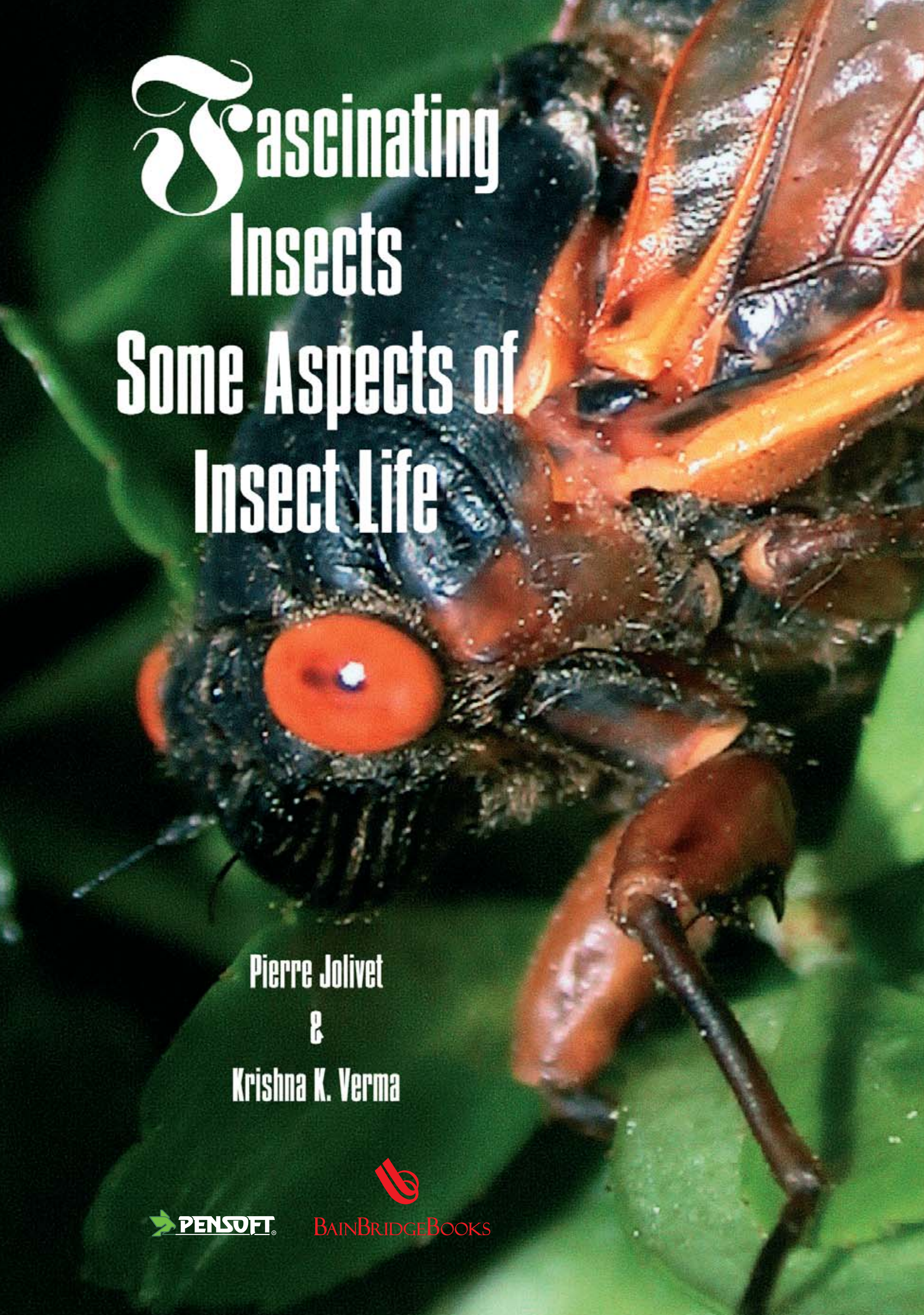

Fascinating Insects

Some Aspects of Insect Life

Pierre Jolivet
&
Krishna K. Verma

PENSOFT.
BAINBRIDGEBOOKS

FASCINATING INSECTS

some aspects of
insect life

TO JEAN-HENRI FABRE,
THE HOMER OF INSECTS, WHO KNEW SO WELL TO DECIPHER
THE SECRET LIFE OF THE CREEPY-CRAWLIES,
THIS BOOK IS DEDICATED.

Pierre Jolivet
Krishna K. Verma

“ L’égalité, la seule égalité en ce monde, l’égalité devant l’asticot”.
(Equality, the only equality in this world, equality towards the maggot.)

JEAN-HENRI FABRE

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some aspects of insect life

Pierre Jolivet
Krishna K. Verma

PENSOFT

Sofia–Moscow
2005

FASCINATING INSECTS
Some aspects of insect life

by

Pierre Jolivet
Krishna K. Verma

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Contents

— 1. Introduction — **11**
— 2. How successful are insects? — **13**
— 3. Insects at sea — **20**
— 4. Insects in frigid regions — **31**
— 5. Omnipresent ants — **38**
— 6. Insect migrations — **49**
— 7. When ants wake up! — **60**
— 8. Chemical defence in beetles and moths — **64**
— 9. Instinct and intelligence in insects — **75**
— 10. Do insects learn? — **81**
— 11. Insects and tools — **84**
— 12. Insect aggregations — **96**
— 13. Infra-red receptors — **102**
— 14. Round defence (cycloalexy) — **108**
— 15. AIDS and insects — **117**
— 16. Living clouds — **121**
— 17. Killer bees — **128**
— 18. Butterfly hunters — **132**
— 19. Interesting ways of bees and dung beetles — **139**
— 20. A memorable month, May 2004, in the USA — **144**

— 21. Digestive strategies in insects — **153**
— 22. Insects and Plants during the carboniferous — **163**
— 23. Jurassic Park or the world of cycads — **168**
— 24. The lost world or the tepuys of Venezuela and insects there — **181**
— 25. Insects and the Gondwana Hypothesis — **192**
— 26. Love match! — **202**
— 27. Damselflies, experts in ballistics — **210**
— 28. Forest on the back — **216**
— 29. Scorpion beetles and lantern beetles — **222**
— 30. Timarcha, a blood spitting magistrate — **230**
— 31. Rotation of the male copulatory organ in insects and biased chirality — **236**
— 32. Carnivorous plants – insect enemies or friends? — **240**
— 33. Parental care in insects — **246**
— 34. Pheromones — **255**
— 35. Parasol ants — **260**
— 36. Do ants make slaves? — **265**
— 37. Do insects feel pain? — **269**
— 38. Pocket mites — **272**
— 39. Aphids and ants — **282**
— 40. Locusts — **286**
— 41. Walking in insects — **293**
— 42. Coprophagy — insect brethren of crowned pigs of Borneo — **295**
— 43. Lamarck's ghost or the Baldwin effect — **303**
— 44. Acknowledgments — **310**

Preface

Insects are a fascinating group, because of the huge biodiversity they present, and of their numerous remarkable adaptations to different habitats and life patterns. Of the various facets of insect life, some are discussed in Entomology classes and find place in text-books. But several aspects remain relatively ignored. This book touches some such aspects as are less talked about, and I hope that it will be a fruitful additional reading for entomology students, as is Norman's "History of Fishes" for Ichthyology learners. At the same time, several chapters in the book are of popular interest, and will help dissemination of information about insects.

Both the authors of this book are well established entomologists. Prof. P. Jolivet's contribution has been voluminous and very significant. His areas of special interest include biology of *Timarcha*, food plants of chrysomelids and ants-plants relationship. In view of his contributions, the Fifth International Symposium on Chrysomelidae in the year 2000 in Brazil was named after him. Prof. Jolivet has very widely traveled, covering almost all parts of the world, not for just seeing places, but for entomological experiences. Some of his experiences find place in this book, for example the sight of mass emergence of the 17 year cicada after 17 years of life underground in May 2004 in USA, morning dark clouds of chironomid midges rising from the Lake Edward and the neighbouring lakes in Africa badly polluted with hippopotamus dung, and 200 metres long procession of army ants entering his tent in a Congo forest, and nothing would check the progress of the ant army.

Prof. K. K. Verma has taught Zoology and Entomology, both at the undergraduate and postgraduate levels in government colleges in India for more than 35 years. He has been an active entomology worker throughout, and is known for his contributions on genitalia, digestion and polymorphism in phytophagous beetles. He has published numerous papers both in national and international journals. He has been my student, and I have always appreciated his clear perception in the subject. I am happy to see that, even after his retirement in 1991, he is still academically active and is continuing to publish research papers and reviews.

Naturalists have always wondered at the adaptive capacity of insects. Some adaptive remarkable mysteries of insects have been unlocked in chapters of this book, which brings out the uniqueness of insects in the animal world.

R. S. Saini, Ph.D. (Sagar), Ph.D. (Cambridge).
Retired Professor and Head of Zoology Department,
Sagar University, Sagar, India.

— 1. **Introduction**

We intended to write a popular book on some fascinating aspects of insect life, but we could not check the temptation of incorporating in it many interesting details, including some recently published ones, and the write up has become semi-popular in nature. While it has retained a popular flavour, it has also taken the form of a collateral reading for students of biology and entomology.

Though a common notion about insects is that they are lowly evolved, several aspects of insect life show that they are highly advanced in the evolutionary direction taken by their group. They present a huge biodiversity, much greater than of the more familiar group, the vertebrates. Their high fecundity, their capacity to adapt to widely diverse sources of nourishment, their presence in widely different environmental conditions on land, including high altitudes, polar regions and deserts, their secondary adaptation to life in fresh water and even in seas, their great migration and dispersion ability, their defence strategies, and the social pattern of life in some of them are amazing. Care has been taken to choose topics which are not commonly covered in textbooks.

The book includes discrete chapters on some aspects of insect life. It may be re-emphasized that it is not intended to serve as a textbook. It is semi-popular in nature and is meant to be used as supplemental reading for those interested in insects.

Entomology is the study of insects. But in this book "Entomology" has been taken in a broader meaning, like some authors (e.g. Fox and Fox,

1964) to include also other arthropods. We have not treated spiders, mites, king crab or *Limulus* and millipedes as “untouchables”.

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FOX, R.M. and FOX, J. W. 1964. Introduction to Comparative Entomology. Reinhold Publishing Corporation, New York.

— 2. How successful are insects? (Insect biodiversity)

We generally consider vertebrates as higher animals, believing that they are more highly evolved than other animal forms. This notion has basis on the prejudice that they are the dominant forms in the living fauna, and the "reigning" species, *Homo sapiens,* is a member of the group of vertebrates. But, while holding this opinion, one aspect is ignored, namely that largeness of body size and development of intelligence are not the only criteria to measure progress in evolution. The following discussion aims at bringing out the spectacular progress made by insects, almost comparable to, if not more than, the evolutionary advancement of vertebrates, though in a different direction.

One of the achievements of evolution is that the members of a group of organisms tend to occupy the various niches in their environment by adapting themselves to those niches, and in this process they come to present increased biodiversity. While man has come to invade different environmental conditions and niches through his cultural and technological evolution, insects have done this through the basic or "classical" organic evolution, and as a result they have come to present much greater biodiversity than vertebrates. We have to admire their evolutionary potential, while we appreciate the cultural and technological prowess of man.

How many insect species are known to us? As one of us (Jolivet, 1991) has pointed out that more than a million and a half species of living animals are known, and groupwise breakup of this figure:

Protozoa	50,000
Arthropoda (Crustacea, Insecta, Arachnida, Myriapoda)	1,250,000
The various remaining invertebrate groups	150,000
Chordates	44,000

That figure was good during the nineties. Since then, the estimates have varied continuously, and, in reality, no one knows how many Arthropoda are there on the earth, and how many living beings exist. Only for vertebrates and flowering plants we have a rather fair estimation.

Arthropoda obviously present much greater biodiversity than other groups of animals. E. O. Wilson (1987), a well known myrmecologist and a protagonist of invertebrate conservation, said., "I estimate that a total of 41,000 vertebrate species have been described, of which 5800 are reptiles, 9040 are birds, and 4000 are mammals. In contrast 990,000 species of invertebrates have been described, of which 290,000 alone are beetles – seven times the number of all the vertebrates together." In 1988, Wilson estimated the described living organisms at 1,392,485, as compiled from diverse sources. May (1988) gave a total estimate of 3,193,800 living beings. But, in his later paper (May, 1992), he does not give any estimate. Not only don't we know the number of living species, but we don't even know the exact number of described species. Wilson too does not give any close estimate in a later publication (Wilson, 1992), but mentions only a rough estimate; he thinks that 3 to 5 million could be the total number of the living species. Of course, in the past the extinct organisms were numbering by millions and that could not be evaluated, as fossils known at present are only a very small part of what are there in nature (Labandeira and Sepkoski, 1993). Flowering plants, for instance, were much more numerous than today. They were quickly increasing in diversity after the Cretaceous (Burger, 1988). Most models suggest that increasing plant diversity was accompanied by increasing animal diversity, and later they both simultaneously regressed.

Insects are small bodied. Though vertebrates are large bodied, their biodiversity could not be accurately decided. In 2004 the number of known species of fishes was 28,500, but we are aware of this that a large number still remain to be discovered and described, specially in the depth of oceans and in the Amazon region. There is a similar situation with Amphibia. We believe that our knowledge of the biodiversity of birds and mammals is most complete. Even then 2 or 3 new species of birds are being described every year, and a few small species of rodents or monkeys are being recorded at times. In contrast beetles among insects are very small, specially members of Staphylinidae and Curculionidae. *Nanosella* (Ptiliidae) is only 0.25 mm long; even then its "architecture" includes a remarkable stridulatory or sound producing organ (Sörensson, 1997). Many beetles, belonging to the family Chrysomelidae are almost 1.0 mm long. In case of beetles the principle that small organisms are usually more diverse than large ones (Dial and Marzluff, 1988) holds well. The famous scientist Haldane once said to an anglican priest, "God has shown an inordinate fondness for beetles". While we are so awe-struck with the biodiversity of beetles, 70-95% of all beetle species remain to be discovered and described (Grove and Stork, 2000). In spite of the body size difference between vertebrates and invertebrates including beetles, at present 900,000 of invertebrates have been described, amongst which 300,000 are beetles alone, and this number of beetles is seven times the number of all vertebrates together.

Let us dwell further on the existing biodiversity. So, how many arthropods are there on the earth? Erwin estimated them to be 30 millions, by calculating the biodiversity of the trees in the tropics (about 50,000 species) (Erwin, 1983). Erwin speculated only about the phytophagous forms, but the number of invertebrates living in the soil, including mites, must also be enormous. Stork estimated once the whole fauna to be between 20 to 80 millions, to come back to a more reasonable figure later on (vide infra). The sad truth is that no one knows, after 250 years of systematic research, a more accurate number (May 1992). PJ asked Basset in 2002, in Panama about this number, and he was not able to answer. There is no answer also in his recent book (Basset *et al.*, 2003), and the present authors believe that global estimates of biodiversity cannot be based on a handful of tree canopy studies. As a matter of comparison, there are a little less than 300,000 flowering plants on the earth. Like the insects, many species of plants also are slowly going extinct on the planet.

Stork (1988) gave later on a figure of 1.8 million, a very underestimated figure, as the number of all the living animal species, about 70% are arthropods, nearly 60% insects, while other invertebrates and vertebrates together would contribute to only about 30% of the total biodiversity, presented by the Animal Kingdom. This biodiversity is much more in tropical forests than in other regions. E. O. Wilson discovered in the trees in forests of Peru 43 species of ants, belonging to 26 genera, which figures are more than the numbers for all the British Isles put together. Stork (1993) said that estimates of global diversity range from about 2 to 50 millons, but 5 to 15 millions seem reasonable. Figures given are totally different from one author to another: Ehrenfeld (1986): 30 to 40 millions; Adis (1990): fewer than 30 millions; Gaston (1991): less than 10 millions; Hammond (1992): 12 millions, including 8 million insects. So the figure of 5 millions, given by Wilson (1992), seems reasonable, but probably underevaluated.

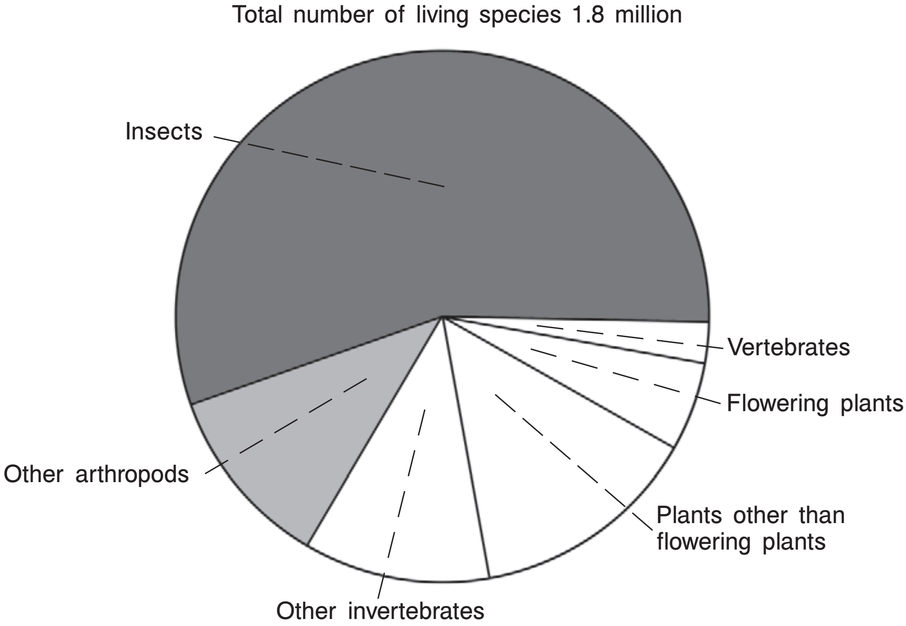
Every year hundreds of new insect species are being recorded. What would be the number of insect species, when all the species have been discovered and described? Studies on tropical forest canopies are yielding particularly large number of new insect species. Terry Erwin of the Smithsonian Institution, Washington has studied the tropical forest insects of Brazil, Panama and Peru; Nigel Stork of the British Museum has recorded insects in the forests of Borneo and Queensland, and Yves Basset the forests of Australia, New Guinea and Panama. All these eminent workers have attempted to estimate the total number of insect species, recorded and unrecorded. Their estimates are, however, widely different. In fact making such an estimate is groping in the dark. Besides, while new species are being described, many species are going extinct. Rate of extinction of organisms is going up every year through human interference.

So let us not venture into estimating the total number of insect species. One situation is obvious, that insects present much greater biodiversity than vertebrates. Evidently it is because the former could adapt themselves to a much wider range of niches than the latter.

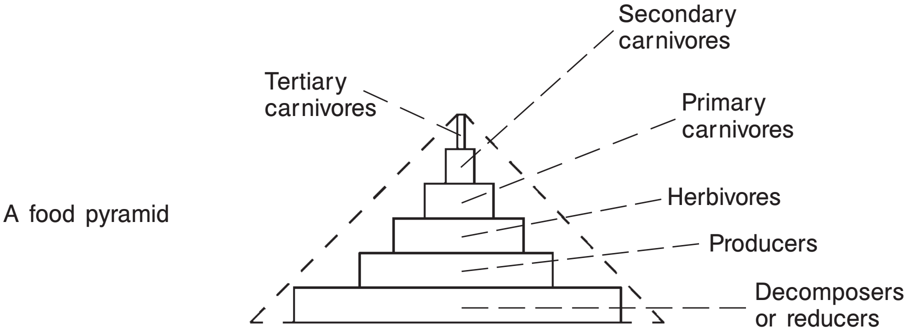
There is another parameter, other than biodiversity, which speaks of great evolutionary success for insects; it is biomass. By biomass is meant total weight or mass of living matter in a certain group of organisms in a certain area. In spite of their much smaller body size, insects present a much greater biomass than vertebrates. This situation is well brought out by E. O. Wilson (1987), "….in tropical rain forest near Manaus, in the Brazilian Amazon, each hectare (or 2.5 acres) contains a few dozen birds and mammals but well over I billion invertebrates of which the vast majority are….mites and springtails. There are about 200 kilograms dry weight of animal tissue in a hectare, of which 93 percent consists of invertebrates". This greater biomass of insects and other invertebrates speaks of their better adaptation to their niches and much higher fecundity.

Insects, mites and other invertebrates, because of their habits, occupy significant positions in the food chain or food pyramid in an ecosystem. Food synthesizing organisms or plants occupy a position near the base of a food pyramid. Above them is the tier occupied by herbivores. Further upward tiers are for primary, secondary, tertiary predators etc., and at the top stands man in a pyramid which includes him. The biomass in a tier goes on declining as we move upward; hence the pyramidal shape of such a theoretical visualization. The organic discharges (excreta, dead bodies, fallen leaves etc.) from the different tiers reach soil or water (depending on whether it is a terrestrial or aquatic ecosystem), where they are decomposed by decomposers or reducers, which include insects, mites, other invertebrates, bacteria and fungi. Through combined action of the reducers, inorganic nourishment is released from the organic waste falling into soil/water. This nourishment is needed by the producers or plants. The decomposers constitute the lowest most tier in the food pyramid. If man disappears or goes extinct, most of the pyramid will survive. But, if the decomposers and the pollinating insects are lost, the whole pyramid will collapse, and the earth will be covered with garbage. That is why E. O. Wilson has said, "The truth is we need invertebrates but they don't need us."

"Gaia, Gaia, don't go away!" Gaia, as per Lovelock, is the auto-supporting blue planet, which has maintained oxygen level in its atmosphere for the past 300 million years. All plant and animal components are contributors of this equilibrium. That is why an undisturbed biodiversity is our absolute need.



— Fig.1. A circle, divided into sectors for groups of organisms in proportion of their biodiversity (after Jolivet, 1991).



— Fig. 2. A food pyramid.

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— 3. **Insects at sea**

Insects are primarily terrestrial. While a majority of insects are adapted to different habitats on land, a small number have secondarily taken to life in water. A typical insect respires through tracheae, which are branching tubes carrying air deep into the body to various tissues. Most aquatic insects also respire with help of tracheae along with some special features to carry undissolved air close to tissue fluid. These special features, one or more of which may be present in an aquatic species, include: (i) A closing mechanism for spiracles, which are little windows, through which the tracheae communicate with the atmospheric air. The closing mechanism prevents entry of water into the tracheae, when the insect is submerged, and opens the spiracles, when the insect rises to the water surface for breathing the atmospheric air. (ii) An air store on the body surface. The spiracles open into the air store, and thus air breathing continues even during submergence. The air store may be renewed during visit to the water surface. (iii) Some aquatic insects possess tracheal gills, which are folds of thin skin, with a rich network of tracheae within them. Diffusion of dissolved oxygen from the surrounding water into the tracheae provides the necessary requirement of undissolved oxygen reaching deep into tissues. A plastron, which is a dense pile of hydrofuge hairs holding a semipermanent thin film of atmospheric air, is used by some beetles in fresh and saline water. Some small aquatic insects have blood gills, which are folds of thin integument full of blood. Direct diffusion of dissolved oxygen from the surrounding water into blood serves for respiration.

These details about insect respiration attest the statement that insects are primarily terrestrial, as almost all of them need undissolved air in their tracheae for respiration.

Though insects are primarily terrestrial, some of them have become well adapted to life in water. But surprisingly most aquatic insects have chosen fresh water environs, and very few have taken to life in sea. Actually 5% of all insect species are aquatic in rivers and lakes, whereas fresh waters constitute 0.01% of the total amount of water in the biosphere, and the oceans cover 71% of the Earth. It is evident that competition was the main driving force in evolution of land arthropods, including insects, in taking to aquatic life only in small numbers, as Crustacea and Trilobites had occupied in the past most of the available niches in water, and fishes were there as terrific predators. Arthropods, like *Limulus*, survived in water, thanks to a strong armored body resistant to any fish attack. Their spiny rounded cephalothorax is probably an obstacle to swallowing by fishes.

Mackerras (1950) has reviewed marine insects, but his paper is very brief. A recent general review of marine insects has been done by Lanna Cheng (in Resh and Cardé, 2003). Among the 15 or so orders of Insects, living in marine or near marine habitats, the most important species are found in Collembola, Heteroptera, Homoptera, Coleoptera and Diptera. Lice, found among sea mammals or birds, present often some adaptation to sea water. Cheng (1976) distinguishes for sea dwelling insects 5 habitat catégories: pelagic, coastal, intertidal, mangrove and saltmarsh. Water can be brackish in mangrove areas, which in Thailand harbour even a frog, whereas Amphibia in general shun saltish water. Insects are common in all those habitats, except in the open sea.

There are always exceptions in biology and you cannot readily generalize when dealing with living beings. To bring home this point let us see some examples among insects found in habitats other than sea. Among freshwater insects, at the larval stage, like Odonata, there is a remarkable exception in Hawaii, where is a dragon fly (*Megalagrion oahuense*), which has a terrestrial larva. The eggs are laid among trash under thickets of a fern, *Gleichenia linearis*. The nymphs live in the damp trash in the mountains of Oahu and are densely hairy (Zimmerman, 1948). Some other dragon fly larvae are arboreal, but they live in phytotelmata. Larvae or nymphs of Odonata or dragon flies are as a rule fresh water forms. No dragonfly has taken to the sea. Caddis flies (Trichoptera) are normally with aquatic larvae, but the genus *Enoicycla* is unique in Europe, having flightless females and terrestrial immature stages. The larva is a typical detritivore and is a typical limnephilid, with the exception of gills, which are absent. The female lays about 50 eggs among mosses at the base of a tree. After hatching, the young larvae construct conical cases, mainly from organic matter and start feeding on mosses, algae and tree-leaf litter (Harding, 1995). In North Africa, there is even another limnephilid, related to *Enoicycla*, *Enoicylopsis peyerimhoffi*, which lives in dry forest surroundings (Masselot and Dortel, 2004).

If we talk of terrestrial arthropods other than insects, no scorpion has come back to the sea, from where they originated. Many terrestrial spiders, mites and insects (from Orthoptera to Diptera and Coleoptera) are adapted to sea life, at least in the tidal zone, along the shores, in the rock crevices, and also mites and collembola in rock pools. Some caddisflies (Trichoptera) around Australia, New Zealand and New Guinea, lay eggs into starfishes and the larva is a tube case maker in the echinoderms (Neboiss, 1988). In Australia there are even parasitoids among larvae of Trichoptera (Wells, 1992), but all in fresh water. That has been a recent finding. Remarkably, no mosquito (*Aedes*, *Culex*, *Anopheles*) larvae live in the open sea, but can withstand a very high salinity in rock pools, streams or lagoons. Perhaps they could not survive in sea because of predators. Chironomid larvae are found in salty marshes with a salinity heavier than in the sea, but there are no predators to worry about. Among the bugs, Corixidae can breed in ponds with a salinity approaching saturation. Unlike *Halobates* (vide infra), corixids are winged and migrate by flight. An old paper by Buxton (1926) describes the colonization of the sea by *Pontomyia natans*, a chironomid midge in the Samoa. It’s a lagoon frequenting species, and it is the only known insect which is submarine in all stages. The male swims actively through the water, using its long first and third legs. *Pontomyia* has an extremely short adult life (30 min to 3 hours) and the pupae float to the sea surface. Of this genus only 4 species are known. Chironomidae, Dolichopodidae and Tipulidae are often associated with intertidal algal turf (Resh and Cardé, 2003).

Many beetles (Staphylinidae, Carabidae, Curculionidae) are found, along with Hemiptera (Veliidae, Hermatobatidae, and others), in rock crevices or in intertidal areas, on the sea shore. They are submerged at high tide like the European *Aepus robini* and the related species. *Bledius spectabilis*, a staphylinid beetle, maintains a burrow that prevents flooding, and provisions the young with algae, prevents mold and protects its larvae from parasitoid attacks (Pelissier Scott, in Resh and Cardé, 2003). In Australia, Britton (1971) reported a Limnichidae, *Hyphalus insularis*, from the intertidal zone together with bugs, and also melyrid and staphylinid beetles. The whole body is covered with a silvery film of air. The genus occurs in interstices of intertidal coral slabs on the Great Barrier Reef. It has been reported from Australia, Cocos, Howe, Norfolk, Japan and New-Zealand. It should exist also in New Caledonia and New Guinea where it has never been searched for. *Hyphalus* larvae have anal gills, a type of blood gills, for respiration (Lawrence and Britton, 1994). Recently, Hernando & Ribera (2004) found the second species of the genus *Hyphalus* from the Indian Ocean (Seychelles). The first one was found in Aldabra. Similar beetles exist all over the world on the submerged part of the sea shore, with spiders, mites, bugs (*Aepophilus*) and various other insects. Many beetles frequent the sea, and one chrysomelid, *Macroplea mutica*, a donaciine, is entirely marine in the Baltic sea, and it feeds on *Zostera*. One dermapteran, *Anisolabis littorea*, in New Zealand lives in brackish-water sponges (Cheng, in Resh and Cardé, 2003), along with other insect larvae. The gill chambers and eggs masses of marine crustaceans are poorly known habitats for immature insects (Humes, 1948). Larvae of Diptera and Coleoptera have been found on crabs in various places in the tropics. Probably, those larvae feed upon detritus and mucus in the gill chambers, but they may be capable of piercing the gill surfaces. Some chironomids seem to live naturally in the gill chambers. A *Luciola* firefly lives on old coral reefs near Madang, in New Guinea (Lloyd, 1973). The entire lifecycle is spent on the reefs.

Let us briefly talk about plants in the sea. Marine angiosperms or flowering plants are rare in the sea (only around 30). They are all monocotyledons, like *Zostera*, and van der Hage (1996) believes that their rarity is due to their pollination mechanism and the absence of coevolution with insects. If angiosperms had invaded the seas, perhaps, she says, the insects would have followed. Perhaps relative absence of flowering plants in sea is because production of a large number of gametes is very costly to the plants, and pollination causes serious problems in the sea. Insect evolution predates that of the angiosperms by some 200 million years, and the reasons why the sea was not colonized is not very clear. The association of insects with green plants on land started very early and probably algae were not very attractive to them.

A marine caddis fly, *Philanisus plebeius* (Trichoptera), on the coasts of Australia and New Zealand, oviposits into a starfish, *Patiriella exigua*, and the larva constructs its tube from coralline sea-weeds, in inter-tidal rock pools. It feeds on bryozoans, copepods, and other small rock-pool animals (Anderson *et al.*, 1976). The adult female has strong ovipositor and this ovipositor is employed to insert the eggs into the coelomic cavity of the starfish where they hatch and develop into larvae. The larvae escape rapidly from the strarfish host and very probably they eat their way out through its body wall. Other case-making larvae, presumably with the same biology, are known on the coasts of the south-western Pacific Ocean. Species of *Philanisus*, *Chathamia* and probably more caddis fly genera remain to be discovered and studied (Riek, 1976). The above described mode of oviposition offers protection to the caddis embryos in the intertidal habitat (Anderson and Lawson-Kerr, 1977).

There is only one insect genus, which lives in open sea; it is the water strider, *Halobates,* a Gerridae; 42 species of this genus are found in sea, but out of these only five species occur in open seas, while 37 species are confined to coastal waters (Pathak *et al.*, 1998). *Halobates* species aggregate into flotillas on the sea water surface, like the bug *Gerris*, the beetle *Gyrinus* or the mosquito larvae in fresh water. It could be a strategy for protection, and possibly a feeding strategy for the Hemiptera and Coleoptera in fresh waters, but the group effect (Grassé) in the flotilla has never been completely understood. Water striders (Gerridae) walk on water. They have non-wetting legs that enable them to stand effortlessly and move quickly on water (Gao and Jiang, 2004). The legs are covered by large numbers of regularly oriented tiny hairs (microsetae) with fine nanogrooves, which enhance water resistance. This holds both for fresh and for the sea gerrids. Only the four long hind legs are used for locomotion, while the two small front legs hold the preys to facilitate the sucking of their juices.

The oceanic species of *Halobates* occur in tropical and subtropical seas, often hundreds of kilometers away from any land. They are specially numerous in areas covered with sea weeds. They are seen walking or skating on sea surface.

Being wingless they must be drifting with water currents to achieve their dispersal. *Halobates* are chiefly indo-pacific, and they are missing in the Mediterranean Sea, and known there only as fossils from the Eocene. Probably the drying of the sea during the Tertiary in the Mediterranean region killed them, as it killed the Merostomata. *Halobates robustus* occurs on the surface of the coastal waters of the Galapagos Archipelago (Foster and Treherne, 1980), close to mangrove and lava edges. Its food consists of dead insects floating on the sea. Predation by fish, birds and reptiles (the marine iguana) is reduced by extremely effective avoidance behaviour by the flotillas. One of us (PJ) remembers the *Halobates* in the Red Sea, on the Ethiopian coast, along the small mangroves of those islands, going often far away into the open sea. Food was rare in those semi-desert environments, as the islands are practically bare, but for halophytic plants.

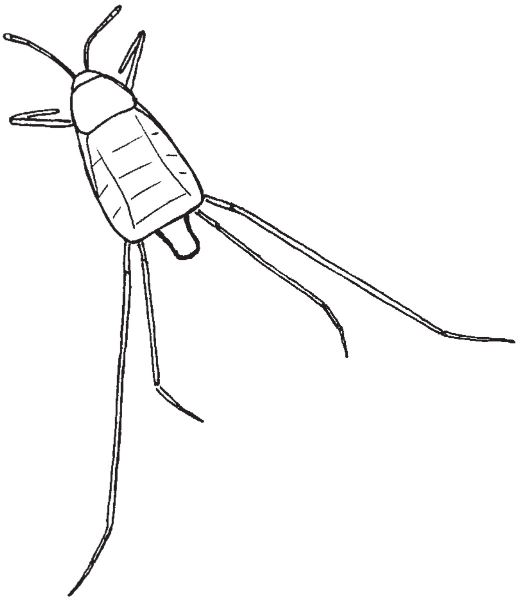
Members of Gerridae, the bug family to which *Halobates* belongs, are almost confined to fresh water bodies, and are seen skating about where water is stagnant and quiet. Their middle and hind legs are very long, and the tarsi of the legs are covered with long branching hairs, which are difficult to wet. These hairs spread out on water surface, and this makes possible for the insect to skate around on the surface of water. If somehow the tarsi go wet, the insect will sink. In this situation the water strider has to climb on some solid surface and expose itself to air for sometime to dry its tarsi, so that it may skate around again on water. Front legs of a water strider are quite short and foldable in such a way that they may hold certain floating objects, which are generally dead insects, which fall to water surface and constitute the main source of nourishment for the water striders. It is surprising that out of the huge class of insects some members of only one family, Gerridae, most members of which live on placid waters, have become adapted so well to marine life.

As has been pointed out above, most sea dwelling species of *Halobates* are confined to coastal waters. Water striders of a related family, Veliidae, and some other bugs also occur in coastal waters. In fact a number of land or shore living insects may venture or fall into coastal waters, but they are destined to perish, unless they swim back to coast.

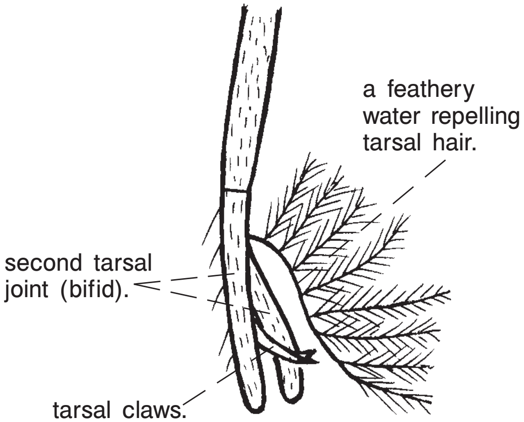
Though truly marine habit is confined to a few species of the surface strider *Halobates*, many other insects are met with in sea. Terrestrial insects, mostly small and light bodied ones, rise in the atmosphere with thermal air columns and may be blown out into sea for long distances by air currents or winds. This way the insects may drift over sea for hundreds or even thousands of miles. Such air drifting insects have been trapped and studied over the Pacific, the Antarctic and some other oceans by several workers, mainly by Gressitt, Cheng and their associates (Cheng and Birch, 1977 and 1978; Gressitt *et al*. 1960 and 1961). More recently insect trapping over the Bay of Bengal and the Arabian Sea and their study have been carried out by Pathak and his team (Pathak *et al*., 1999a and b). The collections made over the Indian Ocean mostly included small beetles, flies, bugs and wasps. These air borne terrestrial insects eventually fall dead to the sea surface. They may be collected floating on sea water. They constitute a source of nourishment for marine life, including the marine *Halobates* (Jolivet, 1991).

