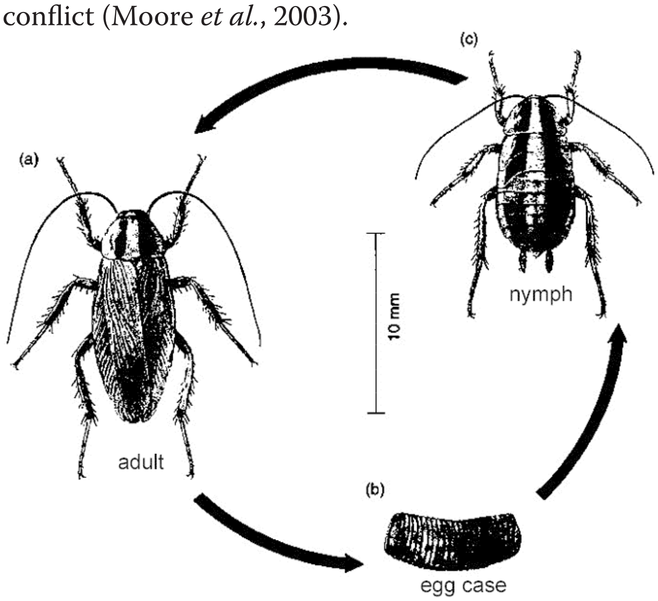


**Fig. 7:** Hemimetabolous life cycle of the German cockroach (from http://www.who.int/docstore/water_sanitation_health/vectcontrol/ch30.htm)

Another interesting factor is the effect of the circadian clock on reproduction: the synchronized male-finding locomotion and the calling behaviour of females are under circadian control, but pregnancy masks the circadian locomotor rhythm (Tsai & Lee, 2000).

As described by Gullan & Cranston (2005) and Roach & Rentz (1997), once the eggs are laid and hatch, nymphs develop in four forms, depending on the species. Oviparous species lay eggs in a protective ootheca, which may be carried by the female (shown in Fig. 8) as a form of parental care, dropped, glued, or buried in the substrate. The appearance and manner of placement of the ootheca can be diagnostic. Ovoviparous species have a specialized form of reproduction in which the oothecae is extruded and then retracted into the uterus or brood sac until nymphal hatching. Other ovoviparous species do not form an egg mass; in this case, the eggs pass directly into the uterus. True viviparity is rare, although it has been studied in *D. punctata*. This viviparous cockroach is able to produce nutritive milk to feed offspring during the gestation period, thus demonstrating the evolution of a new degree of maternal contribution (Williford *et al.*, 2004). Obligatory parthenogenesis occurs in only one cockroach species, while facultative parthenogenesis occurs in a few pest species. Parental care has been documented in an undescribed Australian species in which nymphs cling to the mother's underside for at least two instars. These nymphs use specialized non-chewing mouthparts that fit between the mother's coxae, which may dispense food (Roach & Rentz, 1997). More generally speaking, nymphs gradually come to resemble adults at each molt. Their development depends on temperature, crowding, and diet (Roach & Rentz, 1997; Guthrie & Tindall, 1968), changing photoperiod (Zhu & Tanaka, 2004), and social influences (Holbrook & Schal, 1998). Generally, a slower development leads to a longer life span (Moore *et al.*, 2003).

**Survival of the Fittest**

The cockroach's remarkable form has allowed it to survive many extinction events, in part because of its well-developed sensory systems. According to Copeland (2003), a roach can take as little as 40 milliseconds for an escape response, as well as detect earthquakes as small as 0.07 on the Richter scale. Eisner (2003) demonstrated the cockroach reflex behaviour, proving that the roach can sense chemicals with its body surface. He observed that a decapitated roach still responds to acid by accurately scratching specific body parts where the acid was applied. Besides being used for courtship, the antennae contain olfactory receptor cells responsive to the direction and rate of change in food odor concentration (Hinterwirth *et al.*, 2004). Equally impressive is the roach's range of defensive mechanisms, which include sticky or toxic chemical secretions in response to predators and parasites, hissing via spiracles, and, as observed in *P. semlaunatus*, the capacity to curl into a ball like a pillbug to protect the body against an ant attack (Eisner, 2003; Bullington, 2003; Waldbauer, 2003).