We may find terrestrial insects at sea under another situation. Dragonflies are known to fly following moving objects for reasons not known. Pathak (1996) noticed several dragon flies following and flying over an oceanography research vessel right from Marmagoa Port in the western coast of India to the Lakshadweep group of Islands. They perhaps periodically rested on structures on the ship. It was not a dragonfly in any way adapted to sea life. Pathak *et al*. (1988) noted a butterfly alternately resting on the upper deck of the ship and flying following a loop like course over the sea surface to return to the ship.

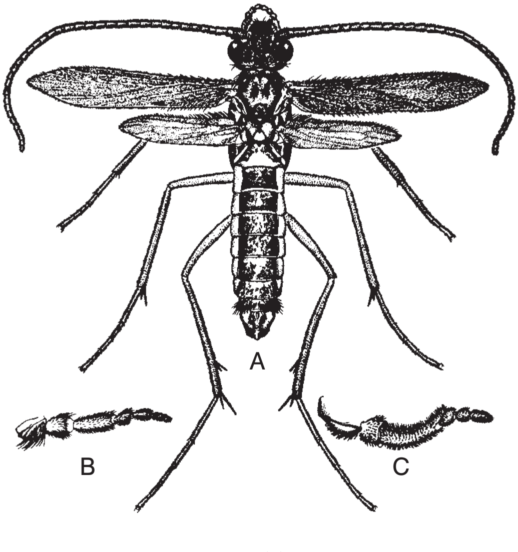
Thus the oceans, not inhabitable for insects in general, are not free from them.



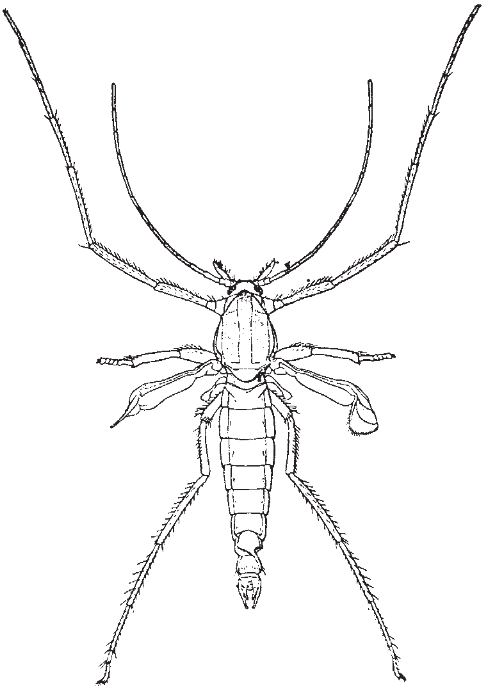
— Fig. 3.1. *Halobates* sp. (Based on a photograph in Pathak *et al.*, 1999).



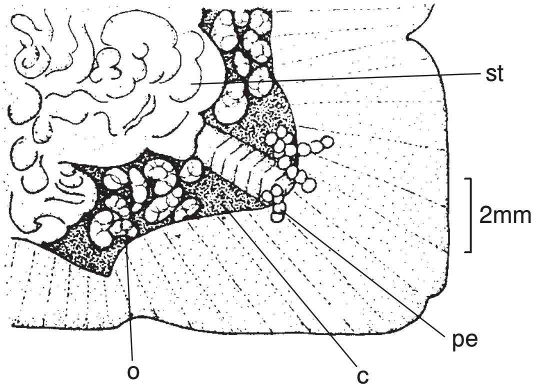
— Fig. 3.2. Middle leg tarsus of a water strider (Based on Essig, 1954).



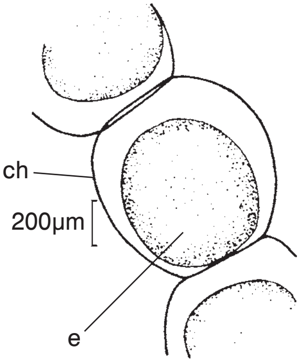
— Fig. 3.3. A marine caddis-fly, *Chathamia brevipennis* from Chatham islands. A: male adult; b: female maxillary palpus; c: male maxillary palpus (after Riek, 1976).



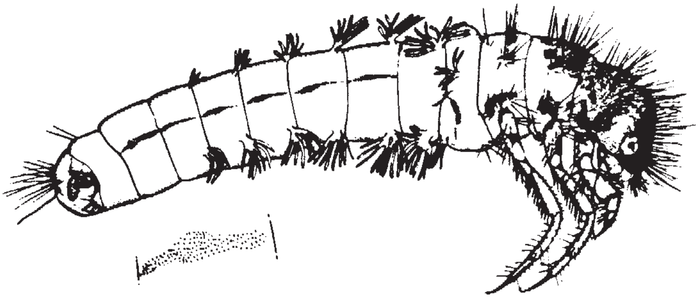
— Fig. 3.4. *Pontomyia natans*, a chironomid midge, in the Samoa (after Buxton, 1926).



— Fig. 3.5. *Philanisus plebeius*, a marine caddis-fly. Eggs exposed by dissection of the starfish, *Patriella exigua*. c: coelome; o: ovaries; oe: eggs of *Philanisus*; st: stomach.



— Fig. 3.6. Egg ribbon of *P. plebeius* enlarged. ch: chorion; e: egg.



— Fig. 3.7. *Philanisus plebeius*, larva outside its tube.

— Fig. 3.8. The larval tube built with coral algae.

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— 4. **Insects in frigid regions**

Insects in fairly good numbers have become adapted to life in frigid areas. Such areas are the polar regions and high altitudes on mountains.

According to M. S. Mani (1974), who has studied high altitude environment of most high mountains of the world, high altitude region is the timber line altitude of 2500 to 3000 metres and above. The Arctic region is considered as extending from 60 to 65 degrees north to further northward. The Antarctic region may be taken as extending from 50 degrees south to further southward. But from the present viewpoint the latter polar region is not so important, as at present our knowledge of its insect fauna is very poor.

In the north polar region insects are found mostly up to 79 degrees north. At high altitudes, which are also referred to as the alpine region, insects have been collected up to 4800 metres and above. According to Mani, insects in the alpine zone are mostly concentrated at the snow edge.

The frigid regions are so referred to because of extreme cold in those parts. In the alpine environment the low temperature is due to semi-rarefied air. Such an atmosphere is very transparent, and its heat retention capacity is low. Presence of suspended particles is very small; it is about 1% of the contents of such particles at the sea level. This further lowers the capacity of the atmosphere of retaining heat from solar radiation. Air temperature, therefore is very low. In polar regions low atmospheric temperature is not due to rarefied air, but due to the angle of incidence of sun rays. While in the alpine regions the sun rays reach the ground level almost vertically, in polar regions the rays are at a wide deviation from right angles, when approaching the ground.

Another special feature of the alpine region is that the solar radiation is much richer in ultra violet rays (UV) than at the sea level. The dense atmosphere at lower altitudes is quite transparent to the visible part of the solar spectrum, but it is opaque to UV radiation. Hence the radiation reaching the lowland regions is almost free from UV. But in alpine zones UV is in a considerable proportion in the sun light. The same is true for the Antarctic zone due to the ozone hole over the South Pole. While the ozone hole in the south is enlarging through human activity, the ozone layer over the Arctic is thinning out due to a similar reason. Even benign chemicals, released from factories and gadgets, condense on surface of the polar clouds, and may become ozone destroying.

Insects in frigid regions show a number of interesting structural, physiological, behavioural and developmental adaptations to the extreme conditions in which they live. Both alpine as well as polar region insects tend to be dark due to heavier pigmentation of the integument. They may be black. That is true also in the Andes, where many insects are dark, for instance, some cassidines and some chrysomelines (*Elytrosphaera melas* in Bolivia and others in Ecuador). They may also be dark blue, dark green or copper. Dark body colours help absorption of heat, when there is sunshine, and they also prevent entry of UV into the body, and thus they protect vital internal organs. In the high tropical mountains, like in the Andes, at the snow level, around 4800 m, there are wingless forms of phasmids, hiding under stones. Many beetles, for instance *Metallotimarcha*, in European mountains remain active during the night and hide under stones or vegetation during the day. It could be a way to avoid the sun rays. All *Metallotimarcha* species are copper-like.

Most alpine and polar species are brachypterous (i.e. with reduced wings) or apterous (i.e. with wings lost). According to Mani, in the north-western Himalayas about 60% of insect species at altitudes above 4000 m are apterous. In the Antarctic Peninsula between 61°S and 65°S, occurs a chironomid, *Belgica antarctica* (Jolivet, 1991; Sugg *et al.*, 1983), the southernmost free-living holometabolous insect. The adult males and females of this species are apterous. In 1984, a new chironomid species was discovered in the Nepalese Himalayas, a species of *Diamesa* living on glaciers. The adults of this species have reduced wings and antennae, and are unable to fly. It was found walking on the surface of glaciers (5130 to 5400 m) and in small cavities beneath them (Kohshima, 1984). The larva grows in melt-water drainage channels under the ice and feed on cyanobacteria (*Phormidium*) and bacteria. The insect spends its entire life cycle in the snow and ice of the glacier, the coldest habitat ever recorded (-16°C). This insect was active at this low temperature. Although several invertebrates have been introduced into the Antarctic, no holometabolous insect has survived there for a long period, except the endemic *Belgica*. However, a chironomid midge, *Eretmoptera murphyi* has been recorded from moss at Signy Island, South Orkney Islands (Block *et al.*, 1984). The fly survived for many years and was thought to have been introduced from South Georgia or the Falklands. Its population is parthenogenetic and capable of supercooling to between -13 and -26°C, but it is not active at such low temperatures. Cryoprotectants have been found in the insect extracts.

The loss of wings and flying capacity is a result of natural selection. Alpine and polar regions have violent storms almost regularly; hence selection operates in favour of reduced wings. That windy environs favour reduction of wings has been experimentally shown in *Drosophila* fly. An entire tropical American genus, *Elytrosphaera*, linked with high altitudes and with the Brazilian plateau, has fused elytra and is totally wingless. It has normally a bright coloration, but shows darkening with increasing altitude. It is close to the Colorado beetle group, which live in lowlands and are good flyers.

Another advantage of wing loss in beetles (Coleoptera), which dominate among insect fauna of frigid regions, is that, due to disappearance of wings, a subelytral space is created. Such an air-filled space acts as a thermal insulation, and prevents heat loss from the body. (In beetles the front pair of wings have become thick and hard. They are called elytra. The hind wings are membranous, and they alone are used for flight. The elytra form a protective cover for the membranous hind wings in repose. Disappearance of the latter leaves a space beneath the elytra, the subelytral space.) Loss of wings is accompanied by degeneration of flight muscles, a change, which makes room for production of larger eggs. Production of such eggs is a part of the strategy for adaptation to frigid conditions (vide infra).

Still another structural change is reduction in body size. A reduction in surface area of the body reduces heat loss.

Frigid region species remain active when it is sunny. When the sky is overcast and at night, they remain without movements and concealed under grass, weeds and under stones.

A specially notable physiological adaptation in insects in frigid regions is cold resistance. Larvae of the Arctic leaf beetle *Chrysolina subsulcata* are quite active at -3 to -4 °C. The Himalayan chironomid *Diamesa,* living on glaciers, is normally active at -16 °C. Springtails (Collembola) are quite numerous around the snow line at high altitudes. They merrily jump about on snow covered fields. Many insects synthetize polyols from glycogen. The cold resistance in these insects is due to presence in their blood of polyols and other anti-freeze substances, similar to those which are mixed with radiator water of cars in cold countries.

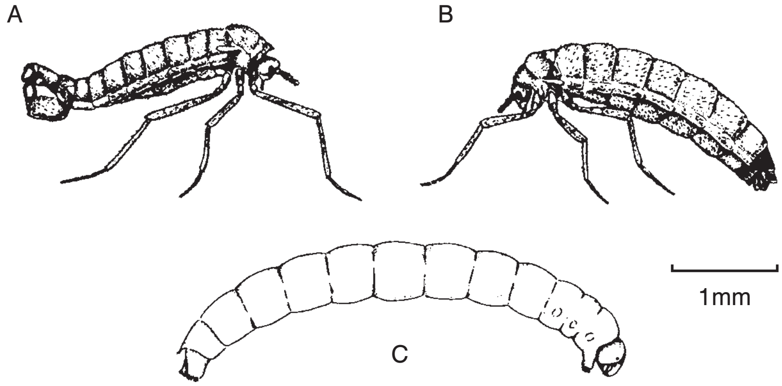
Due to paucity of vegetation in frigid areas most insects are debris and carrion feeders. According to Mani on the north-west Himalayas at 5000 metres only 3% species are phytophagous. All the rest are feeders of dead organic matter and are predaceous. Algae and cyanobacteria are the food source for some of them

Frigid area insects show some interesting developmental adaptations to the cold conditions. Some are viviparous (i.e. the embryonic stages are passed within the body of the mother, and hatched young larvae are given birth to) or ovoviviparous (i.e. early embryonic stages pass within the mother's body, and eggs with a well developed advanced embryos, ready for hatching, are laid). As a result early embryonic stages are shielded within mother's body. In general, frigid area insects lay larger eggs (e.g. *Brachyhelops*, a leaf-beetle in the islands of Southern Patagonia) to permit longer embryonic development due to low temperatures. But *Timarcha,* which is black, has fused elytra and is totally wingless, lays only a few big eggs and lives mostly in plains. It seems to be a result of a very long evolution, at least from the Jurassic, since the pupae are also wingless. Perhaps *Timarcha* originated in steppic areas, probably in Central Asia, and it is adapted well to cold in Europe, being black, with a subelytral cavity and having a complex system of diapauses. Quite an interesting exception, and probably a case of preadaptation.

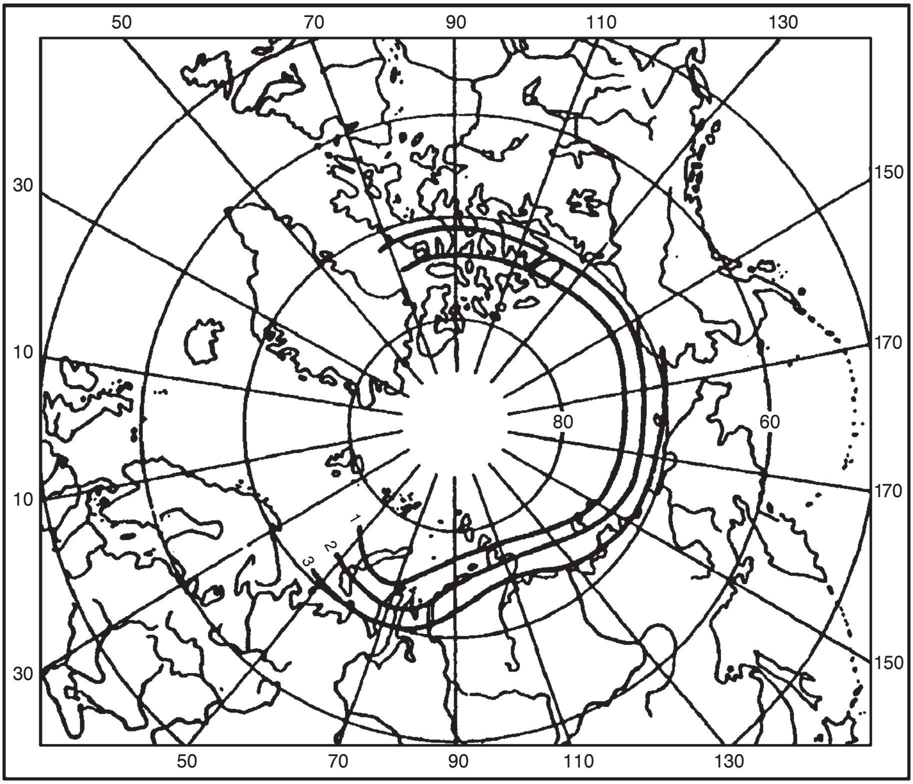
Another developmental adaptation is long periods of hibernation or diapause at more than one developmental stages, so that adverse periods are tided over safely. It may be recalled that food requirement is greatly reduced or is nil during periods of hibernation or diapause. Adult chironomids do not eat generally at the adult stage. As a result of such diapauses the development is a long story. The Arctic species *Chrysolina subsulcata* shows two larval diapauses. In addition, there may be more diapauses in the larval stage. In this species development from egg to adult stage may take as long as six years (Chernov, 1978; Chernov *et al.*, 1994).

There are no insects in the Antarctic, except two flies and the bird and mammal parasites. Beetles are quite common in the subantarctic islands, but the leaf beetles are missing. There are 21 families of beetles in Greenland, and no chrysomelids, but they were abundant at the Pleistocene (Böcher, 1988). Lack of chrysomelids, in those places, means, except for Antarctic itself, of late no opportunity of dispersion. Leaf beetles are quite capable in surviving in the Southern Greenland climate. In the Antarctic, nematodes, tardigrads and rotifers are quite common living on mosses, lichens and cyanobacteria (Convey and McInnes, 2005). Insects, including beetles, so common during the Jurassic, disappeared with the *Nothofagus* forests in early Oligocene.

Insects and spiders from plains are often found lying dead at high altitudes. They have been lifted from plains by warm air columns, and have fallen dead and frozen on surfaces high up on mountains. Lowland arthropods may be lifted to high altitudes in considerable numbers. Mani observed in the Himalayas at 4000 m that, in an area of 100 m^2, over four hundred dead insects of plains were deposited in 20 minutes during May-June. Bodies of these low land forms should be adding to the food available to carrion feeders at high altitudes.



— Fig. 4.1. *Belgica antarctica*, an Antarctic chironomid. A: male; B: female; C: larva (after Sugg *et al.* 1983).



— Fig. 4.2. Number of Chrysomelidae, shown by latitudinal lines, in the northern zone of the Arctic (after Chernov *et al.* 1994).

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— 5. **Omnipresent Ants**

Ants, constituting the insect family Formicidae, are a large group. According to the great American entomologist E. O. Wilson, 11,574 species of ants have been discovered and named (Hölldobler and Wilson, 1990; Wilson, 2003). Many more species remain unrecorded. When all the species will be discovered and described, their number will probably come close to 20,000. Like the humans they are found in almost all parts of our planet. They are there in peripheral parts of the polar regions, and in the rest of terrestrial areas, including deserts, tropical forests, grasslands, sea shores and at high altitudes on mountains. Hence to call them omnipresent is only an excusable exaggeration. Ants are missing in the Arctic, including Greenland, and Antarctic, where there is no food and it is too cold.

In frigid areas of Alaska and north Canada they are plant feeders, and help in pollinating flowers. Away from these extreme north areas, they may derive their nourishment from plants, but they do not act as pollinating agents, as they possess glands, which kill pollens (Jolivet, 1991). However, they are known to pollinate orchids in Australia. Ants have not been found so far in Greenland, but they may be discovered in future. According to the high altitude expert M. S. Mani (1974), the common high altitude ants are species of *Formica, Cataglyphis* and *Camponotus*. He collected *Formica picea* at the height of 4800 m on the north-west Himalayas.

Desert ants show remarkable adaptations to their arid surroundings. They make deep subterranean nests, consisting of a complex system of galleries and chambers. At a certain depth in soil, there is some moisture, there are no such violent temperature changes as on the ground surface and moist soil particles are held together more firmly giving some permanency to the ants' abode. The soil, removed during digging and making of the nest, is arranged as a little heap on the ground surface with mouth of the nest appearing as a crater on it.

A special feature of the life of ants in a desert area is the habit of collecting and storing food during the brief period of vegetation growth, when some food is available in the arid habitat, so that food is there for members of the colony throughout the year.

Among desert ants are harvester ants, which store seeds of various grasses in the nest in some special chambers, which may be called granaries. Vigorous seed gathering is done towards the end of the growing season. One interesting fact about the life of harvester ants is that there may be wars between members of two colonies of the same species. Winners in a war take away the stored grains from the losers' nest to their own. True wars (i.e. organized conflicts between two conspecific groups) are known only in two members of the Animal Kingdom, namely ants and humans. The great zoologist-philosopher Julian Huxley has pointed out that accumulation of property seems to have led to wars both in ants as well as in man. In human history wars are believed to have started after man took to settled life with agriculture and habit of storage.

Some arid area ants are known to store sugary fluid, collected from plants in the brief period of plant availability, within the body of some workers, which act as living banks of reserve food or 'repletes'. Such ants are known to occur in deserts of South America, Mexico, parts of USA, Africa and Australia. As in case of other ants, the honey storing ants are markedly polymorphic. A colony of honey hoarding ants consists of a queen and workers, amongst which are nurses, guards, honey collectors and honey pot ants or repletes. The honey pot ants are workers, which are set aside by nurses, when the former are quite young, and their skin and gut wall are still soft and pliable. During a small period of vegetation growth the honey collectors dexterously drink in liquid nourishment from flowers of cacti, other desert flowers and galls of certain plants. With their swollen abdomens, distended with the collected juices, they return to their nest and reach the chambers with repletes. The repletes or the honey pot ants have their legs dug into the soft roof of these chambers, and they are hanging from the roof. Here the honey gatherers regurgitate drop by drop most of their liquid gut contents close to the mouth of the repletes. The repletes readily engulf those drops. Thus by mouth to mouth transfer most of the food, collected by the gatherers, enters the gut of the repletes. The abdomen of the latter increases several times the original size due to accumulation of liquid nourishment in their guts. The honey storing repletes never move out from the nest, and they have sacrified their individuality for the purpose of food storage for the colony (Poole and Poole, 1963). In dry periods, when no food is available in the surroundings, the inmates of the colony survive on the liquid droplets emerging from the mouths of repletes, when they are stimulated by stroking with antennae of the hungry sisters.

Elsewhere in temperate, subtropical and tropical regions there is an abundance of ant species. They mostly make their nests in the form of subterranean galleries and chambers or under stones and logs. Many ants arrange the dug out earth at the mouth of their underground nests, forming a little hillock. Of special interest are carpenter ants, which make their nest by boring into wood. Some carpenter ants make their way into the narrow space between bark and trunk wood. Using their strong jaws they make their galleries in the hard wood. Some others burrow into rotting wood or wood softened by and already excavated by wood boring beetles. Ants on sea shores and river banks live on drift wood and other organic debris available there.

Tropical and subtropical ants take to some amazing ways of nest making. Some of them make hanging nests on trees with leaves "tailored" together. Their nest making activity has been described in the Chapter 11. "Insect and Tools". Some tropical ants make a flower garden up on a tree. They carry bits of moist earth from the forest floor to a point of forking in a tree limb. Through long and continuous hard work of the ants the earthy deposit takes the shape of a fairly large ball. The ants now start bringing up seeds of the various plants on the forest floor, and putting them into the mud ball. After some time the ball becomes covered with flowering vegetation. While the vegetation is growing, the ants dig galleries and chambers in the mud ball. The vegetation cover makes the earthy ball resistant to the tropical rains. According to Seidel *et al.* (1990), some of the volatile compounds on seeds of ant-garden epiphytes probably play a role in attracting ants to the epiphyte seeds (Jolivet, 1998). It has been questioned by some authors: why do ants make their hanging gardens? Perhaps the attractants present on epiphyte seeds invite them to do so.

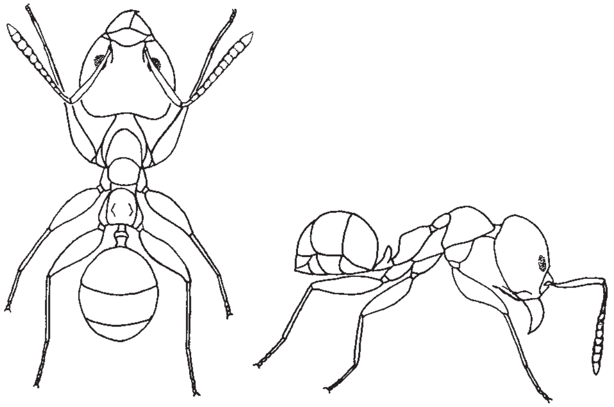
Ant-plants or myrmecophytes are plants which offer to ants natural housing facilities, to be used as a nest and eventually as latrines, and, often, but not always, food in various forms (food bodies or trophosomes, pearl bodies, extra-floral or floral nectaries, edible fruits, elaiosomes or seed outgrowths, containing fats or oils, pith in the stem, saprophytic fungi, oil droplets, etc.). In exchange, the ants are supposed to defend the plant against phytophagous insects and mites, feed it through their excreta and cadavers, prune the climbers and the weeds, reject the eggs of parasites, etc. Sometimes the sugars, supplied by coccids and other homopterans, replace what the ant gets directly from the plant. Lodging for the ants is named as *domatia*. Domatia have been defined as plant-produced chambers that house animals, e.g. the ants, differing from the galls in that they are not induced by their inhabitants. Domatia can lodge also mites or thysanoptera. They are not exclusive habitats for ants. Ant domatia are usually in hollow stems, stipular horns, petioles, hypocotyle axis, pseudobulb, rarely in roots, and also in hollow leave spaces.

Many myrmecophytes are known, more than 510 species, belonging to 65 plant families, around 277 in America (23 families), 66 in Africa (14 families) and 167 (28 families) in Asia and Oceania. Several new myrmecophytic plant families are being discovered in SE Asia and more remain to be described, specially in New Guinea and Borneo. There are myrmecophytes in Northern Australia, but none in New-Caledonia and New-Zealand. None exists also in temperate regions, except perhaps one case in Texas. Their structure is generally preadapted and hollow to harbour ants, but in a few of them the ants dig themselves into the pith. Others have special adaptations in the leaves (leaf pouches or domatia), like the *Tococa* and *Maieta*, and many more Melastomataceae, in America. Some myrmecophytes eventually grow even into the ant-gardens (Jolivet, 1996). Some are remarkable myrmecophytes, like *Myrmecodia* and *Hydnophytum*, in SE Asia, with preformed and specially aerated cavities, some absorbing excreta and cadavers of the inhabiting ants (e.g. *Philidris myrmecodiae*).

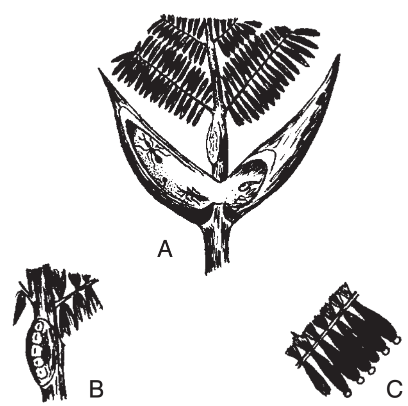
Ants are very variable in their feeding habit. They may be phytophagous, carnivorous or saprophagous. In chapter 39. "Aphids and Ants", ants using aphids for feeding on plant juices have been described. Many ants are fungivorous. They grow fungi in some chambers of their nest. The parasol ants use bits of leaves and their own excreta as the substrate in their fungal garden (see chapter 35, "Parasol Ants"). Other fungus cultivating ants are known to use caterpillars' excreta, fallen anthers of flowers and other soft plant debris for this purpose.

A considerable part of the dispersal of ants across the world has been due to human activities. Ants have been moving with boats, wagons and timber. Entomologists sometimes take to fanciful thinking. They have imagined that, when man is able to establish his covered colonies on the moon or on the Mars, ants will accompany him there. At the moment ants are almost omnipresent on the Earth and new invaders like *Solenopsis, Wasmannia* are slowly extending their area.

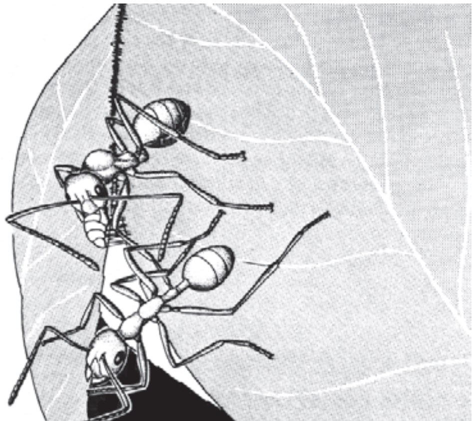
The ants' great adaptability, well pronounced polymorphism (i.e. occurrence of adult individuals with different forms and capability), wide range of food choice, a fine distribution of labour in an ants' colony, and their close association with some articles of human use are the factors responsible for their almost universal distribution.



— Fig. 5.1. *Philidris* (=*Iridomyrmex*) *myrmecodiae*, ant living inside *Myrmecodia* spp. in SE Asia.

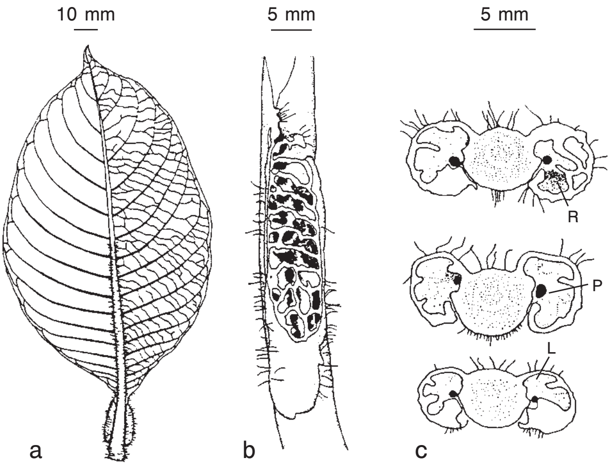


— Fig. 5.2. Neotropical *Acacia*, Mexico. A: swollen stipules or thorns, harbouring ants; B: nectaries on the petiole; C: Beltian food bodies or trophosomes at the end of the folioles (after many authors and Jolivet, 1996).

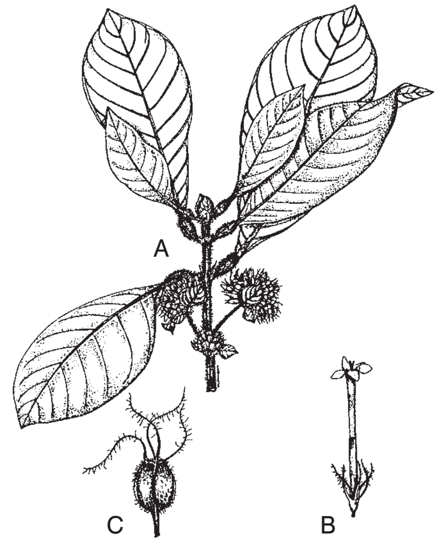


— Fig. 5.3. *Oecophylla* workers building a nest in joining the leaves and using larvae as shuttle (after Dumpert, 1981).

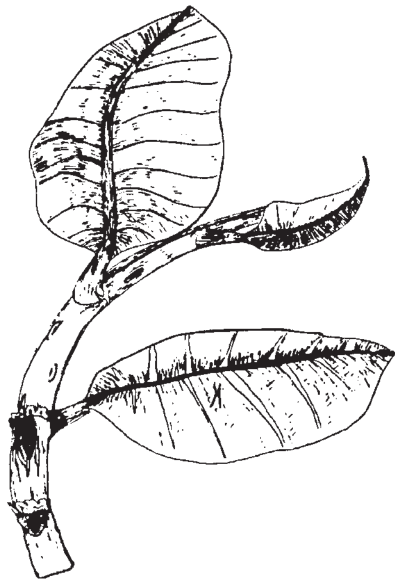
— Fig. 5.4. An ant-garden in Guyana, on a tree (after Jolivet, 1996).



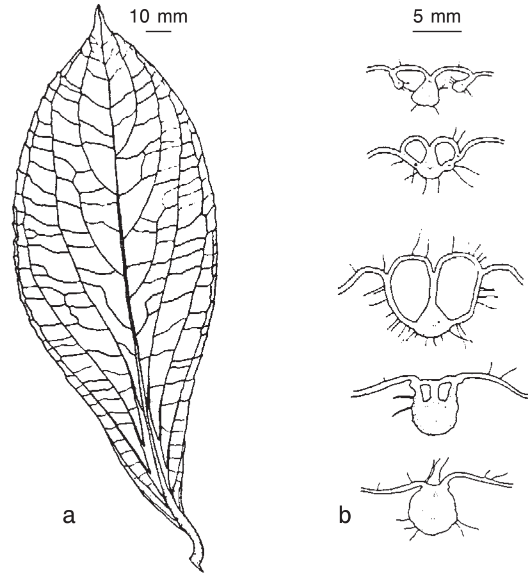
— Fig. 5.5. a: View of *Hoffmannia vesiculifera* (Rubiaceae) leaf (abaxial view) showing location of the formicaria on the petiole; b: a lateral view of the vesicle with a portion of the wall cut away; c: three cross-sections through the vesicles. P: lipid glands; R: refuse deposits (after Windsor and Jolivet, 1996).



— Fig. 5.6. *Hoffmannia vesiculifera* Standley. A: a twig; B: flower; C: fruit. (after Dwyer, 1980). Panama.



— Fig. 5.7. *Triplaris* sp. (Polygonaceae), from the Pantanal, Mato Grosso, Brazil, inhabited by ferocious ants, mostly *Pseudomyrmex* spp. (after Benson, 1984).



— Fig. 5.8. a: a single *Besleria formicaria* (Gesneriaceae) leaf; b: five cross-sectional views of the leaf along the formicaria (after Windsor and Jolivet, 1996).

— Fig. 5.9. *Hoffmania vescicularia* (Rubiaceae), Panama (photo Jolivet).

— Fig. 5.10. *Hoffmania vescicularia*, Panama. Section through the domatia (photo Jolivet).

— Fig. 5.11. *Besleria formicaria* (Gesneriaceae), another myrmecophyte from Panama (photo Jolivet).

— Fig. 5.12. *Myrmecodia sclechteri* Valeton (Rubiaceae), epiphytic on *Casuarina nodiflora.* Goroka, New Guinea (photo Jolivet).

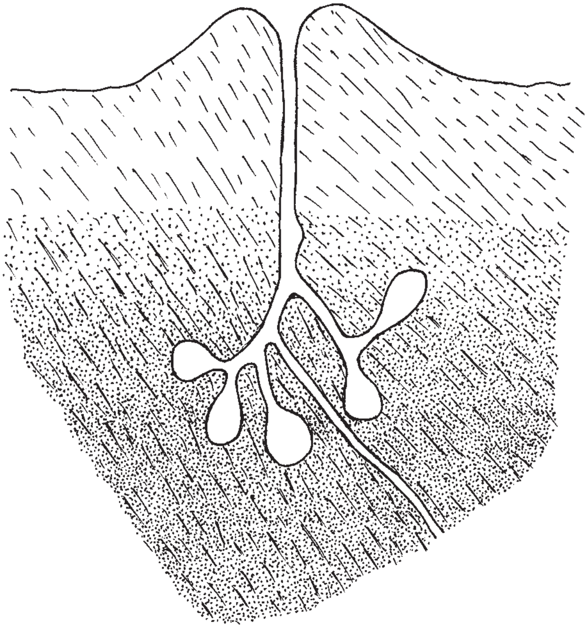
— Fig. 5.13. The same as Fig. 5.12, detail of leaves and fruits (photo Jolivet).

— Fig. 5.14. The same as Fig. 5.12, median section of the inflated tubercles (hypocotyle axis) showing the cavities occupied by the ants (*Philidris* spp.) and some internal roots (photo Jolivet).

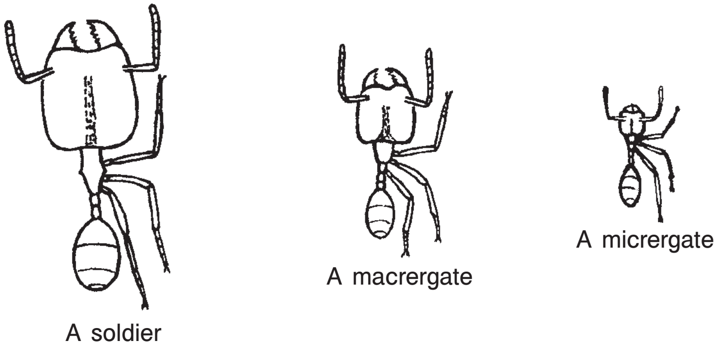
— Fig. 5.15. *Acacia collensii* (Legum. Mimosaceae), Panama, harboring *Pseudomyrmex* ants in the stipular spines. Extrafloral nectaries and Beltian bodies are visible (photo Jolivet).

— Fig. 5.16. *Cordia alliodora* (Boraginaceae) with an opened node containning the ants (*Azteca*), Panama (photo Jolivet).

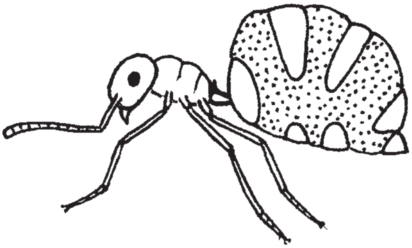
— Fig. 5.17. The same as Fig. 5.16. at a higher magnification (photo Jolivet).



— Fig. 5.18. Diagram of a vertical cut through the subterranean nest of an arid area ant. Dots are intended to show moisture in soil.



— Fig. 5.19. Three types of workers in a colony of a myrmicine ant. (*soldier* = a large worker with extra large head and mandibles; *macrergate* = a large bodied worker; *micrergate* = a small bodied worker).



— Fig. 5.20. A replete of a formicine ant.

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— 6. **Insect migrations**

Among arthropods, insects are provided with wings, as are birds among vertebrates. Presence of wings gives these animals increased mobility. Insects show migrations, which, in some respects, remind one of the better known bird migrations.

Cases of insect migrations may be grouped under three categories:

(1) Seasonal migrations.
(2) Migrations to new lands/areas due to insect's special attributes.
(3) Migrations due to human activities.

Seasonal migrations of butterflies have been known to man quite long. Early explorers of the New World witnessed this phenomenon without clearly understanding it. Even Columbus, when his fleet was approaching Cuba, saw large swarms of butterflies almost darkening the sky. There were huge cricket migrations (*Anabrus simplex*) when the Mormons came to Utah in the USA. The Mormon cricket is a species endemic to western North America.

Seasonal migration of the monarch butterfly (*Danaus plexippus*) has been well studied by American entomologists. When winter is approaching, these butterflies from all over USA and Canada migrate southward, flying in swarms, and cover up to three thousand kilometers, and reach Mexico, Florida and Cuba, where they settle on trees, covering their trunks and branches almost fully. During winter, they remain almost motionless, crawling away at times to escape direct sun. Butterfly covered trees are a tourist attraction. Activities in the migrants return in spring, and now swarms start in a northward journey. During this return journey they often breed and lay eggs on milkweed. Parents die, and the offspring continue the northward migration. By the time the swarms reach their summer station, it is the third generation. In the next autumn the butterflies migrate again, and come to rest on the same trees as their forefathers in the southern destination (Akimushkin, 1973). The migration of the western populations of the monarch in the USA is more complicated. These populations overwinter in aggregations along the coast of southern California.

South American monarchs (a different species from the North American) also show weak seasonal migrations, towards the equator in autumn, and southward in spring (Akimushkin, 1973). *Danaus gilippus* in South America is non-migratory, a feature which has allowed the evolution of several subspecies.

Northward and southward migrations, in spring and autumn respectively, are shown also by some European butterflies. The painted lady (*Cynthia cardui*), the red admiral (*Vanessa atalanta*) and the death's head hawk moth (*Acherontia atropos*) are some examples of this. The painted lady migrates in large swarms. After spending winter in Africa, they gather in swarms again, and fly towards Europe. PJ saw them crossing Morocco, in Rabat, once a year, and flying north during more than one day by millions. The whole town of Rabat was covered with the butterflies. *C. cardui* is widespread on most continents with the exception of South America, where it is rare, and of New Zealand. They fly over the Mediterranean, and fly high over the Alps. They reach north Germany, Britain and Russia. Later they are in Scandinavia. In their migration they cover thousands of kilometers. During summer the migrants, arriving from Africa, breed in Europe. After egg laying the parents die. Their progeny, which are larger and more brightly coloured than their parents, fly southward to North Africa to breed in winter there. The painted lady cannot survive the winter in Northern Europe and Britain.

In the migration pattern of the painted lady there is an indication that they follow warm air currents. For example, they reach Britain, before settling in the Western Europe, which is more southern. This is perhaps because the British coasts are warmed by the Gulf Stream.

There is an obvious similarity in the migration of birds and of these butterflies. In the northern hemisphere both migrate to a southern location in autumn, and return in spring to their northern station. But there is a significant difference between them. Most long range migratory birds have their breeding grounds in a northern station. When winter is approaching, they, along with their young ones, migrate to the warmer conditions of a southern station in search of new feeding grounds. In spring they return to the northern quarters. Thus the same generation performs both southward and northward journeys, whereas the butterfly generation, performing northward/southward journey, is separated by one or more generations from the generation in the previous journey in the opposite direction. A particular butterfly generation, if it migrates, migrates only once, either northward or southward. How do they follow the same route and reach the same station as their parents/grandparents? The only answer we have at present to this question is "instinctively". In fact study of butterfly migrations is in its initial stages. Studies in coming times may unfold some interesting details.

Some dragonfly species also show seasonal migrations. Swarms of dragonflies have been seen flying southward across the Alps in autumn.

Lady bird beetles too are known to undertake seasonal migrations like some butterflies and dragonflies (Akimushkin, 1973). They are believed to swarm southward and northward in autumn and spring respectively. Swarms of lady birds have been seen flying across countries in Europe, Africa and America. In California they have been seen feeding on aphids and other phytophagous insects in fruit orchards in valleys. In autumn they move up on hills as swarms, and high up on the hills they enter into winter sleep or diapause under stones and dry leaves on the ground. When it is warmer in spring, they become active again, and move into valleys, where fruit trees are in blossom, and harbour a good supply of plant feeding insects. The great French entomologist J. H. Fabre saw a small chapel, built on a hill top, with all the walls and the roof covered with a continuous sheet of small red globules. Coming closer to the building he realized that the globules were actually overwintering lady birds.

Now let us turn to those insects which migrate to new lands due to their special features and establish themselves in new areas. The monarch butterfly of North America (*Danaus plexippus*) is a great flier. It can cover thousands of kilometers. It has been able to cross even the Pacific Ocean.

In 1850 these butterflies were first seen in the Hawaii. After a decade they appeared in New Zealand, and later in Australia.

Another striking example of a species, migrating to new lands and extending its range with help of its special attributes, is a tiny flea beetle, *Chaetocnema confinis* (Kalaichelvan *et al.*, 2001). This species originally belongs to North America. But in recent years it has extended its range enormously. Now it is in Central and South America, Africa, Southeast Asia and in some Pacific islands. Outside N. America it was first seen in 1979 in the island of La Reunion by one of us (PJ). After that it has been collected from Mauritius, Madagascar and east Africa. In 1996, it was reported from the Palau Island, Ryukyu Archipelago of Japan, northern Thailand, Vietnam, Taiwan and the Hawaii. In 2001, the present authors (along with Serge Doguet and Mr. Kalaichelvan) reported presence of this insect in India. It is strongly suspected, though not yet confirmed, that it is present in China, and, perhaps, in Australia (Jolivet, 1998, 2000).

The following special attributes of this flea beetle seem to be helping the insect in spreading its range almost throughout the tropical and the subtropical world.

(a) Its light and small body (about 1.5 mm in length), such that it may be readily carried away by winds and air currents.
(b) Its excellent flight capacity.
(c) Its polyphagous habit, as it feeds on leaves of various plants, though basically it is a feeder on a number of *Ipomoea* species.
(d) Its female is facultatively parthenogenic. If a single female reaches a new area, through parthenogenesis she can establish a new population. It may be mentioned here that males of this insect are known only from the New World. Elsewhere there are colonies of only parthenogenetically reproducing females.

Locusts are grasshoppers, with short antennae (Acrididae), with an inherent property of swarm forming and migrating. They show polyphenism, i.e. they, under certain environmental conditions, produce a swarm forming and migratory phase. A locust swarm moves a long distance, destroying all vegetation in the way, and producing a famine like condition in the countries covered. Locust breeding grounds are oases in deserts. They live like any grasshopper species, but, due to continued breeding, the population density in the limited breeding ground increases, and, when the population density has reached a certain high, a shift in the direction of the migratory phase occurs. Eventually the migratory phase is produced, and a swarm leaves the breeding ground. The migratory phase differs from the nonmigratory phase both in structure and physiology.

Some species of seed weevils or bean weevils (the beetle family Bruchidae), which infest stored legumes, show a phenomenon with some resemblance with the migration of locusts. When the density of the seed weevil population in a store becomes quite high, a new phase develops, which has been referred to as the flight phase or the active phase. The active phase individuals have only partly developed reproductive organs, greater flight capacity and a migratory tendency. They are meant for reaching new stores, though they do not fly as a swarm. One of us (KKV), along with his students, has studied this phenomenon in *Callosobruchus analis* and *C. maculatus* (Tiwary *et al.*, 1989; George *et al.*, 1994).

Let us now discuss some cases of insects extending their range and reaching new countries and continents through human activity.

The vine louse or the vine *Phylloxera* is a tiny insect, similar to an aphid. It infests roots of grape vines, producing small swellings in the roots or root galls. It was originally in North America. In 1918, it suddenly appeared in France. In the new country, it soon became a serious pest of grape vines, making the vines dry up, and threatened end of the wine industry, though in N. America it was not doing appreciable damage to grape cultivation. While the French wine industry was trying to survive by importing grapes, the pest spread through the rest of Europe. It was realized that the American variety of grape plants was resistant to the vine louse. The French growers succeeded in saving their grape cultivation by importing grape plants from America, and by using them as stocks, on which they grafted their own variety of grapes (Akimushkin, 1973).

The spread and distribution of the grape *Phylloxera* is believed to have been through human commercial movements. The winged phase of the grape lice is a weak flier, and, therefore we cannot imagine that it crossed the Atlantic on its own.

Another particularly notable example of an insect migrating through man's commercial activities is of the Colorado potato beetle (*Leptinotarsa decemlineata*). This insect was harmless, originally confined to the eastern slopes of the Rocky mountains in North America, feeding on leaves of night-shade, a local weed of the Colorado region. When European, moving across the N. American continent, reached its western parts, they started potato cultivation. The Colorado beetles readily took to potato leaves, and they particularly liked the young and tender leaves of this new food plant. The voracious feeding on potato leaves seems to have greatly improved their fecundity. A single female lays about 700 to 2800 eggs. Larvae grow fast, feeding on young potato leaves, and soon develop into the next generation adults. After recovery from a winter diapause and before it is time for the next winter dormancy, three generations are produced. It has been estimated that a single female at the beginning of an active period theoretically leaves behind 80 million descendants at the end of that period. Predators and parasitoids regulate the numbers.

Soon the Colorado beetle spread through most of N. America. In 1871 it had reached the Atlantic coast of the N. American continent. In 1876 it appeared in Germany, and then quite quickly it moved to reach most of Europe. In 1990s it came to China (Jolivet, 1991a and b; Jolivet, 1994).

In Europe efforts to fight the potato pest was not yielding satisfying result. The governments of Germany and France made laws to prevent any further import of potatoes from America. Germany used its army to fight this severe menace to potato cultivation. The army men dug trenches around an infested field, and then, after sprinkling oil, the infested crop was burnt (Akimushkin, 1973). Next year only some potato plants were grown as a bait for the potato beetle, if any were still surviving. Very few beetles were attracted to the bait. Hence it was inferred that the pest could be eradicated. Then came the first world war. Soldiers had to be withdrawn from their agricultural assignment. In 1914 the pest again appeared in a serious form. Perhaps this second appearance was due to stages of the pest moving with provision and baggage of American soldiers.

Fight against the Colorado potato beetle continues, though with application of modern methods of control, presence of the pest in the field does not cause panic. It seems, at least in Europe, reasonably contained.

A recent insect migrant with help of human commercial activities is the flea beetle *Epitrix hirtipennis* (Jolivet, 1998). It feeds on tobacco. It is originally from Mexico, Central America and USA. In 1984 it reached Italy. In 1993 it was in Turkey. Perhaps it is present in most of the Mediterranean countries.

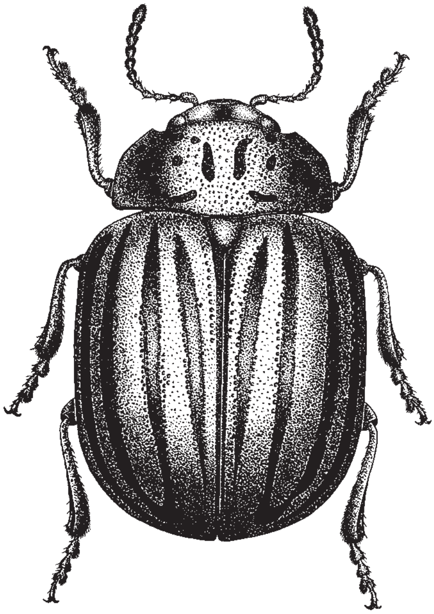
In fact there are many examples of insects moving with crops and plant products from one country to another. The maize root worm (*Diabrotica virgifera virgifera*) of the New World has arrived in Serbia, near Belgrad, in 1992, probably with American planes (Jolivet, 1998). It has then invaded most of western Europe, has reached Paris, France, and a few years ago, Italy, Hungary, and is probably now also in Turkey. The old world *Aulacophora*, another related galerucine, is specially attracted by cucurbits and cucurbutacins, which are toxic compounds present in cucurbit plants, but *Diabrotica* is far more dangerous on other crops, including maize. So far, it does not seem much virulent in Western Europe.

Often for biologically controlling an insect pest or a noxious weed, insects are imported into a country from another country. But this has to be done after a very careful and well planned study of interaction between the species proposed to be imported and the fauna and flora of the receiving country. The case of the Guam Island is well known. A number of parasitoids had been introduced to eradicate some pests, but it resulted in wiping out hundreds of endemic species of moths.

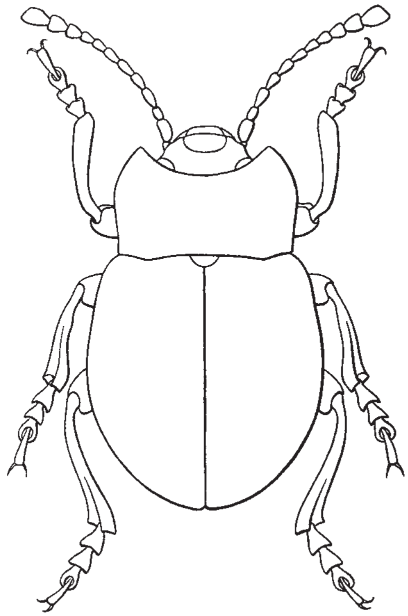
Hugh Dingle (in Resh and Cardé, 2003) has reviewed insect migrations. He has pointed out that juvenile hormone, a time-compensated sun compass, and some other mechanisms, still to be studied, are involved in regulating such migrations. Lepidoptera, namely Uraniidae, the day-flying moths, in tropical America, Madagascar or New Guinea, Pieridae, Nymphalidae, also dragonflies, and large Hymenoptera seem to maintain a constant direction during migration. PJ has seen, several times, the migrations of *Urania* in Panama and Nicaragua and those of *Alcides* (Uraniidae) in New Britain, and it is certain that nothing can make the moths deviate from their course. Sometimes, in New Guinea, a mimetic butterfly (*Papilio laglaizei*) matches the migrating flight and derives its protection from the toxicity of the model, the uranids. Migrations of Uraniidae have been specially studied by Smith (1983) and Lees and Smith

(1991). There are nocturnal, non migrating Uraniidae (e.g. *Lyssa*, syn. *Nyctalemon*) in South East Asia, but the brightly colored day flying ones, *Urania* (tropical America), *Chrysiridia* (East Africa and Madagascar) and *Alcides* (New Guinea and N. Australia) are all migratory, and as caterpillars, feeders on the toxic euphorbiaceous genus *Omphalea* and related plant genera (Smith, 1992). The biochemistry of these plants may be one of the driving forces in population regulation, migration and strategy of the physiology of these butterflies (Smith, 1983, 1992). Hundreds and thousands of *Urania* fly synchronously every year generally in an eastward or south-eastward direction through Central America from Mexico as far south as northern Columbia, always in unidirectional dispersions, probably in response to diminished food in their usual breeding territories (Hogue, 1993). Strangely, contrary to theoretical predictions, the speed of flight among *Urania fulgens* in Panama is independent of both body mass and abdominal lipid mass (Dudley *et al.*, 2002).

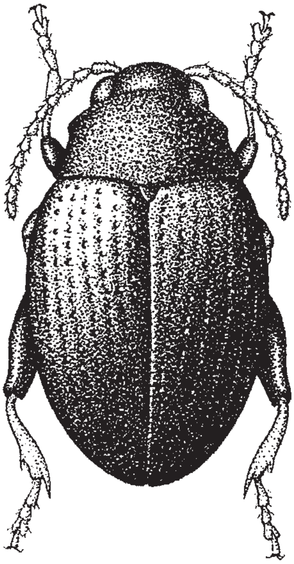
Dingle (loc. cit.) thinks that migrating butterflies incorporate a sun-compass, as in case of movements of honey bees and ants, and, that for the nocturnal migrants, other mechanisms, still not fully understood, are involved. Migration is a trait of considerable complexity and uraniid and danaid migrations are far from being adequately understood.



— Fig. 6.1. *Leptinotarsa decemlineata* (Say) (Col. Chrysomelinae), the Colorado potato beetle, a great migrant (after P. Jolivet).



— Fig. 6.2. *Timarcha* (*Metallotimarcha*) *metallica* Laicharting (Col. Chrysomelinae). A non-migrant, but nocturnal and feeding on Rubiaceae and Ericaceae.



— Fig. 6.3. *Chaetocnema confinis* Crotch (Col. Alticinae) from North America, a great migrant (after P. Jolivet, 2000).

— Fig. 6.4. *Papilio laglaizei* Depuiset (Papilionidae), New Guinea, the mime (photo P. Jolivet).

— Fig. 6.5. *Alcides agathyrsus* Kirsh (Uraniidae), the model. A case of Batesian mimicry (photo P. Jolivet).

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— 7. **When the ants will wake up…!**

According to the famous American entomologist, E. O. Wilson, there are around the world 11,574 species of ants (Wilson, 2003), while previously (Hölldobler and Wilson, 1990), he estimated them to be 8800 species only. Probably there exist more than 20,000 ant species in the whole world, distributed among 350 genera. Ants are adapted to all situations, they are found everywhere, except in Antarctica and Arctica, where they could not reach due to lack of food (see the chapter on "Omnipresent ants"). In the cold area, as north Canada or Alaska, they help, with the mosquitoes in plant pollination. They seem to be absent from Greenland, but we are not quite sure about it. There are Pleistocene ant fossils in the extreme north of the island, in the Peary Land.

Outside the extreme north, ants pollinate plants only exceptionally, since they are inefficient or they possess glands, which kill the pollen. Their dispersing capacity is almost nil. There are, however pollinating ants in Australia, and there they pollinate orchids by pseudo-copulation (see Chapter 26. "Love match!"). Those ants don't have pollen killing glands, and flowers and insects are perfectly adapted to each other.

Ants are very resourceful and adapt themselves to almost any situation. They are very stubborn and nothing stops a herd of tropical ants starting in a razzia or a procession. In that case it is better to evacuate one's tent or one's house, and to leave the ants alone. They will clean everything in their way. PJ remembers once in Kivu, when he was sleeping under a tent in the bush somewhere in a mossy forest, on feeling a bite, he woke up and was obliged to leave quickly his precarious dwelling; compact columns of Doryline ants had for some unknown reason decided to pay a visit to the solitary entomologist. The column measured nearly 200 m long and 20 cm wide. PJ waited outside, a flashlight in hand, expecting that the visitors cleaned the area of termites and all unexpected visitors. After one hour, the ants, probably satisfied, changed their direction and went back to their headquarters. Those ants eat everything, and I never saw again such emaciated chickens, brought there by my cook after the ant invasion. I had tried to stop the invasion with insecticides and fire, but all was in vain and I had to give up.

Mr. and Mrs Larson, a couple of English entomologists, wrote once: "Man is, in fact, reaching for the stars. He may attain them, but life is such that, if he does, it may well be that the ants will go there with him" (Larson and Larson, 1965). They have travelled in the boats, in trains, in cars and have reached continents previously devoid of certain species. The Argentine ant, this big traveller, has now colonized almost all the tropics and subtropics. We can imagine that a little ant will reach with man the planet Mars, and will survive there without space suit with the modest atmosphere existing there. What could she eat? Not much, perhaps only scraps of food, dropped by man.

But if man one day vanquishes, as the Star Trek team, the obstacle of the light-years (warp speed!) and visits a planet with a normal atmosphere in another solar system, it is very probable that ants would also establish themselves there. Science fiction? Yes. But is it not permitted to dream?

The Council of Europe voted recently an Invertebrate Charter. That is easy and costs nothing. That was why it got the unanimity. Protection of insects seems to them to be a duty, while the destruction of trees is tolerated. It is easy to vote for such a text while reckless destruction of habitats continues in Brazil, Borneo and elsewhere. The famous English naturalist Myriam Rothschild became a vegetarian in order to stop eating animals, but, if we must protect all living things, from panda to protozoa, we cannot give the same protection to all. If we do it, as wrote one day a veterinarian, it will become suicidal. Are we obliged to protect also malaria carrier mosquitoes or Chagas transmitting bugs as we protect the beetles or the butterflies of our forests? British naturalists have proposed to celebrate one day the Insect year, the Creepy-Crawly Awareness Year. Why not plan a Year of Awakening of Intelligence and Foresight or a Year of Conscience? More an animal is intelligent, more it will be aware and conscious of its surroundings, and, being most intelligent in the living world, we should be respectful to nature in a holistic way.

Someone with prejudice of "specism" or racism may have low regard for other living forms and even for some of our fellow humans. It is true that the Bible or the Gospels don't speak much of animals except in several passages in the Genesis where God entrusted all living beings to humans. There are other similar passages elsewhere here and there. Buddhists are respectful to all animal life and so are the Indians. It is a fact that we should not torture other animals stupidly. But is it unwise to destroy the *Salmonella* or the amoebas colonizing our intestine? Will it be wise to raid and attack laboratories with cultures of small pox virus and anthrax bacteria with a mission to liberate organisms from cruel hands of man?

An American entomologist from Wyoming, Jeffrey Lockwood, has written in 1987 a well informed paper on the moral standing of insects, published by the very serious journal "Florida Entomologist". He defends vigorously insects and finds even in Protestant theology defenders of the existence of a soul in Invertebrates (Jolivet, 1999, 2002). We must have consideration for our inferior brothers, says Lockwood. Peter Milward (1972) has also written a book full of poetry on soul of Insects. This is far away from entomology, entering the fields of philosophy and poetry. A poet, even if he is entomologist, can be swayed away by emotions.

Let us imagine that the ants, which possess a very sophisticated small brain, will succeed against us on the earth. After all, they have preceded us in evolution by hundred million years, and they are still here, powerful and active. That they become bigger, stronger, better organized (if that is possible) and more intelligent, man then will disappear, victim of his own aggression or of generalized pollution and destruction. The successful ants will impose their own order, mercilessly and ruthlessly. There will be no more forests, no more myrmecophilic plants. The ants will manage by themselves, on a barren floor, covered with some algae, mosses, and lichens.

Will it then be an insect planet? It is much more probable that man will destroy himself through his own foolishness, unless he develops the wisdom of the ants and will struggle to survive in competition against some insects like ants, which have much greater fecundity and capacity to adapt themselves to diverse habitats than the human species.

One may wonder if, among billions of habitable planets, there is a planet with an ant like form as the dominant living species. We can always dream, as probably our capacity of visualisation is much more developed than in any other species on this planet. Let us try to imagine what will happen when ants wake up!

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— 8. **Chemical defence in beetles and moths**

Insects take to various defence strategies against predation. These strategies include homochromy (i.e. resembling the background in colour and marking pattern, very common among adults and developing stages of insects), camouflage (i.e. having a close resemblance with some objects in the surroundings, e.g. the dry leaf butterfly of the Orient, *Kallima*, and various stick insects or Phyllies resembling dried up twigs or leaves), aposematism (warning coloration for defence), mimetism, mechanical devices (e.g. spines on the body of the leaf-beetles belonging to the subfamily Hispinae, springing mechanism in the third legs in members of another leaf-beetle subfamily, Alticinae), reflex bleeding (i.e. coming out of blood through ruptured skin at certain places in the body, e.g. the leaf beetles of the genera *Timarcha*, *Oreina* and *Galeruca* and others, like *Meloe*, show reflex bleeding, on being disturbed, at the tibiofemoral joints of their legs or near the mouth and chemical defence (i.e. through presence of certain toxic chemicals in their body).

Meloe and other blister beetles, like the *Paederus*, secrete cantharidin which is a toxic and dangerous substance. One of us (PJ), while collecting meloids near a dam in Sudan, got many beetles trapped under his shirt. He was covered with blisters and had a high fever during the whole night. People know that cantharidin has the reputation to be an aphrodisiac. It is remarkably toxic, and 100 milligrams are lethal to humans. There are many criminal cases of poisoning due to meloids and meloid powder given to humans. Thomas Eisner, in his recent book (2003), reports that French legionnaires in Algeria, in 1893, were poisoned by frogs that they had eaten, because the frogs had fed on local meloids, which are very abundant there after the rains. As is well known in England, the French people eat frogs and snails; that is why they are sometimes called "Froggies". So no wonder, why those legionnaires in Algeria found and ate the unfortunate amphibians. In North Africa, the larval stage of these meloids feed on nymphs of grasshoppers. *Meloe*, at the larval stage (the larvae of meloids are called triungulins), is parasitic on bees. *Meloe* is now relatively rare now in Europe or United States, but PJ remembers that once on the Tchiaberimu, hilly area situated on the west side of Lake Edward, he saw many of them on *Galium* and grasses all over the mountains. But there *Timarcha*, another beetle, was not present on *Galium*. This other beetle, being apterous and slow moving, did not reach Central Africa. It could not even cross the Sahara and cannot be found in Hoggar mountains, for instance. But *Meloe*, thanks to the triungulins, which climb from flowers to the body of bees, had their aerial transportation, and the Sahara was not an obstacle to their migration.

Bombardier beetle stores in its abdominal glands hydroquinones and hydrogen peroxide. In the reaction chamber, with enzymes, the two substances interact and this leads to an explosion. The resulting spray reaches the boiling point and vaporizes. All entomologists have at least once experienced the heat of the vapour on their skin. One young Danish entomologist lost the use of one eye that way. His cornea was burnt by the quinones. It is like what some millipedes do in the tropics; they can blind you if the spray reaches the eyes.

Leaf beetles (Family Chrysomelidae) live as adults and larvae well exposed on the plant body, as they are mostly leaf feeders. Hence they are readily available to preying insects. Quite naturally they have taken to several different ways of protection against predators, including the interesting chemical defence.

Chemical defence in leaf beetles has been extensively studied by Pasteels and his coworkers (Pasteels *et al.*, 1988, 1889, 1992, 1994). So far only three subfamilies of the huge family Chrysomelidae, namely Chrysomelinae, Criocerinae and Galerucinae have been concentrated upon.

The toxic chemicals, present in the body of leaf beetles, are released to work against predators in several different ways. One way is through externally opening glands, which are glandular pockets of the epidermis. Such glands are called exocrine glands. These glands are located on the pronotum (i.e. the dorsal shield of the first segment of the thorax) and on the hard forewings or elytra. Pasteels *et al.* (1988) have described the discharge from these glands thus: "After disturbance, the secretion oozes out from the gland pores and accumulates in the marginal grooves of elytra and pronotum as well as in more or less defined pronotal and elytral depressions, constrictions and concavities. These contours certainly help to retain the secretions on the insect". Toxins in the blood of the insect may also be released by reflex bleeding. In many insects, as in *Pimelia* (Family Tenebrionidae), there is discharge of fluid contents of the gut either through the mouth or through the anus when they are disturbed. The discharged fluid is likely to contain the toxins present in their plant food, but a definite demonstration of this remains to be done. It often contains quinones, and, therefore it is toxic and repellent. In some places in Morocco, *Pimelia* and *Timarcha* species show some kind of Müllerian mimicry. They are quite similar in appearance and both are toxic: *Timarcha* by reflex bleeding and *Pimelia* by regurgitation. Both are totally apterous. *Pimelia,* being omnivorous, is more adaptable than *Timarcha* and has a much wider distribution in Africa and Asia. *Timarcha*, a chrysomelid, needs its host-plant, not always available, and, therefore it could not cross deserts like *Pimelia*

In New Guinea, the *Polyconoceras* millipedes squirt their very toxic quinones covering more than one meter. The quinones burn skin, and eyes, and can be very toxic. One of us (PJ), around Lae, in the east of New Guinea, got the secretions over his body. He came back with a bee-keeper equipment and all the plastic was badly burnt. The skin after receiving the spray was disintegrating rapidly. Blind dogs are found in the area, and it is said that criminals among the natives used the extract to poison their enemies. The papuans are terribly afraid of them. Similar cases of quinone projections are known in tropical America among several millipedes, but they are rare. Generally they ooze quinones, on their diplosegments, as in Africa, but do not project it. Centipedes bite, but all millipedes produce secretions, cyanide, proteins, as varied as the group to which they belong. This account of millipede toxins is a little deviation from the topic of this chapter, but it may be accepted, as it illustrates what arthropods may do for their protection.

Larvae of some tortoise beetles (leaf beetle subfamily Cassidinae) carry a fecal mass at the end of their abdomen. Besides the repulsive nature of the fecal discharge, secretions of some exocrine glands may be added to it to improve its defensive value. The discharge may also contain some toxic compounds present in their leafy food.

Still another possibility is that toxins accumulate in blood, and affect the predator, when the latter attacks and wounds the leaf beetle. The attacked insect may get killed, but after this agonising experience the predator will avoid attacking kins of the insect killed. This situation has been referred to as "kin selection" by Pasteels. Ferguson and Metcalf (1985) have observed that a preying mantid does not attack galerucine beetles, which have been fed in cucurbitacin rich diet, but it readily attacks galerucines reared on cucurbitacin free diet. (Cucurbitacins are toxic compounds in plants of the Family Cucurbitaceae.)

Leaf beetles get a variety of compounds with their plant food. Some of these chemicals are toxic or repulsive to predators, and are stored in the insect body and used as such in defence. Other compounds may provide material for *de novo* synthesis of defensive compounds in the insect body.

Defensive compounds identified in insect body include:

(1) Nitropropanoic acid and isoxazolinone glucosides.
(2) Cardenolides.
(3) Polyoxygenated steroid glycosides.
(4) Pyrrolizidine alkaloids.
(5) Amino acid derivatives.
(6) Anthraquinones.
(7) Cucurbitacins.
(List from Pasteels *et al.*, 1994.)

Cardenolides are present in the exocrine secretion of some chrysomeline beetles, e.g. *Oreina* and *Chrysolina*, but these compounds are lacking in their plant food. It has been demonstrated that they are synthesized *de novo* in the insect body from phytosteroids, present in food. Pasteels *et al.* (1992) have found that in *Oreina cacaliae* pyrrolizidine alkaloids in the form of N-oxides, present in the food, are retained and concentrated in the insect body as such, and are translocated to exocrine glands, but in another species of the same genus, *Oreina gloriosa*, synthesis of cardenolides occurs within its body from phytosteroids in the food. *Timarcha* has a red blood, the composition of which is poorly known. Its hemolymph is generally rich in anthraquinones. No bird or lizard feeds on it, and day living species (*Timarcha* s.str. and *Timarchostoma*) show an abundant reflex bleeding through mouth or legs. Kids in France and elsewhere play with them; they take them in their hand and say: "Give me your blood, and I'll give you my white wine". There are several nursery rhymes in Western Europe about bloody-nose beetles. Their only enemies are parasitoids (Hymenoptera and Diptera). They have also protozoans in their gut, but those gregarines are harmless and are only commensals. The nocturnal species (*Metallotimarcha* and *Americanotimarcha*), having practically no enemies, do not show any clear reflex bleeding. *Timarcha* blood is extremely toxic and a small dose can kill a dog. *Timarcha* remains toxic with anthraquinones, when feeding on Rubiaceae or on Plantaginaceae. Nobody has yet tested the toxicity of the nocturnal species feeding sometimes on Rubiaceae (*Metallotimarcha*), and also on Ericaceae. Being nocturnal, they don't need so much toxicity in their blood. The American species, feeding exclusively on Ericaceae and Rosaceae, do not show any reflex bleeding. *Metallotimarcha* however shows scanty bleeding on being disturbed.

Some Central American moths, like *Utetheisa ornatrix*, studied by Eisner (2003), emit, from thoracic glands, froth in response to a disturbance. Cells from their blood are present in the froth, as in *Timarcha,* which frequently has blood cells in the ejected blood. One of us (PJ), with colleagues from STRI, has witnessed another member of Arctiidae, Pericopinae, in Panama mountains, a *Hypocrita* sp. (John Heppner det.), which projects a long cylinder of solid paste instead of froth. PJ has named it as the *tooth paste moth*. The observation is still unpublished. This moth feeds mostly on *Crotalaria*, a rather toxic plant. J.-M. Maes, an entomologist in Nicaragua, has told me (PJ) that some Hypsidae, *Chetone angulosa*, which is a mimic of a Heliconiid and an Ithomiid, and *Phaloesia socia* and some others produce a smelly yellow froth from their thorax; it is an effective repellent against birds, lizards and some other predators. Bubbled mass producing is frequent among beautiful acridians in Africa, like *Zonocerus elegans*, feeding on *Calotropis* and other toxic milkweeds (Asclepiadaceae). Perhaps it will be interesting to mention here similar and strange phenomena among some other insects. Pyrgomorphidae locusts are mute, as they lack stridulatory or rubbing sound producing apparatus, but their evil-tasting and foul-smelling secretions, mixed with air, render them very poisonous. Often they are short-winged, but long-winged forms are also found. Aposematic yellow aphids are often seen with them on *Calotropis*. Ejection of blood in reflex bleeding was named *autohaemorrhage* and ejection of blood with air – *haemaphrorrhea*. The first term came from Hollande, a worker on *Timarcha,* and the second from Grassé, who studied *Zonocerus*.

Many beetles, belonging to the leaf beetle subfamily Galerucinae, feed on plants of Cucurbitaceae. They get with their food the compound cucurbit-acin-B. This toxic compound gets conjugated with some smaller molecules, and gets stored in the body of the beetle in a concentrated form. As has been pointed out earlier, the general predator mantid avoids attacking those galerucine beetles, which have fed on cucurbitacin containing diet.

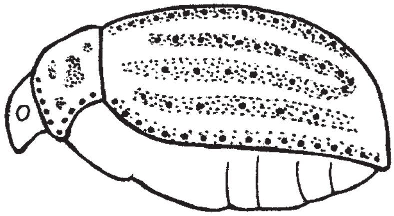
Some insects, due to a small mutational change in their genic set, are able to attack even plants with toxins in their sap. Along with their plant food, the toxins enter their body. They not only tolerate the toxins, but also use them for their defence. This situation is well illustrated in a meticulous study by Labeyrie and Dobler (2004). They have worked on the genus *Chrysochus* (chrysomelid subfamily Eumolpinae). Two species of this genus, *Chrysochus auratus* and *Chrysochus cobaltinus*, feed on plants containing the toxic cardenolides. All other species of the genus feed on plants without cardenolides. The authors have analysed DNA of the cardenolides feeding and cardenolides rejecting species, and have found only one small difference between the two. They have noted that all the species of the latter category have at the position 122 the sequence for the amino acid, asparagine, but cardenolides feeding *Chrysochus auratus* and *Chrysochus cobaltinus* have at this position the sequence for another amino acid, histidine. Thus, just substitution of one amino acid with another not only removes sensitivity for cardenolides but also provides for defence preparedness.

Eisner (2003) in his very interesting book, “For Love of Insects” has attempted to answer the question how insects keep themselves from suffering the effects of the compounds they deploy for their defence, and in the study of Labeyrie and Dobler there is a notable answer to this question.