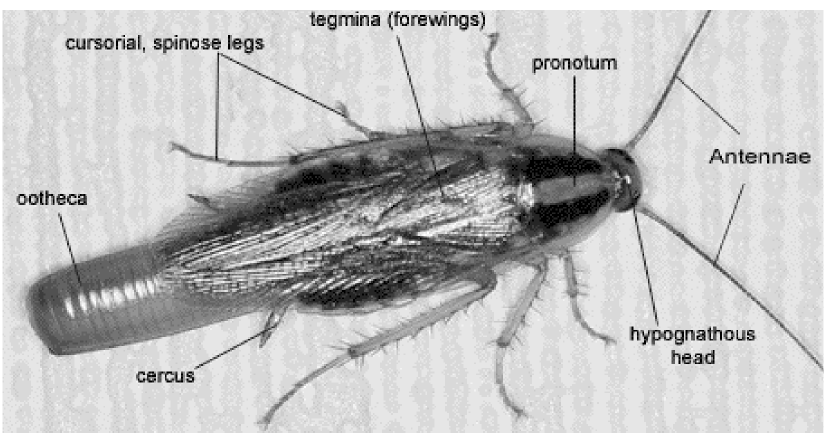


**Fig. 8:** Female German cockroach (unlabeled image from the Dept. of Entomology, Univ. of Nebraska, Lincoln. <http://entomology.unl.edu/images/cockroaches/cockoaches.htm>

Likewise, a number of studies have shown the cockroach's ability to adapt to a wide range of environments. According to Block *et al.*(1998), the New Zealand alpine cockroach, *C. quinquemaculata*, can experience prolonged periods of subzero temperatures (-5° C to -9° C). Mira & Raubenheimer (2002) showed that feral roaches have greater water storage capacities than those in the laboratory culture, and, in addition to their behavioural plasticity, *P. americana* can "alter the number of developmental stadia, the density of endosymbionts they harbour, their size, water storage capacity and starvation duration." It is no wonder that pest species thrive in the urban jungle.

**Importance and Impact**

Cockroaches are important to the ecosystem, particularly because of their dietary habits (Waldbauer, 2003). Being omnivores, they feed and therefore recycle decaying plant and animal matter. As discussed in phylogeny, *Cryptocercus* harbor cellulose-digesting symbionts in their digestive system which allow them to consume dead or decaying wood. The Australian cockroach *Panesthia cribata* can itself digest cellulose using special enzymes (Waldbauer, 2003). Cockroaches are also part of the food chain, feeding insectivores and humans (see Copeland, 2003 for recipe sources).

The medical importance of cockroaches has also been the focus of a variety of studies, including research on food contamination and dermatological and asthmatic reactions (Baumholtz *et al.*, 1997). Although cockroaches may carry certain pathogens, there is no current proof that the roach is a vector for human disease—in fact, roaches have been wrongly blamed for at least seven diseases (Baumholtz *et al.*, 1997). The three popular pest species (*B. germanica, P. americana, and B. orientalis*) and the 16 species of cockroaches that represent a potential threat to human health are not representative of their much wider tropical diversity. The latter include terrestrial, arboreal, and cavernicolous species, some brightly-colored in blue, green, and gold hues with beautifully adapted lifestyles (Copeland, 2003). The pest species introduced accidentally as man's traveling companion learned the advantages of sharing man's food and shelter and consequently grew in population. Infestations inspire more effective means of cockroach control, including the use of insecticides, vapors and gases in enclosed spaces, and boric acid (Ebeling, 2002). Indeed, much of current research is devoted to the control and elimination of these displaced, pest-turned cockroaches.