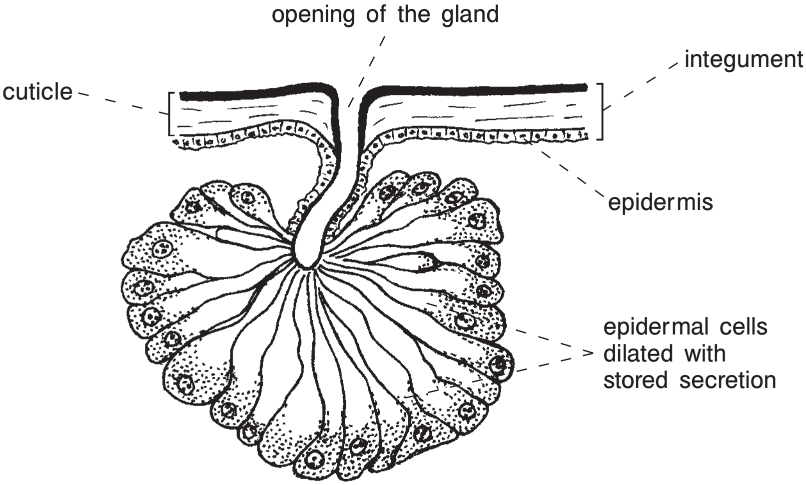
Another mechanism used by many beetles feeding on latex plants, like Asclepiadaceae, Euphorbiaceae and others, having a white latex (containing cardiac glucosides in *Calotropis* and other milkweeds, and diterpenes in Euphorbiaceae) is to lightly cut those parts of leaf which contain veins. They slow down that way the latex flow. The mechanism is very efficient and is used, for instance, by many eumolpines and chrysomelines (Chrysomelidae) and some caterpillars. *Platycorinus* sp. (Chrysomelidae, Eumolpinae), for instance, feeding on *Calotropis procera*, an Asclepiad, avoids this way getting trapped in the elastic latex. In a similar way *Chrysochus, Labidomera* and many other leaf-beetles are able to live on their latex producing host plants (Jolivet & Verma, 2002).

Spiders are as a rule carnivorous and predaceous. Many, as *Nephila clavipes* in Brazil, encircle tightly their preys with silk threads. They do it immediately after the prey is caught. Some of the caught insects are toxic. When the predator realizes the toxic property of the prey, at least some spiders, like the *Nephila* spp., are known to break the silken net and release the beetle or the moth. If it is a moth, it can fly away immediately. Unpalatable butterflies stay motionless when entangled and while the spiders release them. Remaining motionless in webs seems to be a prerequisite to allow recognition of their distastefulness and to escape from getting bitten by the spider. Warning coloration, however, does not produce spider's release response. Spiders reject a toxic prey, but do not spare their palatable mimics. Distastefulness is probably signalled to the *Nephila* by chemical clues. This behaviour was discovered independently by Joao Vasconcellos-Neto and Thomas Lewinsohn (1984) in Brazil and at some other locations by Thomas Eisner (2003), who also describes in his book how sometimes the spider's preys escape from the web by themselves. For this defensive value of insect toxicity see also Jolivet (1991). Let us also note that certain tipulids, mentioned by Etienne Rabaud, because of their so-called inefficient long legs, succeed to rest with impunity over some spider's webs. A web-building spider, *Nephila edulis,* in Australia, attracts prey, the sheep blowfly, *Lucilia cuprina*, by storing decaying matter in its net. It incorporates into its web a band of decaying animal and plant matter and it replenishes the debris to maintain its efficacy for attracting prey (Bjorkman-Chiswell *et al.*, 2004). See Chapter 11, "Insects and Tools".

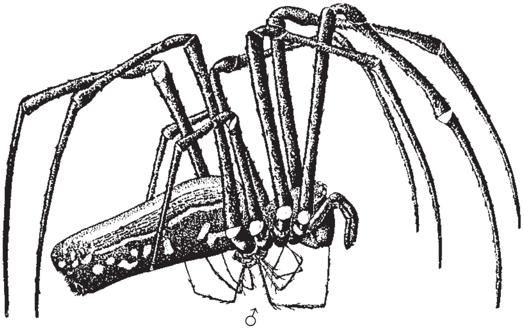
Spiders seem very clever, but sometimes they are deceived by predators which are cleverer than they. On the evening that it will kill its orb-weaving spider host, the larva of the ichneumonid wasp *Hymenoepimecis* sp. induces the spider, *Plesiometa argyra*, in Central America, to build a unique cocoon web to serve as a durable support for the wasp larval and pupal cocoon (Eberhard, 2000). Many parasites manipulate their host's behaviour (Jolivet, 1998), but this case, described by Eberhard, is probably the most remarkable alteration in the host behaviour ever attributed to an insect parasitoid.



— Fig. 8.1. Colorado potato beetle (*Leptinotarsa decemlineata*) in a lateral view. Legs and other appendages not included. Areas, covered with fine dots, denote channels and other depressed areas, and bigger dots openings of exocrine glands (based on Pasteels *et al.*, 1989).



— Fig. 8.2. An exocrine gland in the tegument of the Colorado potato beetle (*Leptinotarsa decemlineata*) in a vertical section (after Pasteels *et al.*, 1989).



— Fig. 8.3. Copulation in *Nephila maculata* (Argiopidae). The small male is placed near the genital opening of the female.

— Fig. 8.4. and Fig. 8.5. *Phaloesia saucia* (Pericopinae), a moth emitting its repellent frost in Nicaragua (photo J.-M. Maes).

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— 9. **Instinct and Intelligence in Insects**

Behaviour of insects is mostly instinct guided. A simple example of this is that of a mantid, reared in isolation from mother and other adults of her species, making an ootheca by shaping a solidifying liquid, coming out of her rear end, by beating it into a froth with her hind legs, and arranging it to cover her eggs. During making of the ootheca she does not look back. She has not seen another adult of her species making an ootheca. Still the ootheca, thus made by her, has the form and details characteristic of the species, to which she belongs. Role of instinct is obvious.

By instinct we mean a behavioural pattern, imprinted in the nervous system, and not learnt by the individual in its lifetime. Insects have been generally regarded as a programmed robot-like tanks with no intelligence. But in some cases we do get a glimpse of intelligence in insect behaviour We shall see a few examples of this.

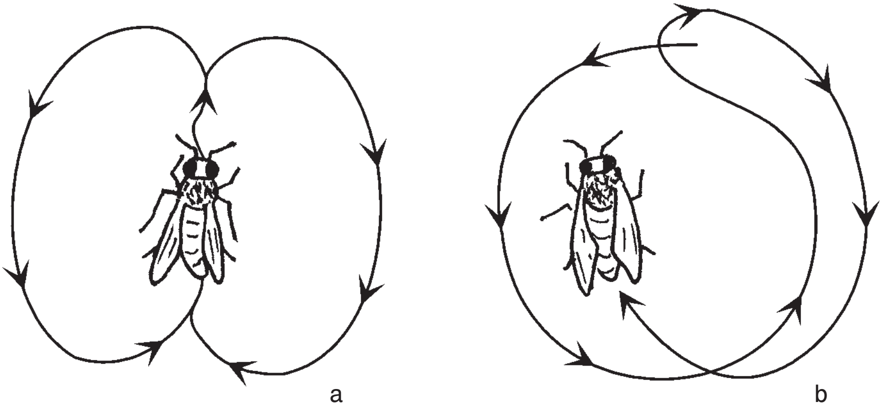
In the chapter "Insects and Tools" the case of a sphecid wasp *Ammophila* has been described. It has been pointed out that, after digging a hole like nest in the ground, the female proceeds to collect a caterpillar, which will serve as food for the future larva. Before leaving on this mission, she conceals the nest by placing a pebble at its mouth, and then some loose earth over it. She then picks up a small stone, and hammers the loose soil to smoothness. She does not pick up just any piece of stone. She picks up a stone, weighs it, holding it between her mandibles, and may reject it. She then picks up another piece, and may reject this one too. Eventually she chooses a piece for smoothening the area with her nest. This choosing of a hammering implement seems to be an intelligence guided action. When she returns to the nesting site with a caterpillar, which has been paralysed by repeated stinging by her, she carefully opens the nest, drags the caterpillar into it, lays an egg on its body, and then again carefully closes and conceals the nest following the previous procedure. All this exercise to conceal the nest is to prevent a parasitoid from locating it and then entering it to lay its own egg.

Another sphecid wasp, the bee wolf (*Philanthus apivorous*), has a very similar nesting habit to that of *Ammophila*. But she provisions her nest with a paralysed bee and not a caterpillar. When, after digging and concealing a nest, she leaves for hunting a bee, she does not simply fly away. She flies in circles around the nesting site, as if she is carefully observing the land-marks around the nesting site, and then she leaves. In one experiment, the experimenter arranged a circle of pine cones around the place, where a wasp was digging a nest hole, and later, when the wasp was on her bee collecting trip, the arrangement of cones was removed some distance away from the nest. On return the wasp was unsuccessfully trying to locate the nest within the cone circle. This observation has convincingly demonstrated that the female wasp memorized the land-marks around the nest before proceeding to collect the larval provision. Memory is a necessary ingredient of intelligence. An intelligent creature remembers past experiences, the elements of which are reorganized to solve new problems.

It is a fairly common knowledge that the honey bee (*Apis mellifera*) worker, returning after foraging (i.e. in case bee collection of nectar and pollen), communicates to fellow workers the location of the feeding source by performing some rhythmic movements or dances. If the source of food is within 100 feet from the bee hive, the bee performs a round dance, in which she moves in a circle repeatedly, reversing the direction of her movement every time after completing a circle. This movement does not convey the direction of the feeding station; it merely communicates that the source of food lies within 100 feet from the hive.

If the feeding source is more than 100 feet away, the returning bee performs another variety of dance, the tail wagging dance. In this type of movement the dancer moves in two half circles alternately on the two opposite sides, the path of such movement looking like a flattened figure of "8". In this, in the straight part of the run between the two semicircles the dancer moves her abdomen from side to side; hence the name "tail wagging dance" given to this rhythmic movement. (To be more exact the distance of the nectar source, at which the round dance changes into the tail wagging dance is 120 feet for the Italian variety, and 275 feet for the Austrian variety of the honey bee – Frisch, 1962).

The tail wagging dance indicates not only that the nectar source is more than 100 feet away, it also conveys the direction in which the food source lies. If the dance is being performed on the horizontal landing board at the entrance of the hive, the straight part of the run directly points to the feeding station. Fellow bees, following the movements of the dancer, memorise the angle between the straight part of the run and the direction of the sun. Then they fly towards the food maintaining this angle between their direction of flight and the position of the sun. If, however, the tail swaying dance is done within the apiary on a vertical surface of the comb in the darkness of the hive, the direction of the feeding station is indicated in a different way. If the nectar source lies on the same side of the nest as the sun, the straight part of the run in the swaying dance is upward. If the sun is on the opposite side, the straight course is downward. When the sun is right above the head in the noon time, foraging and dancing do not take place. The angle between the direction of the straight course and the direction of gravity is memorized by the fellow workers, which maintain this angle between their direction of flight



— Fig. 9.1. Dances of the honey-bee. a: tail-wagging dance; b: round dance.

and the sun's position, when proceeding for foraging. Thus in the darkness of the apiary, as the sun is not visible, the angle is indicated by the dancer with reference to the direction of gravity, and the fellow workers "translate" this angle with reference to the direction of the sun.

The tail wagging dance not only conveys the direction but also the distance of the feeding place. The farther the source of food, the more slowly the dance is performed. Thus, when the food is at the distance of 1000 feet, an Italian bee (*Apis mellifera liguistica*) performs the tail wagging runs 6.4 times in 15 seconds, and, if the distance of the feeding station is 2000 feet, this number is reduced to 4.5. When the dance is performed more slowly, the abdomen swaying takes place with greater frequency per second. As one author has pointed out, "one additional swaying movement per second corresponds to an increase in distance by every 75 metres".

The flexibility and variability of the dancing behaviour of the honey bee suggests involvement of intelligence. But Karl von Frisch, the Austrian scientist who discovered and extensively worked on language in bees, has pointed out that he and his team have removed honey combs from the apiary, and have reared the workers out of contact with older adults, but have found that when the workers reared this way were brought into the apiary, they could immediately indicate position and distance of food through their dancing, and could successfully comprehend what a returning foraging bee tried to convey through her dancing. It means no learning was needed to correctly perform and understand the dancing sign language. K. von Frisch has, therefore, inferred that the language of the bee is truly "innate", i.e. instinctive. But memory is involved in bee's language. A returning foraging bee has to remember the angle between its path and the sun's position. Similarly the fellow workers, closely following the movements of a dancing bee, have to memorise the angle being indicated by the dancer for guidance of their own foraging trip. As has been pointed out earlier, memory is a necessary associate in the functioning of intelligence. Thus, there is a glimpse of intelligence in the bee communication.

The instances, described above, show that some intelligence is mixed with largely instinctive behaviour. But these are not all. Many more instances may be pointed out. All social insects (bees, wasps, ants and possibly termites) show some learning and decision making. Cockroaches learn finding their way in mazes, after some initial trial and error, and ants learn to take the shortest way to food. That, besides their instinctive behaviour, insects have some learning capacity has to be accepted (Papaj in Resh and Carde, 2003). Learning involves, some deviation from pure instinct. At least two books have been written on insect learning (Abramson *et al.*, 1990; Papaj and Lewis, 1993). According to Papaj (in Resh and Carde, 2003), insect learning has been documented in eight different fields in all major insect orders, viz. water consumption, mate finding and choice, territoriality, predator avoidance, dispersal, migration, kin recognition, and thermoregulation. Learning is most pronounced in social insects, but it could be detected in other insects too. In experiments on stored grains beetle *Tenebrio* and in the fruit fly *Drosophila* it has been inferred that the memory, formed in the larval stage, persists through metamorphosis in the adult stage. Many insects learn to avoid toxic food. Butterflies learn to land on the leaf shapes of their host plants, and may wrongly land on other plants having similar leaf shapes. Bees readily learn to associate presence of food through the scent and colour of flowers. They may show some cleverness too. Some insect pollinators may learn to feed on nectar without doing the return favour of pollination. One of us (PJ) has observed in Brazil *Xylocopa* bees making holes in corollas of *Hibiscus*-like flowers to get nectar without visiting stamens and pistils.

About forty years ago, some experiments were performed with flat worms or planarians (McConnell, 1962; Jacobson, 1966). These worms are known for their remarkable capacity of regeneration. When the body of a flat worm is crushed into tiny pieces, even if single cells get separated, a fragment, however small, regenerates into a complete worm. In the experiments some worms, which had been taught to avoid light or electric shock in mazes, were crushed almost to the cellular level, and the resulting debris was fed to some new worms. It was claimed that the fed worms, without any training, showed the conditioned reflexes, which their “food” had acquired through training. Such claims led people to say jokingly, “Students will have to eat their professors to get knowledge”. But such experiments could not be satisfactorily repeated; and therefore, the claims were rejected. Similar experiments, leading to similar claims, were made using other stimuli. They, too, could not be verified satisfactorily. Fortunately, no such viable experiments with insects have come to light. Perhaps, such experiments should be one day repeated, also with some famous prolamarkian experiments, just to prove they are wrong or they are crazy. Who among young scientists will lose time over what seems fully wrong?

Birds, mainly crows, are known to count up to eight, when there are hunters hidden inside a building. Some crows, like the neocaledonian genus, are known for their intelligence, namely in tool making. Probably insects cannot count. People in Papuan tribes, on the higlands of New Guinea, were said to count *one, two, three, many*. Some Amazonian tribes also were not supposed to go above two. However, PJ noted that tribal youths in New Guinea, undergoing education, picked up modern mathematics very well. Children of the above mentioned American Indians had no difficulty with calculation. This observation shows how important learning is in development and manifestation of intelligence. Insects, in their way, do show some capacity to learn.

As we learn more about insect behaviour, we may come across more instances of mix-up of instinct and rudimentary intelligence.

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— 10. **Do insects learn ?**

A common notion about insects is that they are wholly instinct driven in their behaviour like a programmed tank (they are referred to as tanks because of the fairly thick and hard armour of chitin and protein covering their body). That was the basic notion, which we find in the writings of Jean-Henri Fabre and Henri Bergson. In other words, there is no place for learning in insects. Learning is a necessary factor in expression and manifestation of intelligence. Intelligence is the property of using elements of the past learning and experience to solve new problems. It is a general presumption that insects do not have intelligence and that they are fully instinct guided.

But of late such facts have been emerging as suggest that insects, too, have some capacity of learning. O'Donnell and his colleagues have published their observations (O'Donnell *et al.*, 2004), which are of interest in this context. They have studied the brain of the social wasp *Polybia aequatorialis*, which lives in fairly large colonies, a colony including 2000 or more workers. The workers show well marked changes in behaviour as they grow older. Young workers work in the interior of the nest, mainly taking care of developing individuals. After growing older, they start working on the nest exterior, adding more material to the nest cover and defending the colony. When they are still older, they start flying out for collection of food and building material.

With this change of work and behaviour there are marked changes in the brain of the worker wasps. O'Donnell and his team have found that mushroom bodies of their brain progressively increase in size, and they show maximum increase, when the workers start working on the nest exterior. With this change of tasks, their life becomes more challenging. O'Donnell says, "What is happening is that the complexity of the tasks the insect engage in is increasing. They are going from living in a very constrained spatial area with dim light to working outside the nest where is a complex sensory environment with higher light levels. Finally, they have to leave the nest to forage for materials and then to locate their way home to the nest".

It is interesting to note that similar observations have been made in man. In the January 2004 issue of Nature, Dr. Arne May and his coworkers (Anonymous, 2004) studied the brain of persons who were getting training in juggling. The investigators used the technique of magnetic resonance imaging (MRI). They noted that, as the jugglers learnt their new lessons, certain areas in the cerebral cortex showed enlargement. When the subjects gave up juggling completely, the areas, which had shown enlargement, started shrinking. These observations were similar to those which had been made some years earlier on apprentice taxi drivers, who had been asked to move on their bicycles through different parts of London, holding the city map, to become familiar with streets and lanes. These trainees also showed enlargement of the cortex in the hippocampus part of the brain as they went ahead with the training.

The cortex of human brain is a layer of the grey matter, which is made up of cell bodies of neurons or nerve cells, while in deeper parts is the white matter, which consists of nerve processes of neurons. It is not clear whether enlargement of certain parts of the brain during training had been due to formation of new neurons or enlargement or hypertrophy of existing neurons, because MRI is not able to go down to the cellular level. But one thing may be inferred from the above observations, namely that the cortex enlargement is associated with learning and formation of new reflexes. Thus, it may be safely stated that enlargement of certain parts of the brain in the social wasps, as they take to more demanding jobs, is due to learning. There are some other observations, too, on biology and behaviour of insects, which suggest some learning and intelligence, while most of their activities are governed by instincts (see the previous chapter on "Instinct and intelligence in insects").

Several books have been published recently on learning in insects (Abramson *et al.*, 1990; Papaj and Lewis, 1993 and others). As Papaj (2003) mentions, a butterfly learns to search for the shape of its preferred host plant's leaves and for the colour of preferred nectar sources. A grasshopper avoids feeding on a plant associated with recent digestive problems. The same can be said about parasitoid wasps, flies and bees. In *Tribolium* beetles and *Drosophila* flies memory formed in the larval stage persists during metamorphosis. Most of the experiments have been done with bees and wasps (Bitterman, 1996; Menzel, 2001).

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— 11. **Insects and Tools**

Man may be described as the tool wielding animal. Much of his civilization built up, including writing and literature, has been through extensive use of tools and implements.

At the outset let us make clear to ourselves what a tool is. The generally accepted definition of a tool is that it is a foreign object, that is an object outside the body of the user, which is used as such or with modifications to increase the mechanical efficiency of the user. Perhaps the "mechanical efficiency" part of this definition should be replaced with "working efficiency", as a computer is not exactly an artefact for increasing man's mechanical efficiency. Beck (1980) has pointed out the following qualifications for a tool: first the object forming the tool must not be a part of the animal's body; secondly it must not be attached to the environment (climbing a tree is not a use of a tool); thirdly, the user must manipulate the tool and achieve something useful with it. The spider *Dinopis* throws its web at passing insects and so qualifies as a tool user, but the web of a spider, attached to the substrate, is not a tool. This description of a tool by Beck better defines the "tool" than the simple definition, given above.

Though making and wielding of tools is a characteristic of man, instances of use of simple tools by some other animals are also known. Apes are known to use a twig, stripped of leaves, for catching termites for food. If the bank of a stream is so high that a chimp cannot lower his mouth to the water level, he is said to collect some dry leaves, crush them with his hands into a spongy mass, dip the mass into water, then hold it above his mouth and squeeze it to drip water into the mouth. A Galapagos finch uses a twig, held in its beak, to dislodge insects from crevices in a tree to feed upon them. *Melia* crabs brandish the sea anemone, *Actinia,* on their claws to paralyse their preys. Egyptian vultures use stones to break eggs too strong for their beaks. Some octopi slip a stone between a mollusc's valves to prevent their closing. Herons throw objects, even flies, into water to attract fish. Sea otters commonly use tools to open shells, which are flat stones held against their chest, when they are swimming with their belly uppermost. Many other cases of tool use among vertebrates and invertebrates could be cited. A particularly notable example: crows of New Caledonia are known to make an interesting insect catching device (Hunt and Gray, 2003). They cut a twig, remove leaves from it, make a notch near one end of the twig, and then bend the shorter part of the twig to make a hook. This hook is used to collect insects from crevices in the tree trunk. Some white dolphins of Australia hold marine sponges in their mouth for foraging. Young dolphins learn this use of a tool from their mothers.

Cases of use of tools are known among insects, too. Jean Henri Fabre (1908), a well known French entomologist and a contemporary of Louis Pasteur, made some very interesting observations on the breeding habits of the wasp *Ammophila*. His observations have been repeated by Peckham and Peckham (1898) and a number of other entomologists. A female of *Ammophila*, before laying an egg, makes a small tunnel in the ground, using her mandibles and bristly legs (see the chapter "Instinct and intelligence"). This tunnel is a little wider at its inner end, which will be the egg chamber. Before laying an egg in this chamber, the female proceeds to provision it, so that the larva, hatching from the egg, will find its food in immediate vicinity. The larval food is a caterpillar, which has been made insensitive by repeated stinging by the mother. But before leaving to collect a caterpillar, she closes the nest carefully, so that a parasitic insect does not lay its eggs in the nest. The *Ammophila* mother goes through an elaborate procedure to make the nest safe. The mouth of the tunnel is made funnel shaped, a pebble is placed in the funnel, so that the tunnel mouth is closed. Then she scatters the loose earth, which was removed during the making of the tunnel, over the opening of the nest, and then proceeds to do something incredible. For effectively hiding the nesting site, she smoothens the loose earth over the nest. For this she picks up a pebble between her mandibles, and allows it to drop on the loose soil repeatedly. Thus the disturbed earth is hammered to relative smoothness.

Next the female proceeds to cut pieces of grass and scatters them over the nesting site to camouflage it further. When the mother returns with the caterpillar, she opens the nest carefully. After pushing the caterpillar into the nest, and laying an egg on the body of the caterpillar, she closes the nest following all the steps of the earlier procedure. Using a small stone for hammering down the earth is an instance of using a tool.

Some ants, for example *Oecophylla smaragdina* in Asia and *Oecophylla longinoda* in Africa, make vessel like nests, hanging from trees (Jolivet, 1991). The vessel is made up of some leaves of the tree joined together at their edges. For joining the leaves, worker ants hold edges of two neighbouring leaves close together using their legs and mandibles. Another worker holds a mature larva of its own colony with its mandibles. The larva, when ready for pupation, actively produces silk like material from large glands, situated close to its mouth. The silk is for making a cocoon around the pupating larva. The silken thread, emerging from the mouth of the spinning larva, is made to stick to the marginal parts of the two leaves alternately by movements of the head of the worker ant. Thus the edges of the leaves are "stitched" together, and for this purpose the spinning larva is used as a living shuttle. Through cooperative efforts of the workers more leaves are joined together to make a vessel like nest. Thus, the pupating larva is used as a tool.

Some ants, belonging to the genera *Aphaenogaster* and *Pogonomyrmex*, feed their larvae with liquid nourishment, obtained by pressing together bits of leaves. Often hard particles of earth are mixed with the bits of leaves to improve extraction of the liquid larval food (Jolivet, 1991). Ant workers also use leaves as tools to carry large quantities of food, like jelly or any other semiliquid material. Generally, ants are good mothers taking care of their brood and practice social food transfer. The Dracula ant queens, *Mystrium* and *Amblyopone*, in Madagascar, are an exception: they suck hemolymph from their own larvae! They practice a form of nondestructive cannibalism and are exclusively dependent on those larvae as a food source (Goodman and Bernstead, 2004), but, as has been said, it is a case of cannibalism and does not come in the ambit of tool use.

A reduviid bug from Costa-Rica, *Salyarata variegata*, feeds on termites, dwelling in dead and rotting tree branches. The bug uses tools in two ways: to provide camouflage and to bait termites. The nymphal *S. variegata* coats itself with crumbs scraped from the termite nest (McMahan, 1983). Its mode of catching the prey is interesting (Pierce, 1986). It searches out a hole leading into the termite galleries. It approaches the hole cautiously, catches a termite, and immediately withdraws. After sucking up the body fluids of the prey, it moves towards the same hole, holding the carcass of the prey between its mandibles. This time its movement is nonchalant and casual. It drops the carcass, which is readily accepted by termites as food, as they are scavengers or saprophagous. The bug again catches a termite, withdraws, sucks its nourishment, and returns to the nest with prey's carcass. The process is repeated, and termite after termite get killed. The bug's second and the following approaches to the termite nest are obviously not burdened with caution; perhaps it is because the predator offers the dead prey's body as a bait to the termites in these visits, and also perhaps because it has acquired the characteristic odour of the termite colony. Thus it seems to be a case of using a dead termite's body as a tool for raiding prey's habitat. Probably also it is a genetically fixed sequence which evolved because it was successful. The bug can capture 31 worker termites within three hours! In Australia, a predatory spider, *Cosmophasis bitaeniata*, resembles to its prey, the ant *Oecophylla smaragdina*. The spider acquires the cuticular hydrocarbons of the prey by eating the larvae (Elgar and Allan, 2004). This case of using one's prey for enhancing one's mimicry may be taken as a case of tool use, only by expanding the meaning of a "tool".

In Florida owls stand at the entrance of their burrows, surrounded by dung that is positioned to entice beetles (*Phaneus igneus*) to come (Levey *et al.*, 2004). They capture many insects that way. This study builds an elegant case that the owls are using the dung as a tool. Also, web-building spiders attract prey by storing decaying matter (Bjorkman-Chiswell *et al.*, 2004). In Australia, *Nephila edulis* incorporates into its web decaying animal and plant matter to attract blowflies, *Lucilia cuprina*. The spider replenishes the debris when necessary. These are cases of nonhumans using tools for catching insects, like the examples of chimps and a Galapagos finch using shoots to collect termites and other insects.

Larvae of neuropterans, belonging to the family Myrmeleontidae, are peculiar looking plump creatures, with long sickle shaped mandibles and forward directed long legs. Larvae of many myrmeleontid species make a funnel shaped depression in fine grained or dusty soil, and remain buried at the bottom of the pit. When a passing ant happens to move close to the pit, and soil particles, disturbed by its movements, roll down the funnel, and the larva at the bottom perceives possible presence of a prey, it immediately comes up from the resting position, throws some sand towards the prey, and catches the ant with its mandibles, and feeds upon it. Thus these larvae make and use an interesting trap for catching ants, and they throw sand to prevent escape of the prey. Myrmeleontid larvae are also known as ant lions. Larvae of Diptera, Rhagionidae (*Vermilio* and *Lampromyia*) show a similar prey catching behaviour.

Larvae of caddis flies (Trichoptera) are aquatic and caterpillar like, with well developed thoracic legs. They make a thimble like silken case. Abdomen and some of the thorax remain within the case, while its head, part of thorax and legs protrude beyond the opening of the case during normal movements. The larval case is strengthened, by including in the silken material, pieces of leaves, twigs, sand grains or small pebbles. Every species makes a characteristic larval case.

Protecting and/or camouflaging with the help of material, present in the surroundings, is seen in many insect larvae. Larvae of many species of tortoise beetles retain exuviae of the previous instars or fecal discharge or both at the end of the abdomen forming a protective shield. Many Cassidinae use this tool in defense against potential predators. The shield is maneuvered in the direction of the attacking insect, and this wielding of the shield is generally successful in repelling the predator. Removal of the shield renders the larva highly vulnerable to predators, which are mostly ants and bugs.

Webs and nets of spiders for catching prey may in some way be regarded as tools (but it is not a tool, as per the limits defined by Beck, 1980). Some spiders, like the *Pasilobus*, throw their "bola" (a large sticky droplet at the end of a silken thread), like the South-American gauchos, to catch their prey.

Pierce (1986) has mentioned the following instances of tool use by insects:

01. Weaver ants using conspecifics as a gluing mechanism.
02. Ants crossing a streamlet with a bridge made of linked fellow ants.
03. Nuptial gifts by male empidid flies.
04. Foraging female water striders, while copulating, provides a free ride to the male.
05. Use of sand/soil for food transportation by ant.
06. Soil/stone dropping behaviour by some ants.
07. Sand throwing by ant-lion and worm-lion.
08. Nest closure by *Ammophila* and *Sphex* wasps.
09. Camouflage/Bait to capture a prey by the assasin bug.
10. Fecal shield defense by Cassids.
11. Sound baffle use by *Oecanthus* crickets.
12. Structure building by many species (termites, bees, etc.).

Only 5 to 10 of the above items have met with a general acceptance of entomologists. Some reject, others accept some of the other activities (1 to 4 and 11 and 12) as a case of tool making and using. Let us explain what sound baffle means. The male of some crickets (*Oecanthus*) are able to increase the effectiveness of their calling sound by gnawing a small hole in a leaf and orientating it in front of their body (Beck, 1980). The leaf acts as a baffle. Structure building is more questionable in its interpretation as tool making. Perhaps, some justification for regarding nest making as a case of tool making lies in the fact that many insect species fashion structures (burrows, nests) to serve diverse functions (thermoregulation, accoustics, etc). That seems more of an instinctive behaviour than guided by intelligence. Soil or stone dropping has been observed among several ants. Dolichoderine ants (*Conomyrma bicolor*), for instance, surround the nest of ant competitors and drop small pebbles and other objects down the entrances. Hölldobler and Wilson (1990) point out that, in the deserts of Arizona, workers of *C. bicolor* inhibit foraging of a species of *Myrmecocystus* by dropping pebbles into their nest.

One important difference between tools made and used by man and those used by other members of the animal kingdom, including insects, is that the latter are objects in the surroundings, which are used either as such or slightly modified. The former, however, are generally extensively modified to suit human requirements. Even a bow and arrows are much more altered external objects than twigs, with leaves removed, used by chimps or bent twigs, used by the New-Caledonian crows, for collecting termites or other insects. Railway locomotives, aeroplanes and computers are some examples of artifacts, which are very extensively and intelligently modified external objects, standing in stark contrast with simple tools, used by insects and other animals.

One objection raised to regarding external objects, used by insects and other animals as tools: tools and implements, made and used by man, are made and used intelligently, but animal tools are used instinctively, i.e. as per inherited behavioural pattern or as per behaviour programmed in the genome. But this objection is perhaps not as serious as it appears at the first sight. Glimpses of intelligence do appear in insect behaviour (see the chapter on "Insects and intelligence").

There is no doubt that intelligence is greatly developed in man, and human behaviour is largely guided by his intelligence. But glimpses of intelligence may sometimes be seen in animals using their mechanical devices. In its breeding behaviour the *Ammophila* wasp, the case of which has been described above in this chapter, the female does not pick up just any pebble to hammer the loose earth. Before finally choosing a pebble, she holds and weighs several pebbles between her mandibles, and rejects them. The reduviid bug, preying on termites in rotting wood, changes its behaviour as per varying state of rotting in the wood. Recent studies on wild chimp behaviour show that at least 39 aspects of behaviour are passed on to the progeny "culturally", that is through learning and training. One such behaviour concerns termite feeding. Chimpanzees in the Gombe National Park in Tanzania, as observed by the renowned zoologist Jane Goodall, use a long twig, stripped of leaves, for catching termites. When the termites are crawling all over the twig, the chimp with one hand removes all the termites, presses them into a ball, and transfers the ball to its mouth. But elsewhere chimps use shorter twigs, and pick up the termites from the twig with their lips, a much less efficient method. This behavioural difference seems to be through learning, which is a necessary corollary of intelligence.

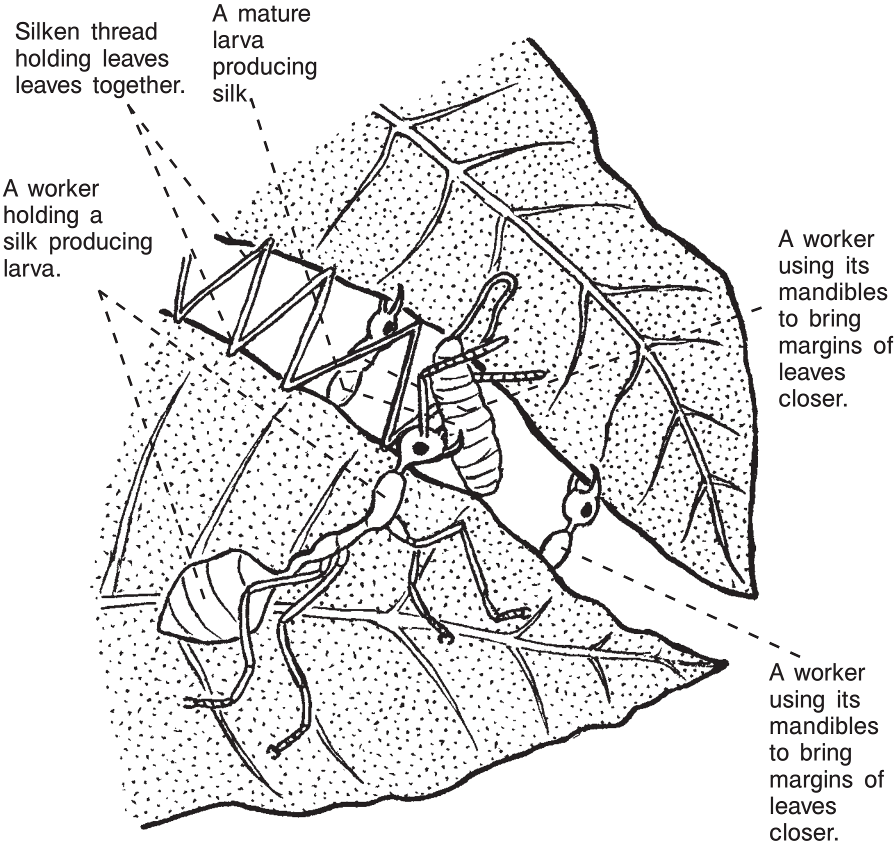
Georgia Mason (1991) insists that individuals in a group can benefit from the experience of those around them. That is why birds flock, fish school and mammals gather in herds. So did the dinosaurs during the Mesozoic and they were not the stupid animals, with a small brain, as pictured in the past. The group learning in chimpanzees has been referred to by a naturalist in good humour as "tool training at the chimp academy". Recent papers on fishes, birds and insects show that tool use is more prevalent than previously believed.

In our opinion, there is not enough ground for sharply distinguishing tool using by animals and that by man. Often intelligence and instinct are mixed up. An example of this situation has been described by Bateson (1983). He says: "It is possible to take a recently hatched laughing gull (*Larus articilla*) chick and show that it will peck at models of adults' bill. Advocates of the first view (that innate behaviour is entirely inborn with no place for learning) would almost certainly want to call the behaviour innate, since the chick had previously been isolated from 'relevant' experience. Nevertheless, as the chick profits from its experience after hatching, the accuracy of its pecking improves, and the kinds of bill like objects it will peck at are increasingly restricted".

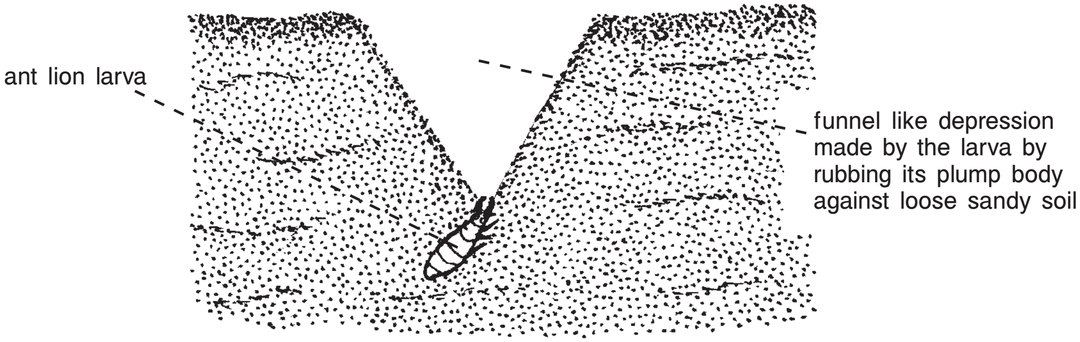
However, it has to be accepted that making and wielding of tools and implements among humans is almost entirely intelligence guided and, therefore artefacts present numerous modifications and versions with variations in needs and local practices and conditions, while use of tools by animals is mostly innate or instinct guided, and, therefore, they tend to be stereotypic within a species. The greatly developed intelligence in man and his nimble prehensile hands make all the difference. With his technological development man has started thinking of producing "cyborgs" (Cyber-organisms), that is producing humans with implanted electronic chips, which will guide his functioning, including mental working and memory. With successful implantation of foreign objects, foreign to his body, like kidneys, liver, heart and orthopaedic implants, he is already moving towards the imaginary cyborg, and moving away from other organisms including insects. Should we regard such implants as "internal tools"? Let biology philosophers decide on this.

Andrée Tetry (1948) produced an important book, "Tools among Living Beings" (English translation of the French title). In this work, the author regarded even functional parts or organs of an organism, such as "ruptor ovi" or egg bursters of a newly hatched insect larvae or the press stud (a snap fastener) of the octopus, as tools. Frish and Otto (1974) wrote also a book in the same sense, showing the basic of animal architecture. But in the present treatment we have adhered to the limits of "tools" as described by Beck (1980). "What's so special about using tools?" said Michael Hansell (1987). "Even a simple amoeba eventually could use tools during phagocytosis". However, man was named *Homo faber* by Henri Bergson, complimenting his capacity of intelligent fabrications.

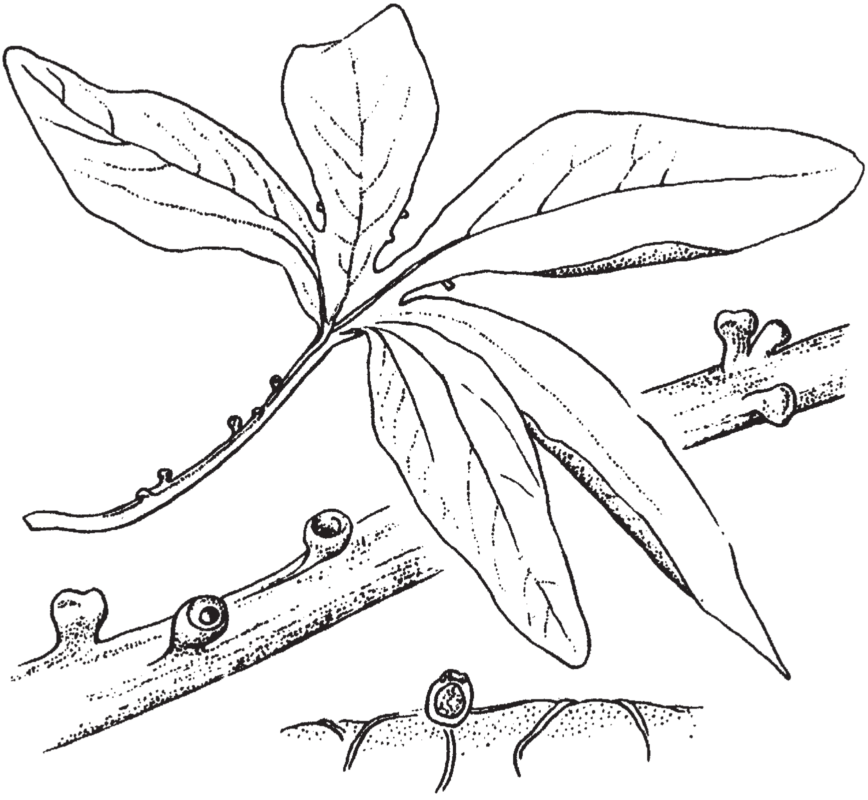
It is also evident that false eggs on *Passiflora coerulea* to prevent *Heliconius* butterflies to lay eggs on the plant are not tools and they are integral part of the vegetal (Sacchi, 1988).



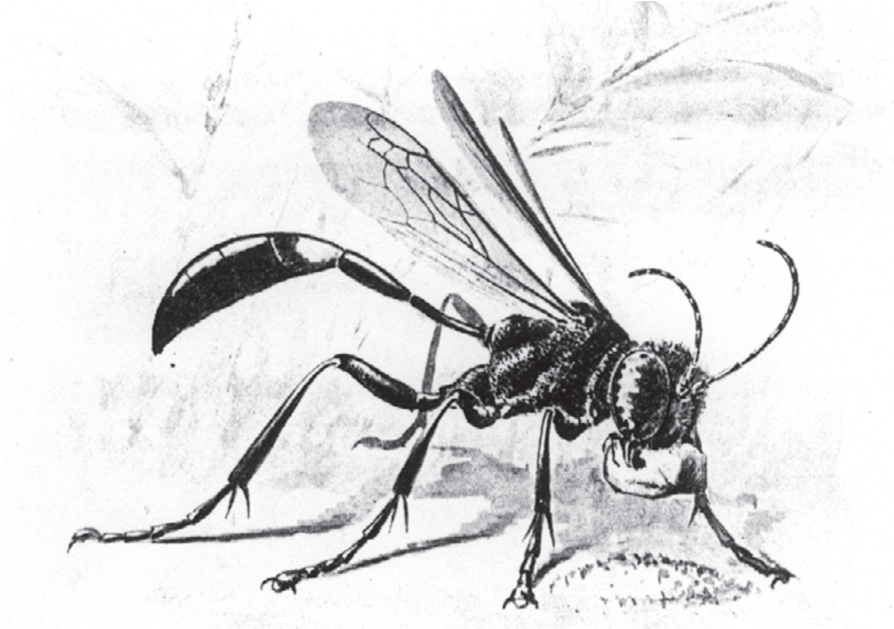
— Fig. 11.1. Weaver ants "sewing" together leaves to make a nest.



— Fig. 11.2. A vertical cut through an ant-lion trap for catching ants.



— Fig. 11.3. False eggs on *Passiflora (Granadilla) coerulea* in Tucuman, Argentina. The pseudo-eggs prevents *Heliconius* butterflies from laying eggs on the plant (after Sacchi, 1988).



— Fig. 11.4. *Ammophila urnaria* using stone to pound down earth over nest (after Peckham and Peckham, 1898).

— Fig. 11.5. *Pompilus quinquenotatus* digging nest (after Peckham and Peckham, 1898).

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— 12. **Insect aggregations**

Insects disappear from our planet at a rhythm of around one species every quarter of an hour. Deforestation, fertilizers, insecticides, urbanisation and construction of roads are the main causes for this fast rate of extinction. However, our activities help certain populations to grow to the size of millions of individuals at some places. Those which disappear and move towards extinction, are insects linked to a specific host-plant, as well as apterous or brachypterous forms, such as *Timarcha*, incapable of flying to populate another suitable area. Those which fly have a thousand chances more to escape extinction. Among surviving insects, many show formation of groups of a considerable size or aggregations.

Cycloalexy (see the chapter "Round defense") is also an instance of aggregation. It is the resting period of insect larvae, or rarely of adults, generally forming a circular group, after a day or a night of activity. This gives a protection against predators and parasites. But here we shall discuss mainly long period aggregation, which is an assemblage of many individuals of one species of insects in a place, at certain time of the year, for hibernation, diapause or any other reason, understood or ununderstood. These aggregations are for a considerable length of time, up to some months. Some aggregations are annual, like the case of the coccinellids (see the chapter on "Insect migrations"), or the Panamean *Stenotarsus*, or there can be in a cycle of a longer period linked with climatic reasons, crowding or any uknown reason.

Large aggregations of certain cicadas in the US are formed every 13 years, or every 17 years, as for the *Magicicada septemdecim* in the USA. In that case the cicad aggregations are related to the simultaneous emergence of a large number from their pupal skin. This happens also in Europe, every 4 years with the cockchafer. In New-Guinea, PJ has witnessed the mass hatching of the local cockchafer (*Lepidiota vogeli*) in the highlands in Goroka. The Papuans, with pieces of cloth, collected them to eat. This sudden mass emergence is linked with the first rains after a long period of drought, and, as good rains come after a gap of several years, the phenomenon of group emergence also shows a cycle repeated after a period of several years. It is a festive day in New-Guinea, when there is such mass emergence of adults, and thank God it is a better way than cannibalism to get proteins. PJ tried one day to eat the beetle also by frying them with butter on a stove. He removed the elytra, the head, the hairy and spiny legs, but not much was left and the taste was not very attractive; it tasted terebenthine or something similar. In the Sahel zone, just north of the Sahara, in Sudan, around Khartoum, and in the North-East of Thailand, *Gonocephalum* spp., tiny greyish tenebrionid, eclode en mass, by millions, immediately after the first heavy rains. They also come to the light and aggregate under the lamp posts. In the Sahel zone also, in Senegal, once a year, following heavy rains, *Calosoma senegalensis* emerge in large numbers, and this nice carabid, normally aphid hunter, fills the streets of St Louis on several days, and then disappears. Similar aggregations of *Calosoma frigidum* have been described in Ontario in Canada. They are all linked with special meteorological conditions. All these cases are not long period aggregations. They are just a result of mass eclosions. Mass emergence may cause temporary aggregations, and we wish to concentrate here on a long time accumulation of an insect species in a given place. The butterfly *Danaus plexippus* makes an aggregate when hibernating in Mexico, in winter, on trees. The neotropical saturniid, *Arsenura armida*, in Costa Rica and in Brazil, is somewhat cycloalexic and gregarious in the larval instars. PJ has observed frequently in Ilha de Maracca, in Brazil, near Boa Vista, the last instar caterpillars feeding during the night on their tree and forming aggregations on the trunk in an oval grouping during the day. They seem to be faithful to their chosen site. The caterpillar skin is soft like silk in the last instar. They are known to use a trail pheromone in the young instars and pheromone certainly helps to keep the group together (Costa *et al.*, 2003). Another saturniid, *Hylesia* spp., which is highly venomous, also has gregarious caterpillars, producing a trail pheromone, in America, but do not show cycloalexy at rest (Fitzgerald and Pescador-Rubio, 2002).

Among insects, Crowson (1981) mentions the aggregations of many aposomatic forms, such as Danaiinae adults, various Zygaenidae and Arctiidae among Lepidoptera, and in Coleoptera the hibernating aggregations of various Coccinellidae. The breeding aggregations of many Lycidae probably belong to this category. It is evident that the small aggregations of Gerridae, among the Hemiptera, and of Gyrinidae, among the beetles, on water respond to different needs, such as food, sex, protection.

PJ was the witness in 1970 of an enormous aggregation of millions of a small tenebrionid beetle over various trees, in one arboretum (Jolivet, 1971). That was in Phu Kae, in the North-East of Bangkok. At the foot of a single tree (*Dipterocarpus elatus*), of 30 m height and with 6 m of circumference, there were 15 millon of these beetles, with an approximate total weight of 170 kg. On all the trees of the arboretum there were hundred millions of insects, all *Mesomorphus*, one species the most common among the three, found there. How to explain that extraordinary accumulation of a beetle? It was probably a sudden massive eclosion, but according to the Thai entomologists, the fact had never been observed before and did not seem to be related to special meteorological conditions.

The case of Coccinellidae, which enter into hibernation, grouped by millions, in a given place, often on an elevated site, is well known. The migrations of those beetles are linked with the density of their population. Cassidinae, leaf-beetles, can also suddenly migrate, and accumulate on a beach, as once seen in Holland. Colorado potato beetles also migrate and can appear by thousands on potato fields. Both migrations are linked with multiplication of the insects with specially favourable climatic conditions. Mosquitoes (*Anopheles, Culex*) hibernate in caves and houses, with their blood transformed into fat bodies. Once in Iran, PJ was witness to thousands and thousands of *Anopheles* on the roof of caves in the Elbourz mountains, near Caspian sea.

A strange case of aggregation is the one of the Endomychid, *Stenotarsus subtilis* (ex *rotundus*) in Panama (Denlinger, 1994; Roubik and Skelley, 2001). PJ saw the beetle for the first time in Barro Colorado island in 1990 on the palm tree, and all the entomologists of the area were there taking pictures. There are two diapause groups in the island with up to 200,000 individuals in each aggregation. Sex ratios varied from 1:1 to 1:4, females often being much more numerous, and one of those groups persisted for at least 20 years. The beetles diapause more than ten months each year. The trees used as rest sites by the beetles were *Oenocarpus panamanus* (Palmae) and *Tetragastis panamensis* (Burseraceae). Fungi do not seem to attract the beetles in the resting sites. Bark and wood substrata do not seem also to be involved in the attraction. The beetles live one year or more and return to diapause sites after completing mating, feeding and reproductive cycle. The reason for this strange behaviour and the reason why the beetles come always to the same site remains a mystery, and perhaps will be solved one day when we will understand better the rest of the cycle.

In most cases long period aggregations are for diapause or hibernation. Reasons for other cases remain to be discovered.

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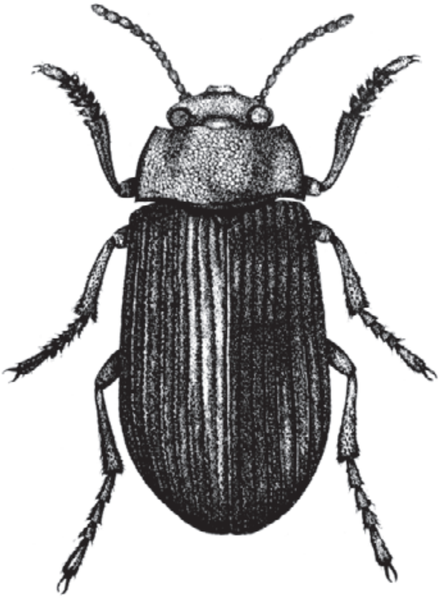


— Fig. 12.1. *Mesomorphus vitalisi* Chatanay (Col. Tenebrionidae). Millions of them were accumulated over the trees of the Phu Kae arboretum, in Thailand (photo P. Jolivet).

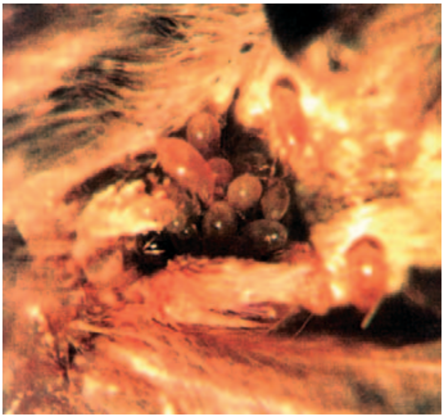
— Fig. 12.3. *Dipterocarpus* tree with the trunk darkening with beetles (photo P. Jolivet).

— Fig. 12.2. Aggregation of 15 millions of *M. vitalisi* over a trunk of *Dipterocarpus elatus* (Dipterocarpaceae). Probably over 50 trees of the arboretum, they were nearly 7 billions beetles (photo P. Jolivet).

— Fig. 12.4. Aggregation in Panama on *Oenocarpus panamanus*, a palm tree, of *Stenotarsus subtilis* (Endomychidae) (photo P. Jolivet).

— Fig. 12.6. *Arsenura* near *armida* (Saturnidae) resting in a quasi-cycloalexy position in the morning. Maracca island, Amazonia (photo P. Jolivet).

— Fig. 12.5. The aggregation in Fig. 12.4, magnified (photo P. Jolivet).



— Fig. 12.7. Colony of the mite *Dicrocheles phalaenodectes* in the tympanic area of *Leucania commoida* male, a moth (after Treat, 1975).

— 13. **Infra-red Receptors**

It is well known that some insects are attracted by the smoke of the blazes of forest fires, for example, little flies like *Microsania* (Platyperidae) and *Hormopeza* (Empidiidae). *Hormopeza* is frequently associated with the beetle *Melanophila acuminata* (Collin, 1918). Many years ago, a Belgian entomologist, Albert Collart, studied in good detail *Microsania* by attracting them to fire made by burning trash in his garden. He collected them also in Congo, around bush fires. These Diptera are common around the earth, but their biology is unknown, and specially the biology of its larvae. It could be inferred that these insects are attracted by the smell of smoke, because clothes, impregnated with smoke, attracted them.

The sense organs of these flies have not been studied, but it seems that they have also special infra-red receptors, which in *Melanophila* (Coleoptera Buprestidae) detect forest fires, and induce the insects to get attracted irrestibly towards the heat source. It may be that smoke smell detection also has a role in inducing this behaviour in some insects.

Evans has described in *Melanophila* sensorial crypts situated on the side of the mesothorax, adjacent to coxal cavities and sensitive to smoke. The sensory organs can receive waves of 2.5 to 4.0 micrometers. These buprestids can perceive them from a distance of 1 km at ground level and up to 5 km in the mountains. This way *Melanophila* is able to reach a fire and freshly burnt trees before any other competitor. It is a common observation that these buprestids are present in a dead tree and can be seen running along still smouldering branches (Evans and Bellamy, 1996).

People capture easily its larvae under the bark of burnt Coniferae. It is believed that the beetle has helped recycling of vegetal matter in the Yellowstone Park, after the big fire of the last century. After hatching, larvae remain in the dead tree for a year or more before tunnelling outward to pupate and to emerge as adults (Hart, 1998). Klausnitzer (1981) reports that these beetles sit and copulate on wood that is too hot to be held in hand. Fire seems to have a stimulating effect on *Melanophila*. However, Crowson (1981) says that charred wood is not necessary for the development of *Melanophila* species. The beetle can be found as developmental stages also in dead and moribund conifers with no trace of fire. It is notable that *Melanophila* does not have bright colours, like other buprestids, it is black, the colour of charred wood on which it copulates.

The charred wood, after a forest fire, has a characteristic fauna of its own, and in that not only Diptera are attracted. Many longhorn beetles, bark beetles (Salpingidae) and even ground beetles, like *Agonum quadripunctatum*, visit burnt wood. There must be specific organs sensitive to the smoke (Evans, 1966 a).

Several authors have discussed the possible utilization by numerous insects of various depressions on body as infra-red detectors. However, most of these organs are moderately sensitive, and only the highly specialized organs of *Melanophila acuminata* detect infra-red radiation with a high sensitivity. Another buprestid, *Merimna atrata*, in Australia, is known as the fire beetle, alighting on steaming branches, even over the parts that are glowing red (Poulton, 1915).

The cephalic capsule of many weevils has a zone, which is sensitive to only red and infrared. In the alfalfa weevil, *Hypera postica*, this extraocular filter is coordinated with compound eyes allowing the insect to use visual markers for locating and identifying its host-plants (Meyer, 1977).

Many cavernicolous beetles have antennae sensitive to heat and humidity. Their antennae are extremely elongated. There are thermosensitive sensilla on the maxillary palpi and the antennal club of *Dorcus* beetles, and in certain *Hypera* (Curculionidae) a part of the cephalic capsule is sensitive to infrared radiation and is especially innervated (Paulian, 1988). Experiments have been done in various laboratories using electroantennograms and electropalpograms. A minute titanium electrode is inserted into a recipient cell. Electric waves are then studied as in an electrocardiogram and we can analyze the insect sensitivity to odour, colour, heat, chemicals.

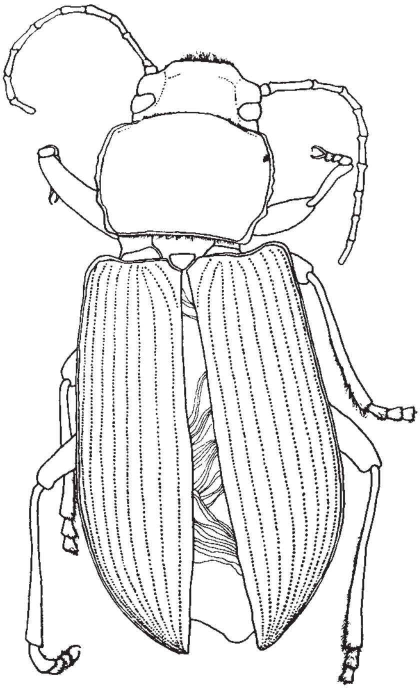
The depressions specially sensitive to infrared in *Melanophila* enclose 70 to 100 sensilla each, which are tiny domes, and a mass of fibrous and waxy material (Evans, 1966 b). Experiments have confirmed the extreme sensitivity of these cells, associated with the sensilla, to infrared. The dome-shaped infrared receptors respond to a slight deformation caused by the radiation, and the resulting impulses are transmitted through nerves. In some beetles, as the tenebrionid *Deretus denticollis*, from the island of Socotra, close to the NE of Africa, only the male possesses three hairy pits under the first three abdominal sternites (Koch, 1970). The female does not have these organs, of which the function remains unknown. Perhaps they are linked with mating. Many carabid and tenebrionid beetles show some similar depressions, in steppic and semi-desert places. Perhaps in these insects the organs serve for hygrometric detection. Sometimes, in special cases, such depressions serve for pollen transport, according to Crowson. Setiferous sex patches and analogous structures exist in 11 families of Coleoptera (Faustini and Halstead, 1982). These structures appear to have several features in common: long ridged setae, cuticular ducts, cribriform pore plates, and the production of a secretion. These structures may be concerned with the production, release and dissemination of pheromones. Presence of such sensory pits in many insects supports the hypothesis that many are capable of sensing infrared radiation (Grant, 1950).

Several years ago, the Italian entomologist, Mauro Daccordi (1980) discovered strange depressions under the abdomen of a small chrysomelid from the Cape area, in South Africa. He named the insect *Gasterantodes*, which means cavernous belly. Those depressions are hairy and certainly sensitive to something, probably to humidity or to heat, since the beetles have to face a long and trying period of dryness, and in this period they hide under stones and vegetation. Even plants, such as the Mesambryanthemaceae, also hide under soil, in a stone-like form, to escape extreme rough conditions.

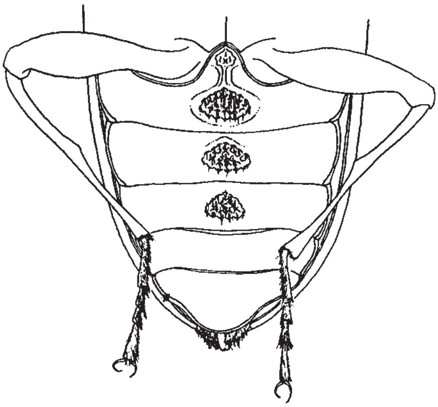
Unexplained invaginations on body surface, with their exact function not known, have been found by Daccordi (1994) also among Australian

Chrysomelidae, like *Peltoschema* (*Pyrgo*) *nigroconspersa*, a species living in dry areas. Those depressions are probably hygrometric sensors or thermoreceptors in steppes or semi-deserts. According to Daccordi (personal communication), *Henicotherus* sp., another chrysomeline from the Atacama desert in Chile, has subelytral bladders which are also probably linked with water detection. Abdominal structures of this nature are present in certain Australian *Callidemum* and *Strumatophyma*, but only in males, and are probably linked to sexual function (Daccordi, 1994; Jolivet *et al*., 2004). Perhaps these organs in some cases are comparable to the sensory pits of the pit-vipers and rattle-snakes, also sensitive to infrared. The specialized structures are located in the snakes below and ahead of the eye, and they act like infrared eyes, with binocular "vision". Boas have 13 pairs of such pits.

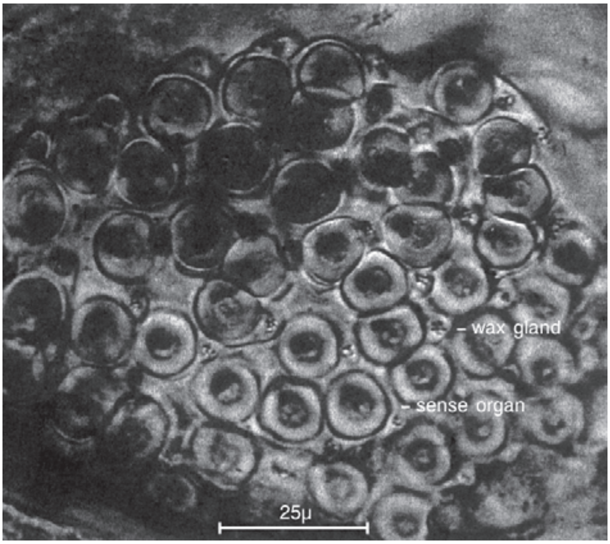
It is sure that such depressions on the abdomen of various beetles have a function, probably concerned with the water detection, but sometimes with sex or pollen transport. It is a domain which remains to be explored. So many beetles have been described without studying their morphology and anatomy; hence it is not known how common such differentiations are among beetles. A micropeplid beetle, discovered by Löbl in Thailand, has the body covered with lamellar secretions all over. It is not wax, and it is not a way to capture humidity since this beetle lives in a permanently humid environment. Is it a protection against predators? There are more things to be discovered and studied among the immense variety of beetles (Löbl and Burckhardt, 1988).



— Fig. 13.1. *Deretus denticollis*, male, a tenebrionid from the desertic island of Socotra, in the NE of Africa (after Koch, 1970).



— Fig. 13.2. The same as Fig. 13.1, with the big hairy depression of the abdomen, probably glandular (after Koch, 1970).



— Fig. 13.3. The infra-red sensitive organs of *Melanophila acuminata* (Buprestidae), as seen when looking at the mesothorax sensory pit (after Evans, 1966).

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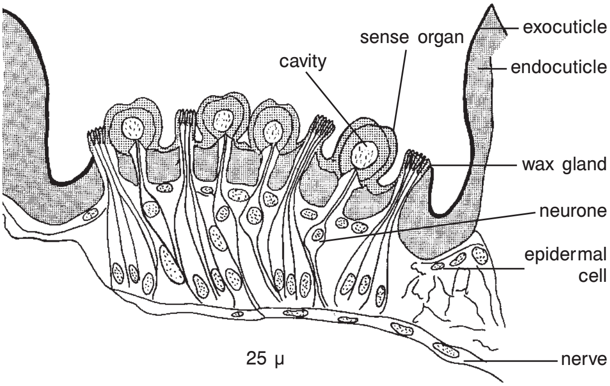

— Fig. 13.4. Diagrammatic cross section of the infrared sense organs of *M. acuminata* showing the wax glands (after Evans, 1966).

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— 14. **Round Defence (Cycloalexy)**

Some vertebrates are known to take to round defence, when a predator is around. Males form a circle, with their heads outward and with females and weaker adults within the circle. This behaviour is shown, for example by penguins, musk oxen of Canada, Canadian deer, etc.

Humans also sometimes resort to the round defence strategy. When Europeans were moving westward in the North American continent in the early days of white settlement, they often faced Red Indian resistance and attack. They then arranged themselves with their horse drawn coaches in a circle, with ladies and infants in the centre.

Curiously enough, the round defence strategy is seen among insects also. Andrade (1981), a Brazilian botanist, was the first to observe this phenomenon among *Coelomera* larvae on *Cecropia* leaves. One of the present authors (PJ), along with a Brazilian colleague (Vasconcellos-Neto and Jolivet, 1988) and with a Brazilian and an Australian one (Jolivet *et al.*, 1990) gave this defence strategy among insects the name *cycloalexy*, and gave the first definite account of this defensive behaviour. In all cases this behaviour is shown by gregarious larvae, when they are at rest, day or night, that is when not feeding or moving. Generally, the larval individuals in a colony disperse to feed upon foliage by night (or by day when they rest during the night), one behind the other, to reaggregate in a cycloalexic arrangement before dawn.

Among beetles (Coleoptera), cycloalexy is known in some leaf beetles (Chrysomelidae), belonging to the subfamilies Criocerinae, Chrysomelinae, Galerucinae and Cassidinae. A member of the family of weevils (Curculionidae) is also known to take to cycloalexy. Examples of round defence have been recorded mostly from the Neotropical (i.e. South America), the Holarctic (i.e. Europe and Asia, north of the Himalayas) and the Australian regions. One of us (Verma, 1996) and Heron (1992) have reported cycloalexy in some tortoise beetles (Subfamily Cassidinae) of India and South Africa, respectively. In *Phelypera*, the processionary neotropical weevil (Jolivet and Maes, 1996; Costa *et al.*, 2004; Fitzgerald, 2004; Fitzgerald *et al.*, 2004), the larvae travel in a loose procession along a branch of their host tree, *Guazuma ulmifolia,* a Sterculiaceae. When larvae loose tactile contact with the larva immediately ahead of them, they rely on a trail pheromone. The larva secretes the pheromone from the ventral surface of the posterior abdomen. The cycloalexic formations maximize the amount of body contact in the aggregate and allow tactile signals to rapidly radiate through the group. In Tam Dao, North Vietnamese mountains, one of us (PJ) saw larvae of some Noctuidae, grouped together on Melastomataceae leaves, standing up all immediately and agitating their heads when anyone approached the plants. They are visually stimulated and are also linked through pheromone production. Among insects, processioning is known only among gregarious caterpillars (Lepidoptera) and in the weevil *Phelypera*. The larvae of *Phelypera*, when resting, arrange themselves in circular formations. As for other cycloalexic insects, this formation functions as an antipredator devise. The cycloalexic chrysomelid larvae and the larvae of *Phelypera* readily bite and regurgitate, when disturbed by potential predators. The entire resting assemblage can be simultaneously alerted by smallest tactile disturbances. The cycloalexic larvae of galerucines or other chrysomelid beetles suddenly raise their heads or tails seemingly for defense. Pergidae larvae, among the sawflies react the same way, and use tapping with the uropod on the leaves to communicate, by means of low frequency vibrations, in the need to reunite a dispersed colony (Carne, 1962). Tapping is also used by larvae of Paropsini, Australian chrysomelines, to reunite the dispersed colony (Meyer-Rochow, 1972). All these larvae of cycloalexic beetles or tenthredinid hymenopterans (Weinstein, 1988) show coordinated movements, threatening attitudes, regurgitation, and biting to repel predators or parasitoids. Some cycloalexic beetles, like *Platyphora* in Brazil, are viviparous and, when the female lays small larvae, the larvae congregate immediately making quickly a circle. Potential predators are pentatomid bugs and ants. Weinstein (1989) has observed an altruistic suicide of a larva of a pergid (Hymenoptera, Tenthredinidae) by biting the ovipositor of a parasitoid wasp.

In addition to some Coleoptera and some Hymenoptera, some Diptera also have cycloalexic larvae, which are known to show this larval defence against predators (ants and bugs) and parasitoids (wasps and flies). Among the flies, pupae and larvae of certain ceratopogonids show perfect cycloalexy in cacao plantations in Central America (Saunders, 1924). More research on ceratopogonids is needed.

All the insects, which take to cycloalexy, are subsocial or gregarious in their larval life. This is not necessarily associated with maternal care. Altruism is obvious among the cycloalexic larvae, as some larvae remain within the circle. In the ring formations, the larvae within the annular arrangement seem younger. Thus, the altruism in this case is with reciprocity, as the larvae, within the circle, will change their position, when they are older. If generally younger larvae are protected inside the circle, this situation should be referred to as reciprocal altruism. But the concept of reciprocal altruism has been recently challenged by Weinstein and Maelzer (1997) for the Australian sawflies in the genus *Perga* (*Perga dorsalis* Leach). The authors labelled individuals with oil paints and recorded their positions on consecutive nights. A subgroup of 20% of the larvae preferentially occupied the outer positions in the resting colony, and also appeared leading the foraging expeditions. Leaders were quick to regain outer positions, if removed and placed in the center of the group. So there seem to be individual differences in the dispersal aggregation behavior of the larvae in time and space, at least for Pergidae; some seem more altruistic than others.

It seems that small colonies of larvae show less viability than big ones among Pergidae. However, in the chrysomelid *Coelomera* on *Cecropia* leaves, a large cycloalexic group divides into two or three subgroups, as the larvae grow in size, and the resulting groups seem as efficient as the original big one, in repelling predators (Jolivet, in Capinera, 2004).

Ring defence is taken to by larvae, when they are more vulnerable, that is at rest or when moulting. In a cycloalexic arrangement the periphery of the ring may be formed either by heads of the larvae (e.g. in the chrysomeline *Platyphora*) (Jolivet *et al.*, 1990), or by their caudal ends (e.g. in the galerucine *Coelomera*). Commonly, when there is an approaching danger, the larvae make coordinated and synchronous threatening movements. Larvae of the Oriental cassidine *Aspidomorpha miliaris* carry a chain of the cast skins or exuviae of the previous moults at the end of their abdomen. The exuviae carrying caudal ends form the periphery. When a cycloalexic congregation of this species is disturbed, the hind ends of the larvae curve upward, raising with them the trains of exuviae. The cycloalexy as such seems to be only partly effective in defence. Perhaps that is why it is supplemented or reinforced by other methods of defence, which include maternal protection (in case of New World forms), emission of glandular or digestive fluid through mouth or anus, reflex bleeding, biting movements of jaws, taking up a menacing posture, camouflage with the leaf surface, etc.

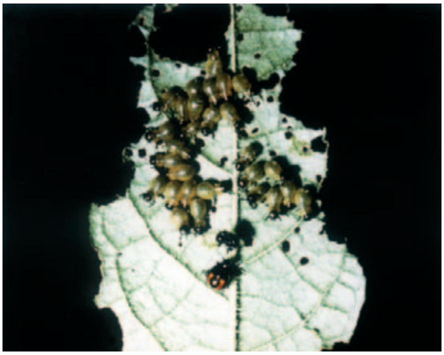
Larvae of some *Platyphora*, an American chrysomeline leaf beetle, form a cycloalexic arrangement on under surface of leaves of the host plant *Solanum*. They have a unique habit of removing hairs from the leaves and attaching them to their own body for camouflage. Other cases of using plant hairs among chrysomelids are seen among Chlamisinae. When those *Platyphora* larvae are disturbed, they raise their heads and an anterior part of the body in a menacing way. A fluid, which is a gastric secretion and seems to be toxic, is ejected from their mouths. If the disturbance continues, they attempt biting.

As has been pointed out earlier, cycloalexic insects are subsocial or gregarious in their larval life. It is believed that the larvae are held together through a pheromone. The chrysomeline Paropsini and the hymenopteran Pergidae, feeding on eucalyptus in Australia, have taken to an interesting way for mutual communication. The larvae of these groups tap on leaves, and the signals, thus produced, are perceived through their special tympanic organs.

The annular arrangement of larvae is generally formed by cycloalexic insect species on leaves of the food plant, on upper or undersurface of the leaves. But, if leaves are narrow, a congregation, with some features of a ring-like arrangement, is formed on a twig, for example those cycloalexic forms which live on narrow leaves of a eucalyptus species. Some instances of polyspecific or even polygeneric ring formation are also known among leaf beetles and sawflies.

Some larval saturniids, such as *Lonomia electra*, in tropical America, aggregate in circular formations (Fitzgerald, pers. com.), and other gregarious saturniids, like *Arsenura* and related ones, rest by day on the trunk of the food plant, not in a circle, as the geometry of the tree does not allow it, but in an irregular group, and use a trail pheromone for procession formation (Costa *et al.*, 2003). Those larvae are very smooth to touch, while other saturniid larvae are dreadfully poisonous. The former have only the group resting position as a defensive mean against predators. Aggregations of an ascalaphid neuropteran larvae (*Ascaloptynx furciger*) around a branch is quite similar to cycloalexy (Henry, 1972).

Cycloalexy or the making of rosette-shaped resting formations is a relatively unexplored area, which deserves further observations and investigations. No sooner has an effective defense developed than a new attack strategy follows; trigonalyid parasitoids for example, have succeeded in producing such eggs as are swallowed by sawfly larvae, thus obviating the need to confront the defensive ring (Weinstein, 1989).



— Fig. 14.1. Third instar of *Platyphora conviva* Stål (Col. Chrysomelinae). Rupture of the cycloalexic ring and predation by a bug of one larva (photo J. Vasconcellos-Neto, 1986). Itataia National Park, Brazil.

— Fig. 14.2. Eggs of *Coelomera lanio* Dalman (Col. Galerucinae), laid on the underside of the folioles of *Cecropia adenopus* (Cecropiaceae). The newly hatched larvae will aggregate (Photo P. Jolivet, 1990). Viçosa, Brazil.

— Fig. 14.3. First instar larvae of *Coelomera lanio* Dalman (Col. Galerucinae). Cycloalexic ring (photo P. Jolivet, 1990). Viçosa, Brazil.

— Fig. 14.4. Second instar larvae of *Coelomera lanio* Dalman (Col. Galerucinae) on a leaf of *Cecropia adenopus*. The ring has doubled. It will increase threefold (photo P. Jolivet, 1990). Viçosa, Brazil.