Love them or hate them, cockroaches have long been a part of our world, and will probably continue to thrive even after the human lineage dies out. It is ironic to note that the same form and biology that have intrigued some into immortalizing the cockroach in folklore, art, and culture have led others to abhor the very sight of these insects. Whatever man's perspective, nature has found a way to preserve these living fossils.

### References

Baumholtz, M.A., Parish, L.C., Witkowski, J.A., & Nutting, W.B. (1997) The medical importance of cockroaches. *Intl. J. of Dermatology* **36**: 90–96.

Block, W., Wharton, D.A., & Sinclair, B.J. (1998) Cold tolerance of a New Zealand alpine cockroach, *Celatoblatta quinquemaculata* (Dictyoptera, Blattidae). *Physiol. Entomology* **23:** 1–6.

Boudreaux, H. B. (1979) *Arthropod Phylogeny with Special Reference to Insects*. New York: J. Wiley.

Bullington, S.W. (2003) The Hissing Cockroach, *Gromphadorhina portentosa* (Schaum). <http://www.key-net.net/users/swb/pet_arthropod/hiss.htm> Viewed April 28, 2005.

Cranston, P.S. & Gullan, P.J. (2003) Phylogeny of Insects. In Resh, V.H. & Cardé, R.T. (Eds.) *Encyclopedia of Insects*. San Diego: Academic Press. pp. 882–898.

Copeland, M. (2003) *Cockroach.* London: Reaktion Books Ltd.

DeSalle, R., Gatesy, J., Wheeler, W., & Grimaldi, D. (1992) DNA sequences from a fossil termite in Oligo-Miocene amber and their phylogenetic implications. *Science* **257**(5078):1933–1936.

Ebeling, W. (2002) *Urban Entomology*. Chapter 6: Pests on or near food. http://www.entomology.ucr.edu/ebeling/ebeling6.html#cockroaches Viewed May 6, 2005.

Eisner, T. (2003) *For Love of Insects.* Cambridge, MA: Harvard UP, Belknap Press.

Grandcolas, P. (1996) The phylogeny of cockroach families: a cladistic appraisal of morpho-anatomical data. *Can. J. Zool.* **74**:508–527.

Grandcolas, P & D'Haese, C. (2001) The phylogeny of cockroach families: Is the current molecular hypothesis robust? *Cladistics* **17**:48–55.

Grimaldi, D. (1997) A fossil mantis (Insecta: Mantodea) in Cretaceous amber of New Jersey, with comments on the early history of the Dictyoptera. *Am. Mus. Novitates* **3204**:1–11.

Gullan, P.J. & Cranston, P.S. (2005) *The Insects. An Outline of Entomology*. 3rd ed. Malden, MA, Oxford, Carlton, Aus.: Blackwell Publ. Ltd.

Guthrie, D.M. & Tindall, A.R. (1968) *The Biology of the Cockroach*. New York: St. Martin's Press.

Hennig, W. (1981) *Insect Phylogeny*. New York: J. Wiley.

Hinterwirth, A., Zeiner, R., & Tichy, H. (2004) Olfactory receptor cells on the cockroach antennae: responses to the direction and rate of change in food odour concentration. *Eur. J. of Neuroscience* **19**: 3389–3392.

Holbrook, G.L., & Schal, C. (1998) Social influences on nymphal development in the cockroach, *Diploptera punctuate. Physiol. Entomology* **23**: 121–130.

Kambhampati, S. (1995) A phylogeny of cockroaches and related insects based on DNA sequence of mitochondrial ribosomal RNA genes. *Proc. of the Natl. Acad. of Sciences (USA)* **92**:2017–2020.

Karny, H. (1921) Zur Systematik der Orthopteroiden Insekten. *Trebia,* I, Weltevreden: G. Koleff. pp. 1–269.

Kennedy, S. (2005) Biomimicry/Bimimetics: General principles and practical examples. <http://bioteach.ubc.ca/Bioengineering/Biomimetics/> Viewed May 1, 2005.