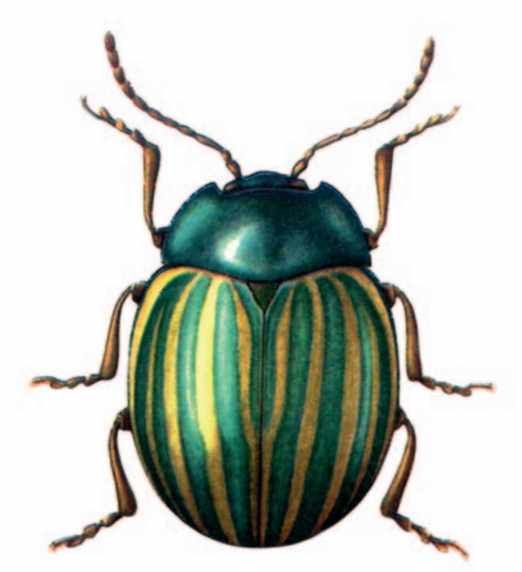
— Fig. 14.5. Third instar of *Coelomera lanio* Dalman on a leaf of *Cecropia adenopus*. The cycloalexic ring is near to be broken and the larvae will go feeding (photo P. Jolivet, 1990). Viçosa, Brazil.

— Fig. 14.6. Cycloalexic ring of *Platyphora conviva* Stal (Col. Chrysomelinae). First instar. The larvae have covered themselves with the hairs of the underside of the leaves of a *Solanum* for extra protection (photo J. Vasconcellos-Neto, 1986. Itataia National Park, RJ, Brazil).

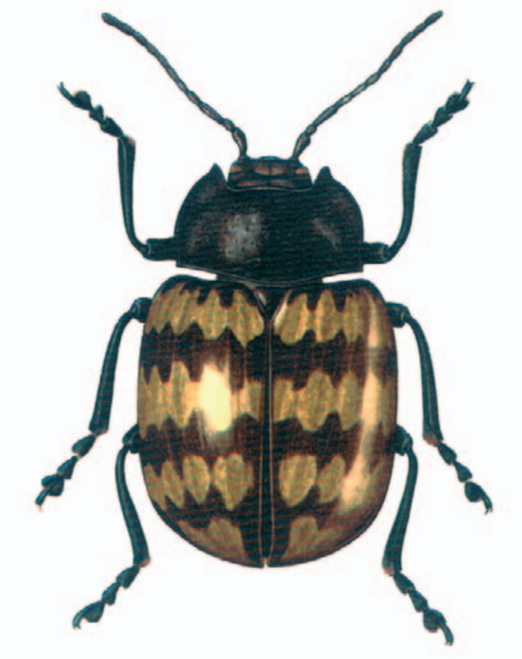
— Fig. 14.7. Second instar larvae of *Perga australis* (Hym. Pergidae) in cycloalexy.

— Fig. 14.8. An ichneumonid parasitoid (*Westwoodia* sp.) attacking the group shown in the Fig. 14.7. Larvae of the pergid are raising their abdomen in defence.

— Fig. 14.9. A heroic larva sacrifies itself (altruism) to grip the ichneumonid ovipositor with its mandibles, rendering the parasitoid incapable of further attack. This is altruistically suicidal (photos P. Weinstein, 1989).



— Fig. 14.10. *Platyphora kollari* (Stal) (Chrysomelinae) on *Solanum* sp., Brazil.



— Fig. 14.11. *Platyphora batesi* (Baly) (Chrysomelinae). Iquitos, Peru. *Platyphora* species are only found in tropical America. Often viviparous and larvae doing cycloalexy (after Jolivet, 1997).

— Fig 14.12. Second instar larvae of *Perga dorsalis* (Hymenoptera: Pergidae) in cycloalexy. White tachinid eggs can be seen on the thoracic sclerites of some larvae (photo Weinstein).

— Fig. 14.13. *Perga dorsalis*, a cylindrical cluster of late instar larvae on an *Eucalyptus* twig. The cylinder appear when the larvae increase in size and the leaf becomes too narrow. In fig. 3 and Fig. 4 no mother protection is shown (photo Weinstein).

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— 15. **AIDS and Insects**

One of us (PJ) got malaria twice in his life, once in Zaire, because he had stopped taking quinine as a prophylactic, and another time in Papua-New Guinea, in the highlands, after collapsing of car on a road and a full night passed there under the stars. PJ was badly bitten by mosquitoes, one of which was infected, but fortunately his wife and kids escaped getting the infection. In both the instances nivaquine promptly put things in order, since it was a benign form of the disease. Then again in New Guinea, PJ got the dengue, a disease transmitted by a day-biting mosquito (*Aedes*), which attacked him in a hotel room, full of those insects without any way to exterminate them. The hotel owners were playing golf and the shops were closed after 4 pm! No insecticide available anywhere. The dengue, this one, close to Murray encephalitis, gives a high fever, skin rash and several bad side effects. Mosquitoes, *Simulium*, fleas, lice and many other insects transmit to man and to animals a fairly large number of diseases, some dreadful and often fatal (Jolivet, 1980).

About 25-30 years ago, AIDS or Sida did not exist or had just started, but the fact was ignored by most people. It started its insidious progress in America and Africa before invading the rest of the planet. At present, we are still powerless, without a vaccine or a real cure against this terrible invader. Antibiotics have effectively controlled sexually transmitted diseases, but they are not effective against the terrible virus HIV. There are no effective vaccines against AIDS, as also against malaria, leishmaniasis, trypanosomiasis, onchocercosis and practically against any protozoan and nematode disease. Tetracyclines, however, seem to work well against Rickettsiae, mycoplasmas and several bacteria-like pathogens.

Several years ago, people hypothesised possible transmission of the HIV by mosquitoes (Jolivet, 1991). Can arthropods really carry retroviruses? We all know that many viruses are transmitted by Diptera or flies, namely arboviruses, and viruses causing yellow fever, dengue haemorrhagic or not, various types of encephalitis (Japanese, equine, St Louis, Nile, Venezolana etc.), and to this list may be added non viral diseases such as malaria, due to a parasitic protozoan, *Plasmodium*, various nematodes, etc. Let us note that, in the case of yellow fever for instance, the virus does not undergo any developmental change inside the mosquito, but simply multiplies itself as in a test tube filled with a culture medium. Bedbugs do not seem to transmit diseases, but Diptera, like Ceratopogonidae or *Simulium*, transmit viruses and worms to man and to various mammals. And lice, fleas and many other insects are also disease carriers.

People thought that, if many viruses multiply in a mosquito and are reinjected into man, why it would not be the same with the HIV? Since many Diptera transmit many viruses, why those insects and many other blood sucking insects, as bedbugs and Reduviidae should not be able to carry and transmit AIDS?

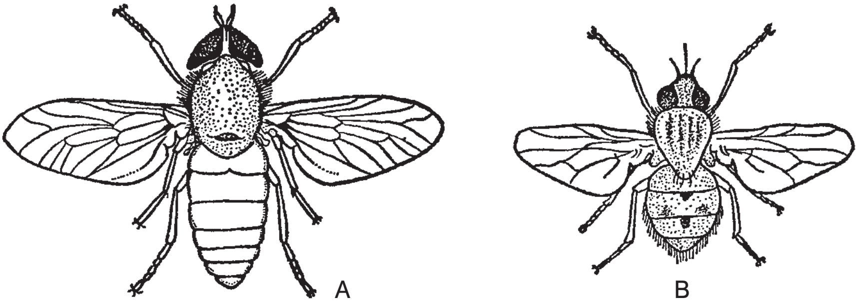
In 1986 a rumour started from Belle Glade, in Florida, that mosquitoes could carry the disease. From 1980 to 1985, 76 inhabitants of this small town (16,500 heads) developed the disease. It amounted to the rate of 461 for 100,000 inhabitants, which at that time seemed substantial. This rate was comparable to other high risk areas, like San Francisco, New York or Key West. Several specialists immediately suspected the mosquitoes to be the carrier of the disease, but inspectors from Atlanta CDC (Communicable Diseases Center) were able to prove that use of drugs intravenously, prostitution and promiscuity were very common in that town. Many Belle Glade inhabitants came from Haiti, the country where seropositive people were numerous. Moreover, most of the cases were found among younger people, and there was no case among young children and among old persons. If the mosquitoes were involved, then persons from all age groups would have been suffering from HIV infection.

Insects (mosquitoes, bugs, fleas, lice) can transmit a virus, a bacterium or any other parasite in two ways, namely mechanical transfer, as with a soiled needle, i.e. without any further development, or biological transfer when the virus or the nonviral pathogen multiplies in mosquito's viscera and then migrates to its salivary glands. However, it does not seem likely that HIV viruses are able to multiply within mosquitoes.

Two other retroviruses, those causing infectious equine anemia and bovine leucosis, are mechanically transmitted by bugs. But in both cases, the donor blood contains the virus at a very high density. AIDS carrier's blood contains not more than 10 viral particles per milliliter, exactly 100,000 times less than in the two aforesaid retroviral diseases. Also, the volume of blood transmitted by a bug is very small. It has been calculated that nurses wounded by a contaminated needle are infected in a very small percentage of cases, around 3 per thousand, and there is 140 times more blood in a syringe needle than that in the proboscis of a bedbug or of a mosquito.

It has been proven that HIV, responsible for AIDS, can remain alive for two or three days inside the gut of a mosquito, but it seems that the probability of a mechanical transmission is practically zero. It may also be pointed out that the virus has had only a recent association with mosquitoes, and it has not so far developed an adaptation to the insect's physiology.

Frequency of AIDS cases, similar to Florida or Haiti, has been found also in Democratic Congo Republic (Zaire). It seems that in the cases there too, it is difficult to attribute the transmission of the disease to mosquitoes. It seems more reasonable to attribute it to promiscuity and prostitution. Until recently, AIDS transmission by a mosquito, though theoretically not impossible, seems highly improbable. We cannot plan experiments on man.



— Fig. 15.1. A: *Tabanus* (Tabanidae), adult. B: *Stomoxys* (Muscidae), adult (after Itard, 1973; Jolivet, 1980).

The only way to make sure about transmission by mosquitoes would be to put under the same tent HIV positive people and healthy people, and to introduce *Anopheles, Culex* and *Aedes* mosquitoes. We could find out if the healthy people get the infection without any contact except through mosquitoes. But such an experiment is unthinkable.

Most of the AIDS specialists reject the hypothesis of mosquito transmission of the disease from man to man. Drug and sex seem to be the main ways of transmission, and yet a recent paper raises some questions (Eigen *et al.*, 2002), and according to it, AIDS in some cases is perhaps horizontally transferred like other arthropod-borne diseases!

The primate *Pan troglodytes troglodytes*, a chimpanzee, has been recently defined as a natural animal host and a reservoir of the human immunodeficiency virus (HIV), not only SIV. Apes are hunted in Africa and sold on open markets. The carcasses are covered with blood-feeding flies, among them the stable fly (*Stomoxys calcitrans*), a biting fly common also in Europe. This fly has been proven to be an effective vector for the retrovirus causing equine leukemia (see above). According to laboratory experiments, the infectivity of ingested HIV virus is not reduced in the regurgitates of this fly. That could explain in Africa a possible primary transmission of HIV from ape to man, through this blood sucking fly.

In view of the dreaded nature of AIDS, it is necessary to investigate further a possible role of blood sucking insects in transmission of the disease.

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— 16. **Living Clouds**

In 1955, when PJ arrived for the first time in Zaire or People's Republic of Congo, formerly the Belgian Congo, to conduct an entomological and parasitological mission in Kivu and Ruwenzori, he spent one month near the Semliki falls, the outlet of lake Edward and one of the sources of the Nile. Those lakes, Edward, Albert, Kivu, Tanganyika, Rudolf etc., have changed names several times according to the dictators reigning in the surrounding countries. Lake Edward has been named for some time as the lake Idi Amin Dada, and lake Albert as the lake Mobutu Sese Seko. They are going to change again following the vicissitudes of politics, and here I prefer to use the older names. All those lakes are pretty different from each other, including the rest of Ethiopian lakes, and they are situated in the earthquake zone in the middle of the Rift valley. PJ has also visited lake Rudolf (now lake Turkana), during an expedition in helicopter along Omo valley, in the period of a yellow fever epidemy, and went to the Koobi Fora park, an extraordinarily area rich in Pliocene fossils (the elephant cemetery of Jeannel!), located along the northern shore of the lake. This area is situated on the border of Kenya-Ethiopia. During this expedition, PJ was once left alone awaiting the next helicopter in an isolated village surrounded by the natives armed with spades and bows. Few hours passed with the villagers speaking no known language and PJ leaning against a big tree. At the end, PJ, a bit disorientated and also not much reassured, remembered Hollywood films and was questioning himself if he will be put in the cooking pot or crowned king of the tribe. Finally the helicopter came and PJ could come back to the camp at his great relief. All those lakes have some peculiarities and some are well known for the sudden hatching of millions of tiny Diptera. Lake Shala in Ethiopia or lake Nakuru in Kenya is covered with pink flamingoes. Others (lake Langano) carry often balls of blue algae (cyanobacteria), floating on the suface; many are frequented by hippos and crocodiles. Hot springs are frequent in all those areas. In some lakes, Gondar, Margherita or Zwai lakes, people use boats made of entangled reeds, as in Egyptian times; also there cows are sent to swim to reach islands. Let us recall that similar reed boats are used also in Titicaca lake in Bolivia. Populations there are rather primitive and hardly touched by civilisation, specially around lake Rudolf or lake Margharita. In many places, during that period, they never heard of the emperor Haile Selassie, at that time the lord of Ethiopia, the king of kings and their direct ruler (Jolivet, 1991).

Between the lake Edward and the lake Albert, the Ruwenzori chain of mountains rises, of which a summit, the Peak Margherita, reaches the height of 5118 m. That chain was named by the ancients as the mountains of the Moon. "The mountains of the Moon feed with their snow the sources of the Nile", wrote, in the third century AD, Ptolemaeus, the pioneer geographer. Remember that around the year 60 AD, Nero sent an expedition to report about the local tribes, their wealth and the origin of the Nile (Cloudsley-Thompson, 1994). Seneca and Plinius the Elder wrote something about the expedition. It is not clear if they were looking for the sources of the Blue Nile or the White Nile. On the way down, on their road, in Sudan, the old Greco-Egyptian civilisations existed, the ruins of which have been left as remains of several temples, Roman baths and hundred of pyramids, and the place is easily accessible by train (Shendi and Meroe). The local writing has not yet been completely deciphered. There was the kingdom of the Candaces, the meroitic civilization, running in parallel with Axum civilisation in Ethiopia. There ruled the Amazon queens, mentioned in the Bible.

It is certain that the Rift valley big lakes, as also the Ruwenzori mountains, have a part of responsibility in the birth of the Nile (White Nile), as has lake Gondar in Ethiopia for the Blue Nile. The Ruwenzori glaciers and snow surely feed the Nile, and in 1954 PJ climbed the mountain and stayed there one month studying insect biology and parasitology. Both White and Blue Niles meet in Khartoum (in the old times Soba) and Nero legions passed through this region while going south in their adventurous mission. When the mission returned, Nero decided that to face the ferocious nilotic populations was not worth the conquest.

In Ishango, a stop-over near the Semliki falls and near Edward lake, PJ met the German zoologist Bernhard Grzimek who was making a film with his son and a cameraman. They were working for the famous film "No room for the wild beasts", which proved greatly successful. Gzimek was then director of the Frankfurt Zoo. He lost his son several years later in a plane accident over the Ngorongoro crater, when filming there rhinos, hyenas, antelopes and lions. On the volcano side, Gzimek planted a plane propeller over his son's tomb and wrote: "He liked so much the wild beasts that he gave his life for them".

In Ishango, hippopotami roamed by the hundreds; they were so numerous and dense in their population that from time to time huge epidemics of anthrax decimated quite a lot of them. The beasts used to give furious head blows against the visitor's boats. Birds were numerous and varied. Elephants and lions used to come by day or night to visit the camp. But during the night, groaning of the hippos and roar of the lions dominated all other noises.

There happened almost every morning a strange phenomenon over the lake; a black cloud used to appear suddenly emerging directly from the water surface. One day we found the key to the mystery. The cloud appeared near us and we were surrounded by millions of non-biting mosquitoes, an explosive mixture of chironomids, chaoborids, and several others. The chironomids were the dominant species in the cloud. The lake was polluted by hippo excreta and was exactly what we define as an eutrophic lake, where mostly chironomids or blue algae enormously multiplied.

Blue green algae, Cyanophyceae or Myxophyceae, now named Cyanobacteria, multiply easily in small ponds or lakes, and even in the sea, when the water is heavily polluted by nitrates. Those cyanobacteria, like *Microcystis*, can be heavily toxic and recently in New Zealand calves and cows died near a reservoir covered with those water-flowers (Wasser-Blüten). Red sea gets its name from that rare phenomenon, and the same happens quite often in the California gulf. Generally farmers are responsible for pollution with excess of nitrates or animal excreta. Intensive agriculture has its drawbacks.

Mosquito clouds are a rather common phenomenon, not only in the Rift valley lakes, but also in Central America, as in Nicaragua. Let us note also that Lake Nicaragua, now heavily polluted, was a place for freshwater sharks and sawfishes. Freshwater sharks are also met with in central New-Guinea in the Murray lake, in the Mindoro lake in Philippines, and in the Maracaibo lake in Venezuela. Sawfishes are also found in the Murray lake. In that last lake, as in the Nicaragua lake, sea fishes probably came through the rivers. As regards the Mindoro, it was a gulf, which was closed accidentally.

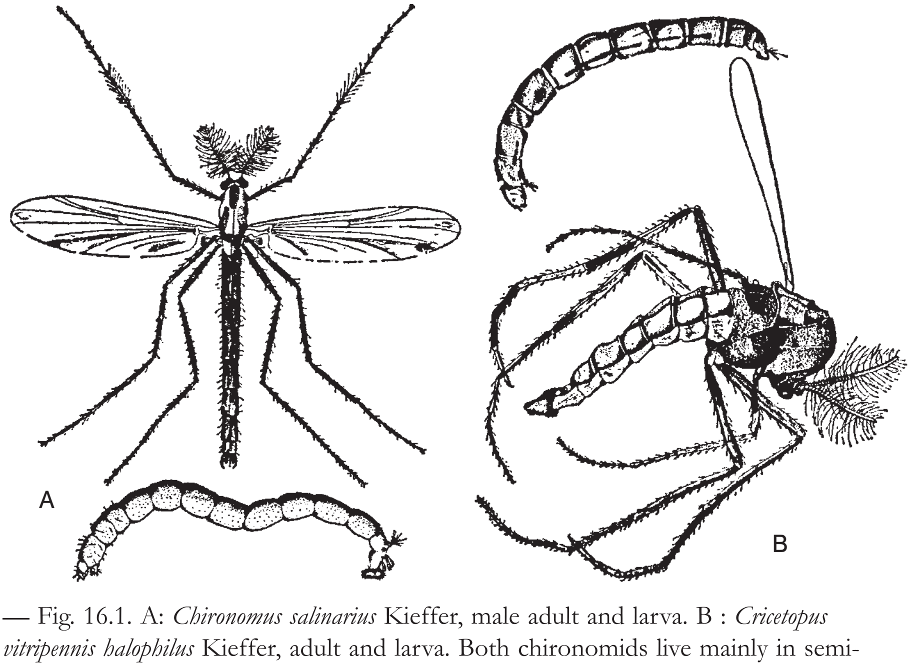
The inconvenience, caused by those minute mosquito clouds, is that they penetrate into the nose, the eyes, the ears… and glasses of wine of the customers of the restaurants along Languedoc-Roussillon coast, near Montpellier. Tourists and locals often complained about it. However, those tiny insects do not bite, do not transmit diseases and are totally harmless in those respects. Of course, people may complain about a few stinging chironomids. But such chironomids are extremely rare, and they are really living fossils in South Africa. Most of the 5000 existing species of chironomids suck nectar of flowers, or generally do not eat at all in the adult stage.

Are the chironomids really pests? Let us consider the examples of various localities, viz. Sudan in Khartoum, Nicaragua lake in Nicaragua and the Languedoc ponds in Languedoc, near Montpellier in France.

PJ was in Khartoum in 1963 when Walker started his study of chironomids. In Sudan, the populations of the midges reach their maximum from November to May, during what we could name as winter, even if there the temperature is rarely below 20°C. Enormous masses of insects, which are named there *nimitti*, makes life almost impossible to the populations living along the Nile and more specially to the hotel customers or the civil servants of the ministries. Rightly or wrongly the midges are accused for all sins of Israel. Serious allergic reactions are attributed to them. The midges penetrate up to 300 m beyond the river shore, and it happens that people quit their houses and once it was necessary to evacuate a hospital. Reactions are mostly neurotic, but people always confuse midges with biting mosquitoes. People even thought about building a new capital away from its actual place. This capital was built in the past by Gordon and improved later on by Kitchener. Gordon built it using the British flag as a plan for the distribution of the streets. Since 1956, a lot of literature has appeared on the midge topic in Sudan. The Nile here plays the role of an eutrophic lake with *Chironomus* and not of an oligotrophic lake with *Tanytarsus*, though that genus is also abundant there. One may explain the dam phenomenon as due the confluence of both the Niles, the Blue and the White, in Khartoum, and also due to many artificial reservoirs created here and there around. The gardens bordering the river are also used for resting by the adult midges. That kind of shelter did not exist in the past, when the country was a plain desert.

In Nicaragua, in 1962, a layer of decomposed midge adults was found having more than one meter of depth. Such accumulations, however more modest, were found in California and on the littoral parts of Languedoc in France. In Carnon, near Montpellier, a layer of more than 30 cm of dead midges once was found around shops.

The chironomids have the defect to provide basis for formation of enormous populations of spiders, which may invade houses, when looking



— Fig. 16.1. A: *Chironomus salinarius* Kieffer, male adult and larva. B : *Cricetopus vitripennis halophilus* Kieffer, adult and larva. Both chironomids live mainly in semi-brackish water (after Jolivet, 1991).

for their preys. When they are small the midges penetrate more easily inside the dwellings through doors and mosquito nets, and may enter eyes. We have already mentioned that in the seaside resorts, in summer time, chironomids invade in the evening the restaurants, dropping into the glasses and dishes. That raises some problems even if it is more psychological than hygienic, but all the customers are not necessarily entomologists and do not realize that the midges are clean, harmless and do not carry diseases.

In the Languedoc area, two midges predominate: one *Chironomus* with red larvae and a *Cricetopus* with green larvae. They are much more difficult to control than the mosquitoes. However, the chironomids, in equilibrium with the local fauna, are a blessing for the environment. They feed the fishes and the birds and bats. They become a pest only when they multiply very rapidly. People tried to contain them by different ways, by mechanical control, biological control, but mostly by chemical means against the adults using the organophosporic insecticides. Success is rare and the insecticides are polluters. Some success was obtained with integrated control, mainly in South Africa.

It seems that chironomids are attracted by certain sounds, the human voice vibrations, certain degrees of luminosity and heat, CO_2, etc. Maybe it is a remnant of their old state of biting mosquitoes and blood suckers at a certain stage of evolution. To develop physical or chemical lure seems to be a relic of the past. Planning a biological control, when they are so numerous, is only a wishful thinking, nothing more.

Finally, the treatment of the chironomidophobia is also matter of education to the population, as the midges are totally harmless. Fight against pollution is also a factor, which should not be ignored, as the midges help reestablish the fragile biological equilibrium, and this balance would be disrupted, if midge population is made to decline through human efforts. Also one must not modify too much the food chains in water and in the air by an irresponsible use of insecticides.

The chironomids are not the only insect clouds to cause nuisances. Clouds of Phryganes, Ephemeroptera, Homoptera (such as *Nephotettix*, so abundant during the typhoons in Hong Kong), Blepharoceridae Diptera or nuptial flights of ants and termites, all may be nuisance makers , mostly in the tropics.

Let us talk a bit about *Nephotettix*. They are Homoptera, small version of the cicads, which hatch in mass in rice fields and invade shops in Hong Kong. They are normally sap suckers, but it happens that they often try to sting and even they are able to remove a bit of blood. PJ has beeen attacked many times, after the rainy season in Ogaden (eastern Ethiopia) by herds of those small insects. They tried to bite like mosquitoes. A very tiny Homoptera, *Orosius cellulosus,* vector of cotton phyllody, a mycoplasma affecting the cotton flowers, in West Africa, has been described, in India as "biting man".

All those small insects are just small nuisances. They do not transmit any disease, and, after all, they are sometimes signs of nature fighting pollution.

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— 17. **Killer bees**

If we are feeble or allergic, we can react very badly to a hymenopteran bite. Only one bite of a wasp or of a bee may kill a man, while it may not affect others. If one is attacked by a swarm, a disastrous result may well be imagined. One can become allergic later on, that is after a few bites, one may develop sensitivity to bee venom. So being careless about bee stinging may eventually prove fatal.

It has been said before that PJ was chased once in Ethiopia by a swarm of *Apis mellifica adansoni*, the Abyssinian variety, which were trying to bite the head, with only vestige of fur in the naked ape (see the chapter on "Interesting ways of bees and dung beetles"). In Africa monkeys, as well as the bears in other countries, are cunning honey robbers. Certain birds in Africa join small mammals in attacking wild hives. Hence bees in Africa have learnt how to protect themselves, and attack readily all furry and feathered animals with ferocity.

Most of African bees, all African races of *A. mellifera*, are ferocious, active throughout year, and build generally their hives in any available cavity. In Ethiopia, the man-made hives are very primitive and made of bundles of firewood suspended from trees. Once PJ travelled there in a DC3, and a co-passenger had inside a metal can full of bees with its top filled with grasses. Slowly the bees escaped one by one, and the cabin was full of buzzing insects. The poor bees were more afraid than we and did not try to bite. It is not rare in Sudan to see the bees installed at the entrance of a swimming pool. This they do to repel potential bathers, when the pool is not to be used. In Dakar, often the bees try to establish themselves on lamp posts. African bees get disturbed easily, and very often in the evening, when the lamps are turned on, the bees, disturbed by the light and the heat, become furious and try to bite. It was the South African variety, which was introduced in Brazil in 1957, *Apis mellifera scutellata,* and its crossing with *Apis mellifera mellifera* which produced a ferocious hybrid, nearly a semi-species, named the Africanized bee.

Bees can be dangerous also due to toxicity of their honey. Recently in France a bee-keeper praised his *Rhododendron* honey. It was forgotten by him that honey collected on *Rhododendron* is toxic for man, but not to the bee. Numerous cases of honey poisoning are known, specially in Asia.

There were in past cases of group poisoning through consumption of *Rhododendron* honey. Xenophon, in 401 BC, has described in the Anabasis that, when the Greeks once camped in Anatolia, the ones who ate local honey lost their mind, vomited and were victims of a terrible diarrhoea. The soldiers who ate only a little honey seemed completely drunk, but recuperated the next day. *Rhododendron*, an Ericaceae, is not the only plant to yield poisonous honey. Toxic honeys result from the bee foraging also on Aconit, Colchica, Jusquiame, and *Kalmia*, a North-American Ericaceae, often cultivated in our gardens. The anthers of that plant are programmed to dust with pollen an eventual pollinator. The toxin of *Kalmia* is a glycoside, the andrometoxin, and its action can be easily neutralized by simple heating at 40-50 °C.

A poisonous honey may be toxic to man, but does not affect the bee, though the insect can be sensitive to certain pollens, such as *Ranunculus* and certain tree pollens. Normally bees avoid those plants, but it so happens that they collect pollen from such plants in case of scarcity or drought, and the toxic pollen poisons the honey both for man as well as for bees.

That the bees can produce in certain parts of the world toxic honey is already worrying people. Besides, a badly controlled and untested hybridisation may become a catastrophe at the continental scale, and that is much worse. It was this that happened when an imprudent apiculturist introduced in Brazil, in 1956, a South African race of *Apis mellifera*, *A. m. scutellata*. The foreign bee crossing with *A. mellifera mellifera* has transformed the latter sweet bee of Mount Hymette, praised in the past by Virgil, into an uncontrollable and aggressive bee, ready to rush against any imprudent visitor. In 1957, one year after the introduction, there were 17.39 % cases of bee stinging among Brazilian beekeepers. In 1969 this figure reached 60.69%, and there were many deaths among humans and domestic animals. Since then, the ferocious bee has invaded Amazonia, tropical parts of South and Central America and has reached California and the South West zone of the US below the overwintering line (Jolivet, 1991).

That bee introduction was made in Iracicaba, in Sao Paulo state, in Brazil, by Warwick Kerr who wanted to produce by hybridisation a new race, better adapted to tropics. In Africa, local races of *Apis mellifera* are more active, and produce, under poor conditions, much more honey. The hives, in Brazil, were equipped with screens allowing exit of honey gathering bees, but not of the queen and the males, which were too big for the size of the openings available. That was the catastrophe. During the absence of the experimenter, a local beekeeper judging the openings in the screens too narrow for the workers coming back with their load of pollen, widened the gaps in the screens. In the following ten days, the colonies swarmed repeatedly and we could count 26 new swarms leaving the hives. The African bees swarmed everywhere, probably by hybridisation with the Italian form (*A. m. ligustica*), and started a new and more vigorous race, almost a new species, more dynamic, more ferocious, and it started the conquest of the New World. Bees, resulting from hybridisation with the African race, established large feral populations and were replacing resident honey bees. Transvaal genes in the hybrid bees dominated the Italian race, and we reached a complete disappearance of European traits (Taylor, in Resh and Cardé, 2003).

These new bees killed beasts and humans (in average 50 men per year) through all Brazil, and there are no years without new cases. In Africa, this insect, though normally aggressive, can be controlled in apiaries. It was not the same in Brazil. Hybridization produced a bee more vicious than the African race itself. The Africanized bees in the New World could be a complex hybrid of *A. mellifera* (Germany), *A. mellifera ligustica* (Italy) and *A. mellifera scutellata* (Transvaal), but certain authors believe that it is only *A. m. scutellata* at the pure stage, probably due to a possible incompatibility of the nuclear and mitochondrial genomes of the remaining three races.

The eventual spread limits of the killer bees in America are difficult to evaluate. All depends on their adaptability to cold. After the accidental introductions in California in 1985, it seems that the Africanized bees will establish in the US in the southwestern states, and eventually in Florida. Due to stinging incidents, American beekeepers will hesitate to accept the bee for local apiculture. The new bee has penetrated in Argentina and a hybrid zone reaches the northern parts of the country.

Economically the Brazilians are rather satisfied with the new bee, which produces twice as much honey as *A. m. ligustica* and four times more than *A. mellifera* s. str. Only many more precautions have to be taken when approaching the hives, and all beekeeper equipment must be used, when collecting honey. The behaviour of these bees is really dreadful, because, when they are disturbed just by someone approaching, it takes one hour before they calm down. In European farms disturbed bees quieten down in five minutes. The movement of Africanized bee swarm covers at least 100 meters, while European bees swarms stop generally after only 10 meters.

In 1988, microprocessors were fixed on the pronotum of the killer bees, to follow their migrations. Solar cells charge the device, which send infrared signals captured by a scanner. That way the wing beatings were measured, and it was noted that the movements were obviously quicker in the African than in the European race. *A. m. scutellata* lives in a more dangerous surrounding than *A. m. ligustica.* Aggressiveness is an answer to the natural aggressions faced by the insect in its original surroundings.

The Africanized bee produces more honey, and it can probably be genetically improved by new crossings. However, so dominant are the African characters that so far all attempts have been futile. As it reproduces in the wild state too, their eradication is impossible. If a well equipped honey keeper can control it, it is not the same with an imprudent walker approaching the hive. It attacks suddenly and stings without pity like all animals, which live normally facing danger to their existence.

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— 18. **Butterfly hunters**

A recent book by a butterfly hunter (Larsen, 2003) reminded me (PJ) of the heroes of the past, those people who collected butterflies or birds in the jungles of America, Asia and Africa, before availability of such facilities as roads, cars, refrigerators, and comfortable hotels, and faced the risk of living among often hostile natives. Those lepidopterists were often victims of diseases, and of arrows, spears or darts from the natives, but they were at the same time often rewarded to see the beauty of a new *Ornithoptera, Papilio* or *Morpho* for the first time. Among those heroes were Bates in Amazonia, Wallace in the Insulinde and Darwin, even if he travelled on the Beagle relatively more comfortably, even if he was seasick most of the time. It is has been said that Darwin got Chagas disease when he was in South America.

Linnaeus during the 18th century described plants and animals sitting behind his desk, as also did the great Buffon during the same period. It was well accepted then that the naturalist stayed in his "Natural History cabinet" and did not travel. Even Jean-Henri Fabre, the entomologist, had not travelled outside his Mediterranean region. He, however, used his time to observe insects in the field, their behaviour in their natural surroundings. He inspired many later naturalist travellers. The understanding of biology of species had to suffer, but in that period, when shipwrecks were frequent, and transportation was slow and hazardous, any trip was an adventure. Even at the end of the 19th century, when Xavier Montrouzier described new plants or insects from New Caledonia, it probably took 4 to 5 months before a letter from the island could reach France. No telephone, no telex, and no software to communicate. How exciting to see a world without pollution, rich with millions of creatures, covered by dense forests, but the main obstacle to nature study was lack of means to study and describe this wealth. Even now, when forests are being cut down, pollution and fires dominate the landscape, buildings and other constructions destroy wild life, there is still a lot of living beings, including insects to be described before they disappear forever. It has been estimated that, at the present speed of description of new species, 3000 years would be needed before everything could be studied and given a name. Will man survive that long on a degraded planet? Molecular biology, cladistics, bar code, even if one day something replaces the Linnaean classification, will never succeed to describe all the living things in foreseeable future.

There were traveller naturalists as well as brave and famous sailors in the past, and the achievements of entomologists, if less well known, were as spectacular as those of the navigators and sailors. Besides Darwin and his famous travel on the Beagle, Wallace, who was codiscoverer with Darwin of the theory of evolution through selection, visited Amazonia and Indonesia. In fact there were many travellers at that time. Thunberg, a student of Linnaeus, went to Japan, Commerson described many plants, and at that time French and British sailors took with them naturalists who discovered the astonishing world of Australia and the neighbouring islands.

The baron von Humboldt explored Central Asia and tropical America. He acted in those parts as a botanist, a geologist and a geographer. He was also a zoologist-entomologist, but to a lesser extent. In such studies there were his predecessors too. In 1651, a Spanish naturalist, Francisco Hernandez, described for the first time the ant tree of the Aztecs, the famous *Acacia cornigera*. Spicy description was done in latin: *Generantur praeterea intra corniculas formicas quaedam tenues fulvaeque et nigricantes*. Hernandez believed very firmly that the inflated stipular spines of those *Acacia* species, in which ants were housed, also generated the ants. As early as 1648, a Dutchman named Macgravius described before him in Brazil the association of ants and *Cecropia*, and another Dutchman, Rumphius, discovered in 1750, in Java, the epiphytic ant Rubiaceae, *Myrmecodia* and *Hydnophytum*. He also believed in spontaneous generation of ants inside the ant nests. It took many more years before Pasteur could finally destroy the myth.

Traveller naturalists, like Belt, who was also a geologist, in 1874, described the ant-plant symbiosis on the *Acacia* in Nicaragua. These plant associated ants constitute an efficient defensive army, which prevents mammals from eating the leaves, and protect them from a more dangerous enemy, the leaf-cutting ants, the famous *Atta*. In exchange of these services, the ants, not only are lodged in all security in the plant, but also they receive a large supply of food in the form of food bodies or trophosomes. Some plants or trees, among the myrmecophytes, *Acacia*, *Cecropia, Macaranga* and several others provide the ants lodging and food. In exchange, the ants protect and clean the plant, destroy weeds, and feed the plant with nitrogenous compounds (excreta and cadavers). It is for mutual benefit, a pure symbiosis. Even if Belt had some perception of this relationship, it took many years before the whole situation was fully understood.

Bates, another traveller naturalist, believed that the leaf-cutting ants cut the vegetation in order to line their nest, a notion based on an old Indian legend. Belt discovered the truth in Nicaragua, that the leaves are brought back into the nest in order to make a compost and to grow fungi, on which adults and larvae in the ant colony feed.