Klass, K. D. (1997) The external male genitalia and the phylogeny of Blattaria and Mantodea. *Bonner zoolog. Monograph.* **42**:1–341.

Klass, K. D. (1998) The ovipositor of Dictyoptera (Insecta): Homology and ground-plan of the main elements. *Zoolog. Anzeiger* **236** (2–3):69–101.

Klass, K. D (1998) The proventriculus of the Dicondylia, with comments on evolution and phylogeny in Dictyoptera and Odonata (Insecta). *Zoolog. Anzeiger* **237**(1):15–42.

Kristensen, N. P. (1995) Forty years' insect phylogenetic systematics. *Zoolog. Beiträge NF* **36**(1):83–124.

Labandeira, C.C. (2005) Pers. comm. to P.J. Gullan, May 9.

Lo, N., Bandi, C., Watanabe, H., Nalepa, C., & Beninati, T. (2003) Evidence for cocladogenesis between diverse dictyopteran lineages and their intracellular endosymbionts. *Mol. Biol. & Evol.* **20**(6):907–913.

Lo, N., Tokuda, G., Watanabe, H., Rose, H., Slaytor, M., Maekawa, K., Bandi, C., & Noda, H. (2000) Evidence from multiple gene sequences indicates that termites evolved from wood-feeding cockroaches. *Curr. Biol.* **10**(13):801–804.

Maddison, D. (2002) Tree of Life Web Project: Dictyoptera. <http://tolweb.org/tree?group=Dictyoptera&contgroup=Neoptera.>Viewed April 9, 2005.

McKittrick, F. A. (1964) Evolutionary study of cockroaches. *Cornell Univ. Agricultural Experiment Station Memoirs* **389**:1–197.

Mira, A., & Raubenheimer, D. (2002) Divergent nutrition-related adaptations in two cockroach populations inhabiting different environments. *Physiol. Entomology* **27**: 330–339.

Moore, A.J., Gowaty, P.A., & Moore, P.J. (2003) Females avoid manipulative males and live longer. *J. Evol. Biol* **16**: 523–530.

Nojima, S., Sakuma, M., Nishida, R., & Kuwahara, Y. (1999) A glandular gift in the German cockroach, *Blattella germanica* (L.)(Dictyoptera: Blattellidae): The courtship feeding of a female on secretions from male tergal glands. *J. of Insect Behavior* **12**(5): 627–640.

Princis, K. (1960) Zur systematik der Blattarien. *Eos* **36**: 427–449.

Ramel, G. (2005) The Blattodea or Cockroaches. <http://www.earthlife.net/insects/blatodea.html> Viewed April 9, 2005.

Roach, A.M. E. & Rentz, D.C.F. (1997) *Blattodea: Cockroaches*. Australian Government Department of the Environment and Heritage. <http://www.deh.gov.au/cgi–bin/abrs/fauna/details.pl?pstrVol=BLATTODEA;pstrTaxa=1;pstrChecklistMode=1#intro> Viewed May 5, 2005.

Thorne, B. L. & Carpenter, J.M. (1992) Phylogeny of the Dictyoptera. *System. Entomology* **17**:253–268.

Tsai, C., & Lee., H. (2000) Circadian locomotor rhythm masked by the female reproduction cycle in cockroaches. *Physiol. Entomology* **25**: 63–73.

Waldbauer, G. (2003) *What Good are Bugs: Insects in the Web of Life.* Cambridge, MA: Harvard UP.

Wheeler, W. C., Whiting, M., Wheeler, Q.D., & J. M. Carpenter, J.M. ( 2001) The phylogeny of the extant hexapod orders. *Cladistics* **17**:113–169.

Williford, A., Stray, B., & Bhattacharya, D. (2004) Evolution of a novel function: nutritive milk in the viviparous cockroach, *Diploptera punctata*. *Evol. & Develop.* **6** (2): 67–77.

Zhu, D., & Tanaka, S. (2004) Summer diapause and nymphal growth in a subtropical cockroach: response to changing photoperiod. *Physiological Entomology* **29:** 79–83.