It would be too long a story, if we refer to the work of all those early traveller naturalists, who, for most of them, have written excellent books, reprinted from time to time. Those books remain precious witnesses of the past, when the forest, still undisturbed, were occupied by tribals, living in symbiosis with nature. The “civilisation” did not reach then the tribal populations, the insects were probably thousand times more numerous at individual and at species levels, and mammals and birds much more common and varied. When Julian Huxley wanted, in the name of UNESCO, to start, in 1946, an international exploration of the Amazon, it was still much the same. Unfortunately, for political reasons, the exploration was slowed down by the Brazilian government of that time, finally cancelled, and Huxley resigned. Brazil wrongly apprehended spread of neocolonialism! Today, we lack taxonomists in botany and entomology in adequate numbers, and innumerable insects and plants have vanished.

The lack of trained taxonomists is general and everywhere in Africa, in Madagascar, in Asia, and in Australia. Big rainy forests are often nothing more than a tourist attraction. The destruction of forests has been fast. In New-

Guinea, tea, coffee, cocoa are planted in the highlands, where were living in pristine forest *Ornithoptera, Troides, Graphium, Papilio* and so many other beautiful butterflies, which will be in near future surviving only in museum drawers.

Le Cerf, the French lepidopterist, in 1933, narrated the explorations of butterfly hunters of the past centuries, including that by Hans Frühstorfer, who travelled into the tropical world, politically then more accessible than now, to capture new species and genera and to enrich his collections. His account includes explorers up to the last century. Let us also note that in that time, it was permitted to catch a butterfly and to collect a beetle. Now the governments of the world, e.g. Brazil, Australia and many others, prohibit any insect collection. People collecting moths and butterflies or plants or beetles, are jailed in New Zealand, Brazil, India, Costa Rica and elsewhere. Small developing countries ask for money, and when money is collected and paper work accomplished, the permit is seldom delivered. It is hypocrisy in the name of nature conservation, as forests are being cut with impunity and with them are disappearing butterflies and other insects, while the poor entomologist can only take pictures of a vanishing world, a ghost fauna and flora. PJ has seen on Bougainville mountains, the unique site of a very rare *Ornithoptera*, Australian pilots spraying defoliants and reducing trees to stumps, as would happen in an artificial lake. Families were living nearby, and we are aware that the chemicals, being applied, are carcinogenic. Mining of copper was being given priority, and people were being told that the underground wealth belonged to the Queen!

Our experience in the tropics has shown that it is very difficult to choose one's collecting area. For collection choosing time is important, because, if the seasons are succeeding, humid or dry, hot or cold, one is never sure to find the "beast" which is being searched for. Seasons vary in intensity greatly from year to year, and specially in Central America with the phenomenon El Niño. In what remains of the Atlantic forest in Brazil, there are dry years and humid years, and years when even it is quite cold. Rarely in winter there is snow in Curitiba.

PJ remembers the year, when crossing the island of Luçon in the Philippines, where he was looking for Negritos, a cousin of *Papilio blumei*, over some blue Verbenaceae. Seeing everywhere the butterfly with its green band on the wings was a gratifying sight. He appreciated his luck, since sometimes the weather is not at all favourable. On the contrary, in New Guinea, we can see all the year in the middle mountains along the rivers the beautiful *Graphium weskei* drinking water in the sand and, in plains; it is no less beautiful than *Papilio ulysses,* looking for its host-plant, an *Evodia*. *P. ulysses* does not like much the imported *Citrus,* and often the caterpillars die on the leaves. On the contrary, in New Caledonia, *P. montrouzieri,* also of an azure blue butterfly, accepts easily *Citrus* leaves, though it is not its normal food-plant. Making a successful collection is not readily predictable.

As Le Cerf (1933) rightly writes, for the butterfly hunter it is a fight all the time, even if he foresees less favourable situations. Sometimes, one does not find anything, the period is bad, the unfavourable season has started much earlier, or the desired season is too late to start, the year is too dry, or excessively rainy, or a poor area turns out unexpectedly rich. Time lost, money lost, pain with no return, and the collector traveller goes back to the coast, happy about safe return, if he could escape health hazards, which is not always the case.

Le Cerf has talked about a good old time, when malaria prevention could be achieved only with quinine, transportation was primitive, roads were nonexistent, and the natives hostile and aggressive. What is it now? Some of these countries suffer from civil war, and it is no more safe now to penetrate into Zaire than during Stanley and Livingstone time. Oases of peace remain: Thailand, Taiwan, Malaysia, and many South American and Central American countries. Many countries now are modern and well equipped, but butterfly or beetle hunting remains forbidden. In most of the areas, forests are being cut down, monoculture reduces the insect breeding, and nitrates and pesticides destroy a great part of the remaining fauna. Malaria, once nearly eradicated, has returned with force, and is resistant to most of the synthetic antimalarials. *Plasmodium* has developed resistance to drugs, as mosquitoes have become resistant to most insecticides. As an effective protection against malaria WHO offers now pyrethroid impregnated mosquito nets! However, repellents remain quite efficient against bites. In some areas, like Papua-New Guinea, legal collecting of insects has become replaced by underground poaching, which is not easily controllable. Some kind of conservation hysteria has developed now among nations, when the best means of conservation is to stop forest cutting and criminal fires. Unfortunately, there is little we can do about population increase and consequent growing urbanisation.

Let us think about those butterfly hunters of the past, when the forests were intact and the insects abundant. Some of them lost their life, e.g. Goudot disappeared more than a century ago in Madagascar; Lix, who was hunting in New Ireland for the Paris Museum, was killed and eaten by the natives in 1892. New Ireland has always been an unproductive and barren land. It is there that in 1879 the unfortunate expedition of marquis de Rays, a Breton gentleman, started. He devised an enormous swindle and proclaimed himself king of that imaginary kingdom. Bretons, Normands, Vendeans, Italians died there, victims of fevers or eaten by the natives. Others were rapatriated to New Caledonia, some went to New Britain and successfully established there plantations. In Port-Breton, we can see the ruins of the town founded by those unfortunate adventurers. Their millstone is exposed now in Rabaul, in New Britain. It is not surprising that 14 years later, Lix was captured and killed in the area. The French writer, Alphonse Daudet, inspired by his adventure, wrote Port-Tarascon.

New Guinea, formerly an impenetrable land, has been responsible for the death of several butterfly hunters, and recently a young Rockefeller disappeared there on the northern coast. Werner died after six months of hematuria. Doherty escaped by miracle from the spear of a native, who reached one of his carriers. Xavier Montrouzier received in his back in the Solomon the spade of a native, and it took him 6 months to get the wood pieces out of his body. Another time a spade barely missed him in the north-east of New Caledonia, in Balade, where he was trying to establish a new mission.

Today the plane carries the modern butterfly hunters. They have electricity and UV for their traps, bungalows for sleeping, and asphalted roads for their jeeps. But those roads are also crowded by trucks, loaded with logs from rare trees. It is a current situation in Thailand, Borneo, Ivory Coast, Venezuela, and it will go on until the death of the last tree. In Amazonia, after clearing the land, the trees are left decaying on the spot. Then African grasses are planted to feed the local zebus, of which the future is to finish as hamburgers in various American fast food stands. The sandy ground is covered by a thin humus layer, which is soon washed out by rains. In Amazonia, the biomass survives in a few centimeters of soil, and, what was once a forest, has been cut, only to grow shrubbery *Solanum* and several species of *Cecropia*. In the north of Panama, along Costa-Rica border, a formely dense forest, has been cut down for farming, and later abandoned. There exists now a forest of *Cecropia* trees and nothing else. PJ has visited in Banfora (Burkina Fasso) several years ago, and saw there a rich endemic forest, formerly protected by the former colonists, totally cut to replant eucalypts. All that with the blessing of FAO! And eucalypti burn like matches in an area renowned for its bush fires.

Those, who are worried about decline of insect biodiversity have to realize that generally insects are highly fecund, and that collecting some specimens by beetle or butterfly hunters does not bring about any considerable decrease in the insect population size. The main factor, responsible for driving insects to extinction, is habitat loss. This situation is well illustrated by the case of the Lange's Metalmark butterfly (*Apodemia mormo langei*), which was fast disappearing in California (See "WINGS", Summer, 1987, published by the Xerxes Society of USA). Naturalists noted that the butterfly was breeding on a weed, naked buckwheat growing on sand dunes along the banks of the river San Joaquin, that the sand dunes were being destroyed through sand mining, and that this was the reason for the disappearance of the butterfly. Steps were taken to prevent destruction of the sand dunes over a large area, and thus the butterfly could be saved from extinction.

The effective way to conserve insect biodiversity is to save insect habitats. A careful field study reveals what a particular insect needs for its breeding and feeding, and this is what a naturalist does. But to identify the habitats, needed by different insect species, would take long, though setting up national parks would help make the process faster. Meanwhile we should take care to protect our forests, wetlands and other natural environs as well as we can.

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— 19. Interesting ways of bees and dung beetles

It is well known now, through Jean-Henri Fabre's observations, that many Hymenoptera hunt spiders, caterpillars, locusts and grasshoppers, which they paralyse with their sting to feed their offspring. The paralysed prey remains fresh and without any rot for a long period. This preservation of the prey, which is in a state of prolonged coma, is a primitive substitute of the modern refrigeration. The honey bees (*Apis mellifera*) amass honey, which they collect and produce from the nectar and pollen harvested from flowers. Honey with pollen is used to feed the larvae and the adults in their colony, and, according to the quality of the food, larvae will become workers or queens. The honey includes the worker bee's saliva, which has preservative quality. Hence the honey remains free from fermentation and decay indefinitely. The larva, which is meant to develop into a queen, gets a special food richer in proteins, the royal jelly, secreted by labial glands. Sex is mostly determined by the number of chromosomes, males or drones being haploid, i.e. having half of the number of chromosomes in the females, which may be sterile workers or egg laying queens.

There are in the tropics, small bees (*Melipona* and *Trigona*) which produce excellent honey, and they are stingless, but are often aggressive for their defence.

In Brazil, some *Trigona* bees come in groups over your hairs, and try to bite the scalp. Others surround the intruders with a buzzing cloud to thus create fear, but there are also, among the species of this genus, some very sweet bees, which never attack. PJ remembers, in Burkina Fasso, near a river, when using lemon grass as a mosquito repellent (phthalates and other repellents were not available on the spot), he could escape mosquito bite, but he was surrounded by clouds of *Melipona*. Repulsive to mosquitoes, the lemon grass juice was strongly attractive for the stingless bees.

Why *Trigona* bees were attacking the hairy surface? The British naturalist and traveller, Thomas Belt, reporting his experience in Nicaragua, wrote that it was because the bees had the habit to attack the furry mammals, mainly the sloth. It is also likely that bears, which are fond of honey, may also be a potential enemy of the bees. The bees may also be attacking in Africa hairy apes. As these bees are stingless and having no other means of defence, they take to biting. In Viçosa University, in the state of Minas Gerais, in Brazil, there is a round laboratory for apiculture and meliponiculture with a good number of wild bee hives around. They are free to gather pollen outside, but their nests are visible through a glass in case of each of their hives. The nests are of different species. Outside, there are also hives of the Africanized honeybee, so it is called there. There, if as you get close to a hive, the bees suddenly start emitting a buzzing noise, and appear agitated, and a prompt retreat from the hive becomes necessary. PJ with a team of students, once in Ethiopia, in the Ogaden, was suddenly followed by angry African bees. They were trying to bite, and he was protecting his eyes, but the insects were coming over his hairs from everywhere. Obviously his scalp, covered with hairs, was attractive to them, and he (PJ) was running away, trying to crush the insects over his head. The pursuit lasted after few hundred meters. One of his colleagues, in Zaire, was bitten over the head by an enormous wasp, and went into coma. He got out of it one month later, 90% disabled. He was constantly shaking, since the wasp had probably bitten a vital centre of the brain. Attraction for hairy surfaces seems general among these Hymenoptera, though some wasps mainly aim at the eyes. PJ has still the bitter souvenir of a wasp bite on the upper eyelid, when as a teenager he was trying to displace a wasps' nest. Thank God he was not allergic to the sting poison, and the bite resulted only in an enormous swelling. A classic case is that of the German naturalist, Fassl, who died of malaria in 1922. He was hunting for butterflies in Amazonia, when he was stung into the eye by an enormous wasp. He spent 8 hours in terrible pain, before succeeding to remove the sting.

To come back to *Trigona* bees, another peculiarity of these insects is that, when they feel a danger approaching their hive, they arrange themselves in a circular group around the entrance of the hive. It is what we have named cycloalexy (see the chapter on “Round defence”). Only in Viçosa University, you can observe them in semi-freedom in a wonderfully equipped laboratory. Beekeeping with *Trigona* and *Melipona* in Mexico and in South America declined rapidly with the invasion of the African variety of honey bee.

Most of the bees collect pollen from the stamens of flowers, squeeze them into special pollen baskets located on the tibiae of their legs. In East Africa (Ethiopia, Sudan, Kenya), some races of *Apis mellifera* steal smelly flours, instead of pollen in village markets. They like most of all shirro flour, *Cicer arietiinum* or chickpea. What is strange is that those bees, so aggressive when you approach their hives, do not bite when you take the flour in your hands to transfer it into bags. When disturbed, they go away to come back immediately, exactly as do the flies when chased out from a pot of jam. Under that situation the terrible bees are peaceful.

Von Frisch wrote to one of us (PJ) in 1963 that European bees collect sometimes any pulverised substance, like brick or coal powder. It is evident that the nutritive value of these substances is nil, and one may consider this behaviour as a mistaken instinct

It must be noted that the purple emperor, *Apatura iris*, the beautiful European butterfly, sucks humid bricks or even humidifies the brick with its excreta before sucking with its proboscis. It seems that the male sucks this way to get sodium, potassium, and calcium present in the brick to be used in making its spermatophores, and used by the female in egg making. It is also possible that Von Frisch’s bees get calcium with the brick dust.

Melipona and *Trigona* are known to collect enormous quantities of pollen and their stock cells in the hive are full of almost pure pollen. To feed their larvae with pollen and honey is the normal method for the 400 known species of these small bees. In Mexico and in Guyana, they pollinate well vanilla. In the areas, where they are absent, the pollination has to be done by hand, a method, which was learnt through a fortunate discovery by a slave, named Albius, in La Réunion. Outside Mexico, in the Mascareignes, New Caledonia, and Madagascar this method is now commonly used. Let us add also that *Trigona* males participate nest building and in defence of the hive, a rare situation among honey bees, as in almost all bees these activities are confined to sterile females or workers.

It must be said that, though melipones and *Trigona* are excellent pollinators, they often perforate flower's corolla, as do the bumble bees and carpenter bees (*Xylocopa*) and then go straight to the nectaries. Like the honey bee, those small insects use also cochineal dew, sugar from extrafloral nectaries, smashed fruits, and collect sap and resin, which exude from buds and stems. For a long time people were surprised to find some *Trigona* resting upon the putrefying cadavers, animal excreta and bird droppings. Then one day entomologists discovered that some species of these bees are partially or totally necrophagous (Roubik, 1982), that is feeding on dead and decaying matter. Roubik (1992) mentions that those carrion feeders shun animals that have been dead for more than a brief period or are infested with fly larvae. They efficiently collect new carrions, which they convert into a greenish grey pasty mass, adding their saliva. The pasty material is then stored and used as though it were pollen. This substance has lower energy than pollen, but is richer in protein.

In Amazonia there are no *Necrophora* beetles, as in temperate areas. Those big beetles, yellow and black, practice a family life and carry and bury cadavers of their dead. There feeding on cadavers is practiced by big dung beetles, the *Phaneus,* and wild bees like *Trigona* and also the ants of the genus *Crematogaster*. At least three species of *Trigona* are entirely necrophagous: *T. crassipes*, *T. necrophaga* and *T. hypogea*. Among these species, the pollen baskets remain vestigial or small and ill developed, since they collect only putrefying flesh together with monkey excreta. A mixture of honey-excreta-cadavers does not seemed very attractive, but honey, if they collect some, and predigested flesh are separated for storage into different cells in the hive. No pollen is found in either store. It may be added that *Lestremelitta*, obligate robbers of food from nests of other stingless bees, are totally unable to gather pollen from flowers because they have short mouth parts and regressed pollen baskets. To survive they plunder the pollen reserves from the hives of those species of *Trigona*, which collect it. As among parasitic ants, those social parasitic bees are closely related to the species they plunder.

Roubik (1982) studied in detail the biology of the necrophagous bee, *Trigona hypogea*, in Panama. Cadavers of monkeys, snakes, lizards, toads, fishes and even of big insects are foraged, used as a source of proteins, digested and regurgitated to other individuals (trophallaxy), when the bees go back to the nest. To dismember the cadavers, the *Trigona* bees possess toothed mandibles, specially adapted to tearing. They communicate with their partners using pheromones, smelling molecules, used by many insects as a kind of chemical language. The foraged material is stocked as partially digested flesh. The stored material is fermented by bacteria. Those bees are extremely aggressive towards flies, which are tempted to lay eggs on the cadavers.

Another peculiarity of *Trigona* bees is that around 23 species live inside termite nests and at least five species in ant nests. The association is peculiar and not adequately understood, and these small bees are well tolerated by the termites, and by the ants, which do not seem to get any reward out of the association. This phenomenon is mostly known from tropical America and Malaysia.

The specific behaviour of the necrophagous bees has never been found in the tropics of the old world. It is also true that the Amazonian forests harbour many other extraordinary events. I just mentioned *Phaneus* and other dung beetles, which instead of collecting excreta are necrophagous. We find there, in the canopy of forests, some coprophagous beetles, e.g. some species of *Canthon*, which collect exclusively monkey droppings. Those dung beetles make a ball with the excreta, as our land dwelling ones do, then they, attached to their ball, drop to the ground and drive this ball into the forest soil some dozen meters away. PJ walking in Barro Colorado island in Panama in the morning was always wearing a hat, since the beetles started to drop their excreta balls from the trees at 9.30 am and you could find your head covered quickly with balls of monkey feces. It is surprising that people have just started studying biology of these canopy dwelling dung beetles. There are also phytophagous dung beetles in Australia and also there are coprophagous weevils. Really it is a world upside down there!

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— 20. A memorable month, May 2004, in the USA

The year 2004 was really a year to remember. One of us (PJ) was there during spring time. He went through Canada to Washington, to be in the Smithsonian. In Fairfax, Virginia, he could see the emergence of millions of *Magicicada septemdecim*, the big 17 year US cicad, which, after seventeen years of larval life, spent underground feeding on the roots of trees, were coming out. They were emerging at the beginning of May in great numbers, but were not singing yet. Perhaps they were shy and busy in extending and drying their wings after leaving the pupal skin. The pupae, which were still awaiting adult emergence, were numerous around, on the trunks and at the foot of the trees. It is said that certain mammals, birds, amphibians and reptiles feed on them. Really, the feeders were quickly disgusted due to the abundance of food available. Some restaurants in Washington offered fried cicadas and had published attractive menus wherein those poor creatures were listed as the most original dish. I inferred that humans were the main predators of the cicadas.

This appearance of those poor cicads, totally inoffensive, do not resemble the Egyptian plagues or the Hitchcock birds. They were totally harmless. But daily newspapers were exaggerating a lot about their nuisance potential. It was the 1987 brood, which was coming out from the ground, and the period of their emergence was around one month or even less. That allowed those adults to dry in the sun. The males produced slowly their song, a rather discordant, a song which has tempted some composers, eagerly looking out for some novelty.

Happy are the cicadas, since their wives are mute, wrote one day some macho writer at the beginning of an entomology book. Yes, among the cicadas, only the males sing, or better screech to be more correct. They can all together produce sounds as strong as a subway train entering a station, or a child yelling, or working of a pneumatic drill. At 90 decibels, their song competes with a lawn mower. That is not at all exaggeration. People complained that in some golf clubs it was this year really deafening. The players could not hear each other to count their score. These cicadas are present in the District of Columbia in Washington, and in 15 eastern states of the USA. If their song is not really a love song, it is at least a mating call. The females are not completely mute. Well heated under the sun, they answer with a rattling of the wings. The rattling is an OK to the male singing.

As I said before, those insects are harmless, and it is only their eggs, laid in young branches, which can damage some of them. Sensitive journalists have strongly protested in Washington against children who remove their wings, throw them under the cars and torture them. This behaviour is alarming, and should be discouraged. La Fontaine, speaking of the youth, said that their age is merciless and Seneca used to say that the future cruelty of Nero was already visible when, as a child, he removed the wings of flies, still alive. Those journalists correctly proposed the denunciation of a “cicada abuse”. Those creatures waited 17 years to get out of the soil. Should not people leave them alone and allow them to take the sun in peace?

Another American cicada, *Magicicada tredecim*, has a 13 year cycle. It is tempting to explain these strange cycles as being a means of self-defence against the predators. Evolution of such long life cycles, as also in case of cockchafers, seems to have the advantage of protection against a multivoltine predator. The pupa gets out of the soil only when the ground temperature reaches 17°C. During those 17 years beneath the ground surface there are 5 moults in the soil, near tree roots. The adults are expected to live for only 2 to 4 weeks outside, under the sun. Egg laying takes place within a small incision in tree branches. The eggs hatch on the twigs and the larvae drop to the ground beneath, and immediately enter the soil. A female deposits 400 eggs at an average.

It is said that, in the countryside in Serignan, France, Jean-Henri Fabre shot twice with a cannon to see if the cicadas would stop singing. It was in vain;

they did not stop. As Messiaen has imitated in his operas the bird songs, several American musicians tried to imitate the cicadas, without attaining the original harmony, if we can speak of harmony. Are the cicadas happy, when singing ? Probably they are, since this appearance under the sun, after having being jailed during 17 years, seems to take them to the peak of happiness, as if they have found again the lost paradise.

In May, says a French proverb, do what you like. I think I obeyed the proverb. May is probably in the United States, every 17 years, the cicada month, but it is also the season of love for the *Limulus*, those archaic and strange Arthropods, with blue blood, the famous haemocyanin, in which copper replaces iron, but which is dissolved in the serum and not incorporated into cells, like haemoglobin. *Limulus* are direct descendants of trilobites from the Palaeozoic. They also develop through a trilobite-like larva. They come directly from the Ordovician-Silurian junction, more than 450 million years ago. *Limulus polyphemus* or horseshoe crabs are, at spring time, pressed against each other, in the Mexican gulf, and the females, surrounded with their suitors, are laying eggs on the sandy beaches and are fertilized by aggressive males, which fight each other to achieve maximum fertilization. They are everywhere, but their number is certainly regressing, because they are hunted to be used as fish bait or to pump out their blood, which is believed to have a strong antibacterial property. New regulations ask the fishermen to release them to the sea after draining their blood. But, after this blood "donation" can they survive bacterial infections?

Limulus are everywhere along the Atlantic coast in the US. The Mexican gulf is a remnant of the Triassic Sea Tethys. Another genus and several species exist also in Indonesia and in Thailand-Vietnam-Japan, which are the other end of the palaeogeological Sea Tethys. They have been eradicated in the Mediterranean sea, because of the drying of the sea sometime at the end of the Tertiary. In Thailand people hunt the females to eat their eggs, which taste like caviar. Thai people eat even the big *Belostoma*, the aquatic bugs. They don't eat them entirely; they use only the glands of the male to produce a sauce, which tastes like bed-bugs, and is very much appreciated there. Killing the horseshoe crabs for a small number of eggs, from which they produce only a few grams of food, is a hopeless slaughter. That reminds one of the massacres by the Romans, killing the flamingoes by thousands, to eat their tongues. Mating among the *Limulus* are well synchronised and massive. Some young individuals mix with the others, and this phenomenon is not very well understood. Birds on the shore watch the females, so that they may later dig into sand to get their eggs. In spite of all this predation the species has managed to survive from such early days of animal evolution to this date.

A book has been recently written on these Arthropods in the US by Shuster *et al.* (2003). We should not forget that the horseshoe crabs descended directly from the trilobites and must have retained the same biology, since they have the trilobite larva. The trilobites have disappeared, and the horseshoe-crabs have survived. It is true that the recent discovery, of a living graptolite, a Notochordate, *Cephalodiscus graptolitoides*, in the ocean bed, near New-Caledonia and Norfolk island, shows that there is possibility of discovering some more forms, which at present seem extinct. *Cephalodiscus* dates much before *Limulus* and from a period close to the origin of life; almost at the Burgess shales!

And, looking at the seventeen year cicadas, at spring time, in Virginia, it was interesting to realise that again they will be seen in 2021. I had the rare luck to witness an extraordinary phenomenon. But looking at the horseshoe crabs on the Mexican gulf beaches, I got the feeling of going back in time, in the age of the trilobites, during the Palaeozoic. I thought that perhaps the trilobites also had blue blood, with copper oxide, when they had been laying eggs on the shores of the primitive Sea Tethys. Their eyes, supposedly made of calcite, as they are preserved in the fossils, were perhaps made of proteins similar to those of *Limulus*. I have always doubted this. Of course, their visual organs were very complicated, often with a double vision, in and above the water or inside the mud. Some others were practically blind. Those Silurian, or even Cambrian beaches, were still free from any vegetation, amphibians were to appear much later, over a mat of Cyanobacteria; the Stromatolithes, and progressively proto-green plants, like the Psilophytales grew their meagre stems, then later on, mosses, lycopods, horsetails etc. appeared. Fishes were then the dominant group, algae were numerous, amphibians started to diversify. The trilobites were laying eggs along quasi-desert shores and very probably behaved frenetically like the horseshoe crabs in heat. The ancestors of spiders, trigonotarbids appeared, and still later the terrestrial scorpions and, much later the first insects. Thus the horseshoe crab belongs to that ancient stock from which insects evolved.

Having seen *Danaus plexippus* (L.), the monarch, flying in the greenhouses of the Mc Guire Center for Lepidoptera, in Gainesville, FL, PJ had admired this magnificent realisation in the natural conditions of a tropical forest, reproduced in greenhouses, which allow exotic butterflies and even dragonflies to fly about and live healthily. We hope that one day some severe cyclone will not take away the greenhouse and the butterflies to the kingdom of Oz. In that greenhouse, there are a stream, a water fall and all the grasses and trees, needed to feed the caterpillars. There are, of course, still unknown food for some beautiful butterfly larvae, as for *Graphium weskei*, from the mountains of New Guinea. To one of us (PJ), it is the most beautiful butterfly and he has seen hundreds of them along the streams in the mountains drinking water. Sedlacek, an entomologist, at Wau field station, told him one day that he saw a female laying eggs on a plant. He did not look carefully because he was going to Australia on leave the next day. He came back and could never find again the mysterious host-plant.

In the Gainesville greenhouse, it will be necessary to introduce mosquitoes, if we want to feed the Odonata, and if their larvae accept to multiply in a slightly chlorinated water! The local climatic conditions will permit, with a moderate ground heating, *Morpho*, *Ornithoptera* and *Papilio*, to survive with their caterpillars, on their original plants. It is the third butterfly greenhouse in Florida after the old one in Fort Lauderdale and the new one in Key West. A superb working tool for the scientists and a nice attraction for the tourists. The poor *Danaus* attempt aborted migrations against the screen, so strong is the effect of their migratory genes. Will they survive long in this condition? Jean-Michel Maes, an entomologist from Nicaragua, proposes to use Central American species of *Danaus*, the one which is non-migratory.

This greenhouse is partly what the scientists have attempted to do in creating their Biosphere II in the American desert, with more or less success. However here, in Gainesville, it is an ultrasophisticated butterfly greenhouse. We could compare that to the English experiment of the creation of an artificial jungle in the island of Ascension in the middle of Atlantic Ocean, a concept, which originated, in 1843, in the mind of the great Scottish botanist, Joseph Hooker and which has survived for more than 150 years. When Charles Darwin stopped in the island in July 1836, he described it as "entirely destitute of trees". Really he did not see one bush: *Oldenlandia adscensionis*, one African Rubiaceae, probably then already rare. Eighty years before, Peter Osbeck, a Swedish priest, described the island as "a heap of ruinous rocks", with a naked mountain in the middle. The volcanic island is only one million years old and, as it has a tropical and potentially humid climate, it was covered rapidly after 1845 with a heteroclite jungle, coming from the whole of the tropical world from Argentina, to the Cape Province, and Australia, up to Norfolk island to the East. Kew Gardens and the Navy, following Hooker's advice, contributed to that flora enrichment with importation of hundreds of seeds and tropical trees, such as guava, banana, ginger, *Opuntia*, bamboos, *Clerodendrum*, Malagasy periwinkle, *Cataranthus (Vinca) roseus*, Australian eucalyptus, and Norfolk *Araucaria*. They all found the surroundings suited to them, and multiplied rapidly. Contrary to all expectations and contrary to ecologists' predictions, that "genesis" of a tropical flora in miniature was a total success. There are actually beetles, butterflies and caterpillars, coming from nowhere, in that pot-pourri of the jungle, totally man-made and the experiment goes on. As we are far in Ascension from any land and in the middle of Atlantic Ocean, any contamination is prevented. The island discovered in 1501, was still unhabited in the middle of 18th century and now it harbours nearly 1,100 inhabitants. Situated at 2,000 km from the nearest continent, the island has a basic limited flora of around 20-30 vascular plant species, of which about 10 are endemic. Most of the ferns have survived, only 4 are extinct and 5 are actually endangered. The Green mountain, the actual name of the formerly bare rock, has provided rain and prosperity. A new biotope, a mountainous, man-made, tropical forest was born and functions perfectly. It is a unique experiment, based on seeds from the whole world and chosen at random. That concept, Hooker created, has survived to the great displeasure of the ecologists and theoreticians. Hooker knew exactly what he was doing, because he wrote: "the consequences to the native vegetation of the Peak will, I fear, be fatal, and especially to the rich carpet of ferns that clothed the top of the mountain when I visited it". After all, the Navy saw greater benefit in improving rainfall and encouraging more prolific vegetation. The effect on the native vegetation finally was not so great.

A fascinating experiment in a natural landscape was done in Ascension island and is more enriching than what the Gainesville beautiful greenhouse has achieved. It would be interesting now to introduce in Ascension, since the experiment has been irreversibly made: *Ornithoptera*, *Morpho*, *Papilio*, *Agrias*, *Urania* and related, and their host-plants. Why not also try *Timarcha spp.*, dear to one of us (PJ); there are some living in a similar climate and *Galium,* the host plant of *Timarcha*, grows anywhere. The evolution of this artificial biotope would be fascinating to study.

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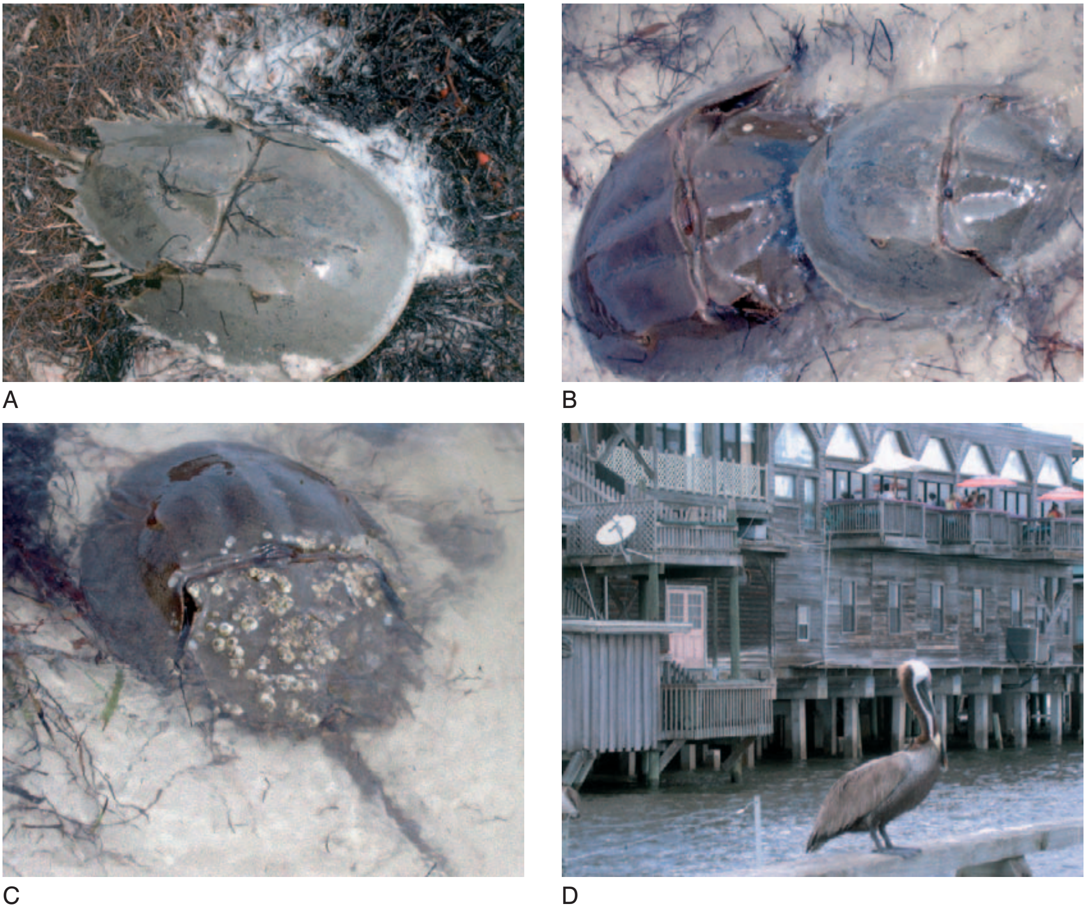
— Fig. 20.1. A-F: Various stages of *Magicicada septemdecim*, in May 2004 in Fairfax, CA, USA. The nymphs are coming out and the adults are just freshly ecloded from the pupal skin (photos Jolivet).



— Fig. 20.2. A: *Limulus polyphemus* taking to water;
B: *Limulus polyphemus* in copula;
C: *Limulus polyphemus* covered with barnacles;
D: Brown pelican, *Pelicanus occidentalis*, on the shore.
(All photos by Jolivet in Cedar key, Florida, USA, May 2004).

— 21. **Digestive strategies in insects**

In the chapter "How successful are insects?" we have noted that insects present a much greater biodiversity than vertebrates. Among insects, the number of the known species of beetles (insect order Coleoptera) alone is about seven times the number of all the vertebrate species put together. The main factors, responsible for so extensive biodiversity presented by insects, are: (i) their great dispersal capacity due to presence of wings, (ii) their highly developed fecundity; a single female laying some hundred to some thousand eggs, and (iii) their remarkable digestive adaptability to different types of food. The last mentioned property allows insects to adapt themselves to different sources of food, and thus diversify to exploit different trophic niches.

A large number of insects are plant feeders or phytophagous. They feed on leaves, buds, flower nectaries, pollen, stem and roots. Some insects are wood borers, attacking healthy and rotting wood. Some insect groups have organs of feeding in the form of feeding needles, and they suck plant sap. Stored grains and other forms of stored food products are infested by many insects. Numerous insect species are carnivorous and predaceous. Some insects groups are parasitic on other insects. In entomological jargon they are referred to as entomophagous insects. Among insects are external parasites of birds and mammals. Mosquitoes and the tse-tse fly (*Glossina*) are blood suckers. Saprophagous insects (that is insects feeding on dead organic matter) are important among decomposers (that is those organisms which consume organic debris in soil and water, and release nutrients for plants). Among insects some are feeders of fibrous proteins (wool, keratin, silk etc.); they are pests of carpets, clothes, furs and museum specimens. Termites and book lice attack libraries and book stores, as they are efficient, thanks to their symbionts, in digesting and assimilating cellulose.

A few words about the infamous blood sucking habit of insects. Blood sucking in some cases of various tropical moths is an adaptation from fruit feeding to sucking on the secretions of the eyes of mammals and finally blood from small vessels. Blood sucking among the fleas probably dates from the Mesozoic, even if the pre-fleas, of questionable origin, were possibly parasites of pterosaurians. Real fleas are found from the Eocene (Rasnitsyn and Quicke, 2002). Blood sucking is very old among the tse-tse flies (Oligocene) and Culicidae (Cretaceous).

Let us first become familiar with the different parts of the insect digestive system. Between the bases of the mouth appendages, referred to as mouth parts in insect anatomy, is located the mouth. Mouth opens into a small buccal chamber, followed by a narrow tubular oesophagus. Opening into the buccal chamber are the ducts of a pair of salivary glands. The oesophagus enlarges posteriorly to form a sac like region, the crop, which is meant for storage of ingested food. In those insects, which feed on solid food, e.g. cockroach, the crop is connected behind with a globular and muscular part of the gut, called the proventriculus or the gizzard, which crushes the food and reduces its particle size to help digestion. The proventriculus leads behind into the mid-gut or the mesenteron, which is generally a soft simple tube, but in many insects it is differentiated into certain regions. Arising from the anterior end of the mid-gut are a variable number of pouches or diverticula, called the mesenteric or gastric caeca. Digestive enzymes are mostly secreted by the glandular epithelial lining of the mesenteron and of the caeca. The mid-gut presents a special feature, a membranous tube within it, preventing food particles from coming in direct contact with the epithelial lining of this part. This membranous tube is called the peritrophic membrane. It is believed to protect the epithelium of the mid-gut from abrasion, as does the mucus in the digestive system of vertebrates. The mesenteron is followed by the last part of the digestive tube, the hind-gut, which is a tubular region leading from the mesenteron to the anus. Generally the hind-gut is differentiated into an anterior simple tubular portion, the anterior intestine, and a dilated last part of the hind-gut, the posterior intestine or the rectum. While most of digestion and absorption of the digested food take place in the mesenteron, absorption, mainly of water, occurs in the hind-gut.

At the junction of the mid-gut and the hind-gut arise a variable number of tubular structures, opening into the gut, and with closed ends away from the gut. They are urine forming organs, and are called the Malpighian tubules. They discharge the excretory fluid, secreted by their glandular epithelial wall, into the first part of the hind-gut. In the hind-gut most water in the urine is absorbed, and thus conservation of water is brought about, and the excreta in a highly concentrated or solid form is voided along with feces. This is an account of the digestive organs in a typical insect; several variations are seen in different insect groups.

While the chief secretory part of the insect alimentary tract is the mesenteron with its gastric caeca, secretion is also the function of the paired salivary glands, the ducts of which open into the buccal chamber. The salivary secretion moistens the food to help mastication by the mandibles among the mouth parts, and also lubricates the food to help its posteriorly movement. But the latter effect disappears by the time the food reaches the mesenteron, as in the cockroach *Blatella*. In some insects some digestive enzymes may be present in the salivary fluid.

Now let us turn to the enzymatic part of digestion. The three broad categories of enzymes, which occur in the digestive system of vertebrates, are present in insects too. They are protein digesting enzymes or proteases, carbohydrate digesting enzymes or carbohydrases, and fat digesting enzymes or lipases. In omnivorous insects, like cockroaches, the mesenteric secretion contains maltase, invertase and lactase among carbohydrases, trypsin and erepsin among proteases, and lipases. But exclusively predaceous and carrion feeding insects have mainly proteases and lipases in their mid-gut secretion. In blood feeders, like the tse-tse fly (*Glossina*), there are special proteases for digestion of haemoglobin. In exclusively phytophagous insects carbohydrases predominate in the mesenteric secretion. Insects feeding exclusively on nectaries of flowers have an abundance of invertases, which are carbohydrases for digesting disaccharides into simple sugars, in their mid-gut. The carnivorous larva of the blow-fly *Lucilia*, which burrows deep into the body of sheep, causing grave injury, has a special protease, called collagenase, which digests the proteins callagen and elastin, present in connective tissues of sheep. Wood boring larvae of the beetles, belonging to the families Anobiidae, Buprestidae and Cerambycidae, have a special carbohydrate digesting enzyme, called cellulase, to digest cellulose present in abundance in wood. The cattle grub (*Hypoderma*), the larvae of which penetrate through tissues of cattle, has a special carbohydrase, glycogenase in the larval mid-gut, in addition to the proteases trypsin and erepsin and also lipase. Glycogenase helps digestion of the animal starch or glycogen. Thus the nature of the digestive enzymes present in an insect are related to the food the insect consumes, and, as the food of different insects varies very much, there are corresponding variations in the enzyme contents of the digestive system.

As has been pointed out above, some wood boring insects have cellulase in their mid-gut secretion. If we make an extract of the mesenteron wall of a larva of a long horned beetle (Family Cerambycidae) and try to filter it, using a filter paper disc, a hole is made in the disc. This is due to cellulase action on the cellulose fibres in the filter paper. Most phytophagous insects, however, do not have cellulase in their digestive secretion. Plant cells have a cellulose wall around them. Hence, before the nutrients within the cell are released and made available for digestion, the cellulose cell wall should be broken. This is done by the mechanical action of the mandibles among the mouth parts and of the proventriculus. But 100% cells in the plant food do not get ruptured this way. Many cells remain unbroken, and come out intact, with their organization unaffected, with feces.

Many insects digest cellulose in their food with the help of symbiotic bacteria and Protozoa. Such insects are *Rhagium* (Coleoptera), *Tipula* (Diptera), the cockroach *Cryptocercus* and termites. In termites, cellulose digestion occurs in the hind-gut. A part of the hind-gut is dilated, and lodges a number of different flagellate Protozoa. The flagellates ingest pieces of cellulose and digest them. The termite host gets nourishment by digesting dead flagellates and by absorbing their secretion. The symbiotic Protozoa make about 1/3rd of the weight of the nymphs of *Zootermopsis* (Day and Waterhouse, 1953). When in an experiment the flagellates are removed from the gut of termites, the insects are unable to digest cellulose. When refaunated with the Protozoa, they are again able to live on a diet rich in cellulose. Dung beetles (Family Scarabaeidae) also feed on cellulose rich diet. In these insects, too, a part of the hind-gut is dilated to form a fermentation chamber. The cuticular lining of the chamber forms a number of branching spines. The cuticle is specially thin between the bases of these spines, and is provided with fine canal like gaps (Wigglesworth, 1953). Pieces of cellulose are held among the spines for days together, and are digested by cellulase produced by the cellulose fermenting bacteria, which abound in the fermentation chamber.

Some insects take help of fungi to digest cellulose rich material. But this is done outside the insect body. Many ants and termites maintain "fungus gardens" inside their nest. The fungus in the gardens grows on a cellulose substrate (bits of leaves in case of parasol ants; see the chapter "Parasol ants" for details), and the fungus is the immediate source of nourishment for these insects.

Larvae of the wax moth (*Galleria*) tunnel through the hive of the honey bee, and feed on wax. Digestion of the wax is also believed to be brought about with the help of symbiotic bacteria.

Fibrous proteins are another category of materials difficult to digest. Clothes moth (*Tinea*) feeds on woolen clothes and carpets. Larvae of this moth are able to digest about 47% of wool ingested. The proteases in the mid-gut of this insect require a very high pH (about 9.5) for their action, but they are not able to break disulphide bonds (S-S) in the wool proteins. However, the high value of pH, existing in the mid-gut of the insect does the job; it breaks the disulphide bonds. The resulting smaller length polymers are then readily digested by the mesenteron proteases.

The mid-gut is typically a simple tube, undifferentiated into further regions. The mid-gut caeca serve to extend the area of its secretory and absorptive epithelium. But in some insects there are some functional divisions of the mid-gut. In the larva of the mosquito *Aedes* there is an anterior portion of the mid-gut, in which digestion and absorption chiefly of fats take place, while in second half those of glycogen. In the adult of the blood sucking tse-tse fly (*Glossina*) three regions may be made out in the long and coiled mid-gut. The first half of the mesenteron is a little broader tube, in which no enzymes are present, and only absorption of water takes place to thicken the ingested blood. This is followed by a middle region with deeply staining and enzyme secreting epithelial cells. In this region digestion mainly occurs. This second region continues behind into a long narrow tubular region, which is mainly for absorption of digested food. In the tortoise beetle *Aspidomorpha miliaris* the mid-gut is divided into a broad sac like anterior region, and a narrow tubular and coiled posterior region (Shrivastava and Verma, 1982). The two regions have been referred to by the authors as MS1 and MS2. The peritrophic membrane of the MS1 presents a special feature, namely presence of certain cells in its thickness, the peritrophic membrane cells. These cells are actually mesenteric epithelial cells, which have left the epithelium and have come to lie in the thickness of the forming peritrophic membrane. No such cells are present in the peritrophic membrane of MS2. The peritrophic membrane cells disintegrate releasing a cluster of tiny globules, seemingly secretory globules which pass into the lumen bound by the peritrophic membrane (endoperitrophic lumen) of MS1. Verma and Shrivastava (1989) have recorded a differential distribution of enzymes in the mid-gut of this tortoise beetle. They have noted protease and lipase activity specially pronounced in the endoperitrophic lumen of MS1, amylase (a carbohydrase) activity in the ectoperitrophic lumen of MS1, and lipase and amylase activity in MS2. It appears that the specially high protease activity in the endoperitrophic space of MS1 is due to the peritrophic membrane cells, and that it serves to dissolve away the cytoplasmic cover around the cell inclusions in the leaf cells, and then the released starch grains and lipid globules move on to the extraperitrophic lumen of MS1 and to MS2 for their digestion.

Mid-gut is the main producer of digestive enzymes. But in some insects enzymes may be detected in the crop. This is due to the mesenteric enzymes moving forward as a result of antiperistalsis, i.e. peristaltic contractions moving from behind forward. Some digestive enzymes may be present in the salivary gland secretion. In many insects the salivary secretion is a watery fluid without any enzymes, and is meant to moisten the food during mandibular action. But in some insects the salivary fluid includes some enzymes. In the leaf hopper *Empoasca*, which sucks plant sap, the salivary secretion contains an amylase to dissolve starch grains in situ in plant cells. In plant feeding insects amylase and invertase (both carbohydrases) are commonly present in salivary fluid. In blood sucking insects the salivary fluid includes anticoagulin to prevent clotting of blood.

As has been pointed out in the preceding paragraph, the amylase in salivary fluid of plant sap feeding insects is meant to bring about digestion of starch grains outside the digestive system. Such extraintestinal digestion is known in some other insects too. In the larvae of some predatory ground beetles (Family Carabidae) and in carrion feeding *Panorpa* (Family Panorpidae of Order Mecoptera) digestion is largely extraintestinal, as during feeding mesenteric secretion is regurgitated, and digestion takes place outside the buccal cavity. The larva of diving beetles (Family Dytiscidae) is very active and predaceous. Its long sickle like mandibles are nearly tubular. They are made to pierce the body of the prey, and then a fluid is seen moving down the mandibular canal, and getting injected into the prey's body. One can see under some magnification that, following the injection of the fluid, which is actually the mesenteric secretion, the tissues of the prey are getting liquefied in its body, and getting sucked up through the mandibular lumen into the body of the larva. In Oedemerid beetles which feed on pollen grains, the pollen grains germinate in the gut and pollen tubes grow slightly before being digested (Arnett, 1962). Other pollen-eating beetles crack the cuticles of pollen grains with the mandibles.

These diverse digestion strategies among insects have been an important factor in development and evolution of the huge biodiversity they present. This situation is well illustrated by the case of the species complex of the tree hopper *Enchenopa binotata,* discussed by Rodriguez *et al.* (2004). The species in the complex are obviously closely related, living on different host plants, in process of diversification, and found in the same geographical area. It has been inferred that in a common geographical area members of one species, due to small changes in their digestive physiology, have moved on to different hosts. There are differences in such characteristics of the different host plants as length of flowering period, time and extent of autumnal shedding of leaves etc., and this has led to developing different timings for the tree hopper's life history, such as mating and egg laying time, length of larval period, diapause time etc. This has brought about some reproductive isolation among the tree hoppers population, living on different host plants. As a result of this isolation different patterns of vibrational communication between prospective mates have developed, the reproductive isolation has been strengthened, and diversification has gone ahead. How a single point mutation in the genome of an insect species, resulting in replacement of one amino acid molecule with another in a protein structure, permits the insect to invade a new host plant is well demonstrated by the studies by Labeyrie and Dobler (2004) on species of *Chrysochus*. This work has been cited at some length in the chapter "Chemical defence in leaf beetles."

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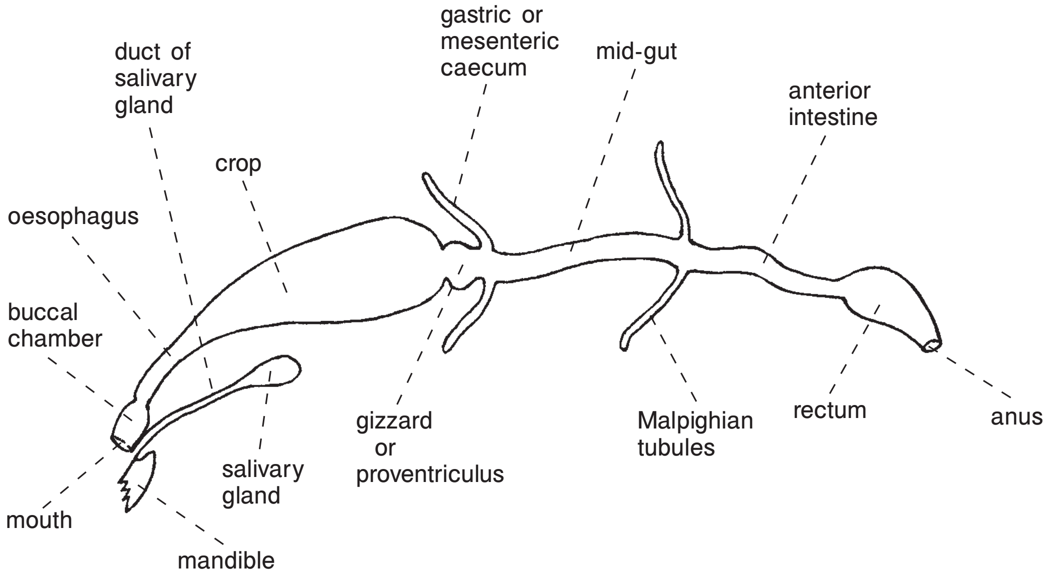
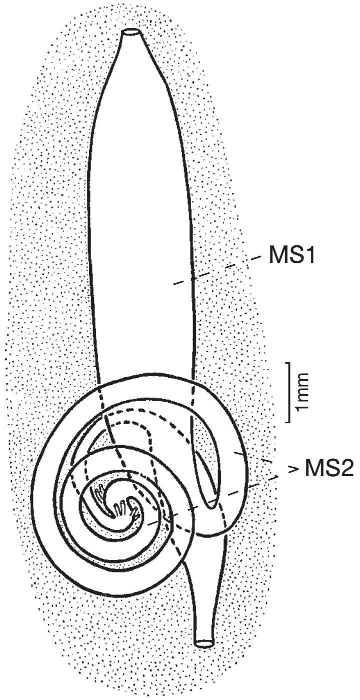
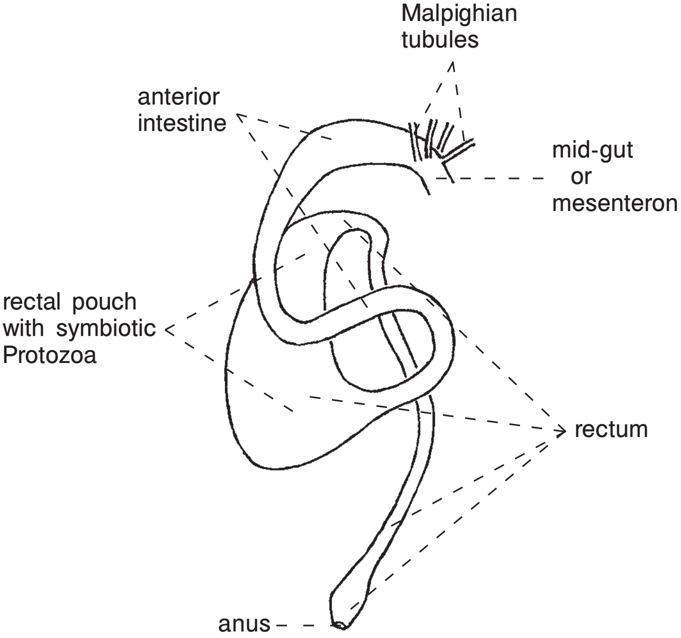


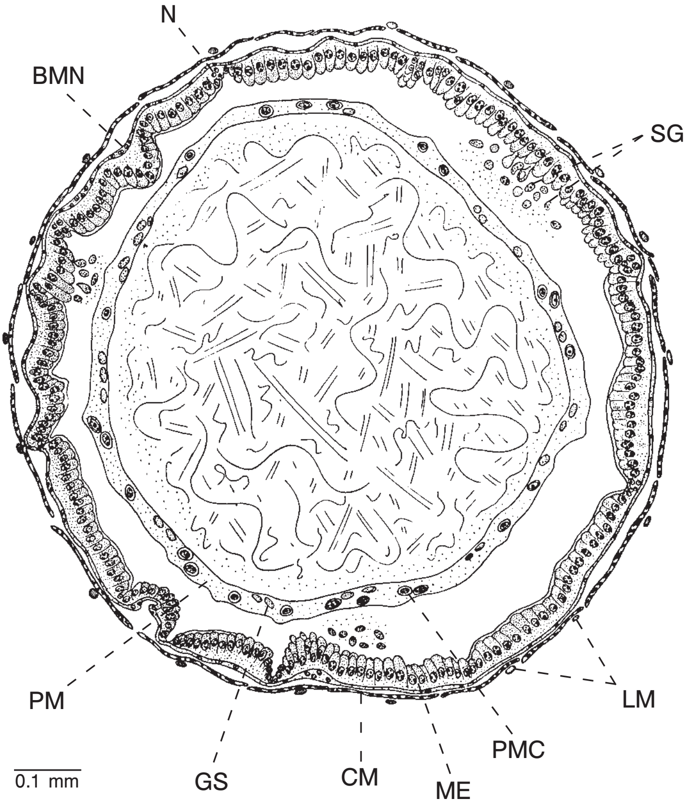
— Fig. 21.1. Typical insect digestive system in lateral view (original).



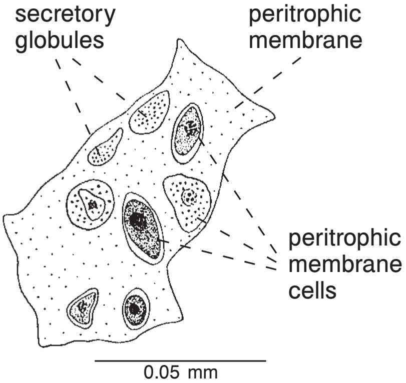
— Fig. 21.2. The gut of the tortoise beetle, *Aspidomorpha miliaris*, showing two regions of the mid-gut, MS1 and MS2 (from Shrivastava and Verma, 1982).



— Fig. 21.3. Hind-gut of a termite, showing the rectal pouch, in which symbiotic Protozoa are lodged (from Wigglesworth, 1953).



— Fig. 21.4. A cross-section of the mid-gut (MS1) of the tortoise beetle, *Aspidomorpha miliaris*. PM: peritrophic membrane; PMC: peritrophic membrane cells. Other labelling of detailed anatomical interest; hence not explained (from Shrivastava and Verma, 1982).



— Fig. 21.5. A part of the peritrophic membrane of *Aspidomorpha miliaris* (from Shivastava and Verma, 1982).

— 22. Insects and Plants during the Carboniferous

An American professor used to frequently ask his students, “If you were able to use H. G. Wells’s time machine, which epoch would you like to visit?” Some said Carboniferous, others Triassic, and still others wanted Eocene. Many, without any hesitation, chose Cretaceous, the era which witnessed the fall of dinosaurs, the time of the ferocious *Tyrannosaurus* and the enormous flying reptiles *Quetzaltcoatlus*, with wingspan reaching 15 meters. It was the time for the expansion of the flowering plants, of the ants, and of the chrysomelid beetles, after their timid start during the Jurassic.

It seems probable that flowering plants, the Angiospermae, were derived directly or indirectly from the Bennetitales, a kind of cycads, with complete bisexual flowers, living in the Jurassic and the Cretaceous. This view is at least a reasonable hypothesis. Does it mean that we have finally solved what Darwin used to name “the abominable mystery of the origin of the flowering plants”? It is too early to answer that. Pre-angiosperm fossils are very old and some are not cycadoid. However, it is not forbidden to think that in the forests of that time, the last Bennetitales had coexisted with the Phanerogamia. Let us recall a prairie in Southern New-Guinea, where *Cycas* prospers near palm trees, the Coniferae, and the flowering plants, and we can get a fair idea of the flora of that old time. Only the proportion of these plant groups might have been different.

However, another fascinating period must have been the Carboniferous, one of the last stages of the Palaeozoic. An enormous quantity of fossils is available in coal deposits of that time, and it has been possible to reconstitute the ecosystem of the forests of that period, with its swamps and its inhabitants. This age lasted 70 million years, 236 million years ago. We can speak already of a certain coevolution between plants and animals, and there were already cases of mimetism, but not yet of myrmecophily, as the ants did not exist then. Also carnivorous plants and the phanerogams had not appeared yet.

In the Carboniferous amphibians were carnivorous and insectivorous, and reptiles, first carnivorous, and some became herbivorous at the end of the period. Beetles appeared a bit later, during the Permian. However, insects were diverse, some of them giants, and adapted to all sorts of diets. Most of them, however, were herbivorous. The giant myriapod *Arthropleura* was trilobite-like, two metres long, and was mostly feeding on lycopods. Many insects had then long proboscis, and were sap suckers, as are our bugs. Certain species were phytophagous or saprophagous, as are the present cockroaches; they were numerous and were detritivorous or truly phytophagous. Grasshoppers then were evidently phytophagous, and scorpions, having left water, were eating what they could find in forest litter.

One can imagine that lycopods, horsetails and giant ferns, mixed with primitive conifers, were forming great humid forests. In swamps, giant dragonflies were breeding, with Ephemeroptera and Perlidae. *Meganeura monyi* was living then with its 75 cm wingspan (see the chapter on "Damselflies, experts in ballistics"). It was so strong that no spider could catch it with or without its web. *Meganeura* must have escaped any predator in air.

It has also been discovered that among insects and plants of the Carboniferous there were strange cases of palaeomimetism, e.g. pinnules of ferns *Neuroperis* and *Odontopteris* closely resembled to the wing innervation of certain coackroaches, like *Phylomylacris*. That could explain why in the literature there was sometimes confusion between leaves and insects. Jeannel, in his time, reproached Nicolas Theobald (1937) for some confusion in his book on Oligocene terrains in France.

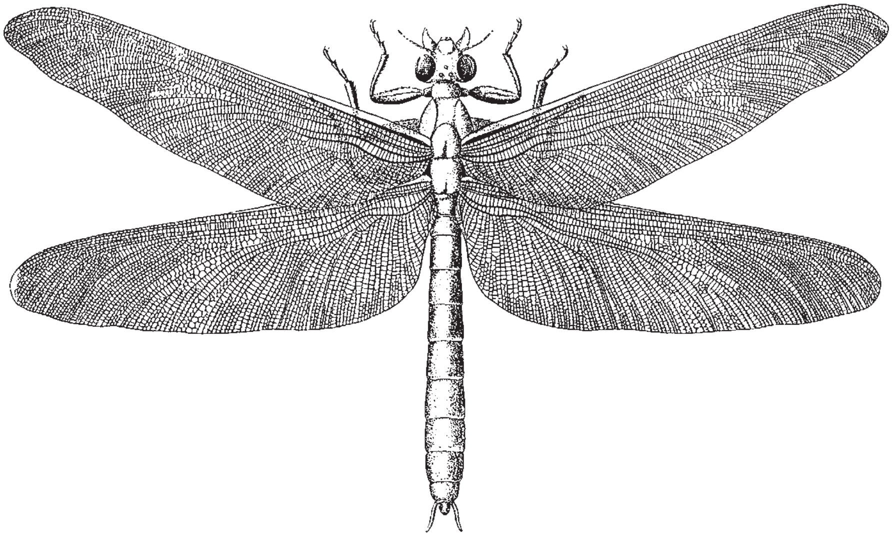
Pollen grains and spores were already carried by arthropods, including *Arthropleura*, which has been mentioned above. Fossils of this myriapod carry the proof it. Seeds probably carried attractive glands for attracting the disseminators. Plants protected themselves against herbivory through sclerified layers, glandular hairs, etc., but they were even then attacked and eaten. Some leaves and stems of, for example *Neuropteris* of that period, strongly attacked by herbivores, have been found. But perhaps phyllophagy was still in its infancy. To suck the sap or to feed on soil detritus were probably the most current modes of nutrition. It was, however, noted that among the arborescent fern, *Psaronius*, entire stems were full of insect excreta, and were much eaten. There were also galleries inside wood, with coproliths or fossilised insect feces containing vegetal debris.

Carboniferous insects were mostly living on the ground, inside forest litter, on the plants and certainly on the forest canopy of that period. We don't know much more. There were carnivorous, saprophagous, and phytophagous insects. Those enormous arthropods moving two meters inside the litter must have been very impressive. Were they toxic and venomous? Probably yes, but that we will never know for sure.

It does not seem that large scale extinctions affected the insects, either because they multiplied rapidly, or because they escaped long cold periods, thanks to diapauses, or because the temperate zones, less affected, became readily repopulated. A great extinction at the Cretaceous-Tertiary (K-T), marked by the Alvarez iridium layer, does not seem to have much touched the insects (Whalley, 1987). At least, it was never found among the invertebrates indications of the effect of the catastrophic events, which are supposed to have killed the dinosaurs. Some people, e.g. Labandeira, however, have objected to the notion of non-disappearance of insects. It is very difficult to review the oldest extinctions, due to lack of definite data, and also because much of the rich amount of insect fossils available has not been examined and analysed by experts. One thing is certain, that no important insect group disappeared from the earth, the old orders being the ancestors to the present orders.

— Fig. 22.1. Diaphanopterodea, *Uralia* sp., a fossil species from the Permian, feeding on a primitive flower head (from Rohdendorf and Raznitsin, 1980; Jolivet, 1986).

— Fig. 22.2. Upper Carboniferous tropical forest, with Lepidodendraceae, Sigillariaceae, Equisetales, Gingkoales and tree ferns (Pteridospermae) (after Jeannel, 1946).



— Fig. 22.3: *Meganeura monyi* Brongniart, a primitive dragonfly (Meganeuridae). Carboniferous, from Commentry, France (after Jeannel, 1946).

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— 23. **Jurassic Park or the World of Cycads**

Cycads are very primitive plants, and their association with beetles and other insects should also be very old. This association is of special interest to those entomologists who are trying to make out palaeohistory of insects.

Cycads are ligneous, palmiform plants, with pennate fronds, i.e. leaves with leaflets, and they produce seeds. They resemble palm trees, but are not at all related to them, and are much more primitive. They are classified among the Gymnospermae, together with the Ginkgoales and the Gnetales, which also do not look like Coniferae. Like Gnetales, they are very toxic and they concentrate a great part of that toxicity into the cones. It seems that beetles feeding on the cones and the leaves do that partly for pharmacophagy. Cycads constitute a unique group of plants, very ancient, probably dating from the Permian, along with the precursors of flowering plants. Cycads had their maximum development during the Mesozoic. They all produce male and female cones, the sexes being separate (dioecism). This production of cones can be annual or spaced out by several years. Coevolution between beetles and cones remains sometimes difficult to understand, the Coleoptera having generally an annual cycle.

Cycads are very primitive, and are among the actual seed plants. They are practically unique, sharing this feature only with the Ginkgos, in producing mobile male cells. They also represent an important link with the old seed plants, the Pteridospermeae and the Bennetitales. Cycadales were flourishing during the Mesozoic (-206 to -65 myr), and they were in this period, mostly during the Jurassic and the Cretaceous, very largely distributed over the planet. They were then much more varied than the present survivors. Cycads are actually relics, with a disjunct distribution, essentally tropical, with the exception of Japan and Florida.

Cycadales at present are a small group, consisting of around 185 species and 11 genera (Jones, 1993; Norstog and Nicholls, 1997). But the number is increasing with the intensity of the taxonomical researches (Schutzman, 1984, 1987, 1989). There are certainly synonyms, but many species remain undescribed. The real number may approach 210 species, all archaic survivors of once a large group, which covered the planet, with the Bennetitales, during the time of the dinosaurs and the *Archeopteryx*.

Among all those genera, the American *Zamia* shows an incredible variability, since it can be arborescent, subterranean, epiphyte, myrmecophile, or cremnophile, i.e. adapted to abrupt cliffs. It shows also all sizes from the minuscule *Zamia pygmaea* Sims from Cuba, actually endangered, up to the enormous *Z. lindenii* Regel from Ecuador and Peru. *Zamia's* preferences vary enormously, from the cloud forest in mountains, up to the mangrove, the plain forest, and the savannah. The genus lives as well on sandy soil as on red ferrugineous laterite, on rich humus, in plains and in dense forests, on the cliffs or along the torrents. *Zamia* species can be arborescent trees as well as plants with hypogean roots. The biggest density of the group is in Central America. Hybrids exist, and have contributed to the general evolution of the genus.

A peculiarity of the Cycads is that some individuals may suddenly undergo change of sex. Another abundant group during the Mesozoic was the Bennetitales. They disappeared by the end of the Cretaceous, but cycads survived. Relationships of these fossil plants with insects are proven, mostly with the beetles. However, Bennetitales had bisexual cones, surrounded with petaliform bracts, sort of floral corolla. Those plants did not possess male or female individuals like the present Cycads and cross pollination was probably not a problem with them. Bennetitales did not have “flowers” on the trunk, as shown in the old drawings, but the cones, which were closed, except perhaps in *Williamsonia* with an arboreal form. The insects visiting those cones were necessarily borers, and we think that it was that way that they fertilized those plants. Cycad seeds, as probably also in case of now extinct forms, are disseminated by the mammals, the birds, the reptiles and by water. Probably during the Mesozoic, the big reptiles were important disseminators.

Cycad cones produce, during certain periods of the day (Tang, 1989; Tang *et al.*, 1987; Terry *et al.*, 2004), volatile components and various odours, resinous, fruity, mouldy, etc., certainly to attract pollinating insects. The cones are visited by more or less specific beetles, and the young fronds by Lepidoptera, mostly lycaenids, and many beetles. We suppose that the beetles attracted by male cones and their nutritive sources go later on to female cones by "mistake", and in doing so pollinate them. It, however, remains to be adequately demonstrated for certain species of beetles and cycads, because female cones are generally very tightly closed, and are often without insects within them. That is why anemophily (i.e. dissemination by wind) was, until mid-1980s, supposed to be the only fertilizing mechanism for the cycads. Beetle intervention is now fully proven, for example the Australian cycad, *Lepidozamia peroffskyana* (Zamiaceae), which is pollinated exclusively by *Tranes* weevils (Hall *et al.*, 2004). Many supporters of the coleopterous fertilization have written about it (Norstog *et al*; 1992; Rattray, 1913, Tang, 1987a and b; Jones, 1993; Norstog and Nicholls, 1997). Crowson mainly (1981, 1989, 1991), in his remarkable study of the relationships beetles-cycads, has strongly insisted on the pollinating role of the beetles. Some *Macrozamia* in Australia are pollinated only by some species of thrips (Terry *et al.*, 2004).

— 1. **Insects and beetles frequenting cycads**

It is always difficult to see cycad beetles on these plants, because their appearance period on the cones and also on the fronds is very short, and it sometimes happens during the night or at dusk (Windsor *et al.* 1999). PJ observed them on the fronds in Panama paying a very short visit. The insects come to the plants one week after the strong spring rains, in May normally, and their visits stop totally one month later. They seem to survive as diapausing egg and larval stages hidden somewhere. The appearance of the insects on the male cones is linked with the latter's maturity and can be autumnal, as in Florida. Some Aulacoscelinae (Chrysomelidae) appear on leaves in spring in Central America and in December in Bolivia.

As mentioned by Crowson (1989), the beetles frequenting cycads are found mostly on the male cones and on the leaves, and rarely on the trunks (only some weevils). A few have been observed on female cones, where they help fertilization, often in the evening. None has yet been found on the roots, but that is probably due to lack of careful search. Some larvae are certainly adapted to radicolous life and probably the larvae of aulacoscelines are seed borers, as those of the bruchids, but these probabilities remain to be confirmed.

— 1.1. **Insects on cones**

Insects frequenting male cones and eventually female cones during the pollen production are not many. They are mainly Coleoptera. Oberprieler (2004a) has summarized our knowledge about the cycad-associated weevils.

The idea of anemophilous pollination of cycads comes mainly due to an analogy with Coniferae. A male cone can produce enormous quantities of pollen, up to 100 cubic cm for *Cycas circinalis* cones. Actually, except for *Cycas,* the cones are firmly closed, and it seems difficult that wind alone can allow the pollen to enter into the micropyle, often situated several centimeters down inside the cone itself. With a few exceptions, only the entomophile solution, rarely observed, seems possible. Often weevils seem involved in this, as mentioned by Rattray (1913), in South Africa in cases of *Encephalartos altensteini* Lehm. and *E. villlosus* Lehm. Species of the genus *Phlaephagus* visit first the male cones, then visit the female cones. Doing that they fertilize them. According to the same author, *Strangeria kaatzeri* would be, on the contrary, exclusively anemophilous, which should be the reason why the cones of that plant do not produce heat.

Zamia furfuracea L., in Mexico, is pollinated by the weevil *Rhopalotria mollis*. *Zamia pumila* L. in Cuba has two pollinators, and also *Zamia floridana* A.D.C. (=*integrifolia* L.), in Florida, the male cones of which are visited by *Rhopalotria slossoni* and by a Langurid, *Pharaxonota zamiae*. Larvae and adults of these beetles feed in the male cone tissues and get covered with pollen. These insects get attracted by the female cones, probably by the heat produced by the cones and their specific odour. In a recent paper (Norstog *et al.*, 1992), pollination of various *Zamia* has been detailed.

Dioon califanoi in Mexico (Vovides, 1991) is pollinated by various species of *Pharaxonota*. These langurid beetles (actually for some people: erotylids) frequent equally the male and female cones of *Ceratozamia* in Mexico. In Costa-Rica, in La Selva, several *Pharaxonota* frequent the male cones of *Zamia skinneri* Warsz. There are also, sometimes, on *Zamia* cones Lepidoptera eggs larvae or pupae, including those of Lycaenidae (*Eumaeus* spp.), which feed on the fronds.

In Australia, the cycads *Macrozamia communis* and *Lepidozamia peroffskyana* are associated with the weevil *Tranes lyterioides*, a big noctural species, which develops inside male cones and eats the pollen. Many other beetles are associated with male cones of Cycadales, viz. Tenebrionidae, Rhizophagidae, Languridae, Anthribiidae, Boganiidae, and Nitidulidae. Other insects frequent male cones of cycads, like *Trigona* bees, a genus known from the Cretaceous, suggesting a very ancient association.

In Costa-Rica, Gomez has observed and photographed in Wilson Botanical Garden quantities of langurids, probably some *Pharaxonota*, invading the male cones of *Zamia fairchildiana* Gomez, devouring the starch. Those small brown beetles could be easily confused with *Aulacoscelis melanocera* Stal or *A. costaricensis* Bechyne, if it was not for their much smaller size.

Crowson (1981, 1989, 1991) has pointed out that certain beetles frequent specially the cycad cones, namely the Boganiidae, dating from the lower Cretaceous and linked with Australia and Africa, then loosely connected, as suggested by the Gondwana Hypothesis. In South Africa, it is a Boganiid, *Metacucujus encephalarti,* which pollinates *Encephalartos lunatus,* and, in Australia, *Paracucujus rostratus*, which is met with on the male cones of *Macrozamia riedlei* (Endrody-Younga and Crowson, 1986).

Brentids of the genus *Antliarrhinus* breed inside the ovules of *Encephalartos* in Africa, and feed on the almond. *Antliarrhinus zamiae* digs with its rostrum through the sporophylls and ova, and lays, with its telescopic ovipositor, its eggs inside the cones of *Encephalartos longifolius* and *E. altensteini*. *Antliarrhinus signatus* comes directly inside the cone to lay its eggs (Oberprieler, 2004b). Crowson (1989) mentions many other curculionoids attacking cycad male cones, namely the genera *Porthetes* and *Amorphocerus* (both Cossoninae) in

Southern Africa. According to Crowson, many beetles, supposed to be cycad pollinators, possess in their mandibles cavities used to carry pollen grains. Others, such as the Allocorynidae and certain Curculionidae, have antennal cavities, perhaps for this purpose.

— 1.2. **Insects on fronds**

Crowson (1989) has mentioned on *Macrozamia* fronds, in Australia, buprestids, such as *Xyroscelis crocata* and *X. bumanna*. The sagrine, *Carpophagus banksiae*, which looks like a big bruchid, has been also found on the fronds of *Macrozamia*. The relationship of these insects with cycads has not been fully elucidated.

Really, there are many frond frequenting insects on the cycads, in tropical America as well as in South East Asia. Good observations in Africa are lacking, as well as in Madagascar. We must observe the time of appearance of these insects, which have only a short adult life, most of their life being in the larval stage.

In South East Asia, *Lilioceris,* normally a Liliaceae feeder, frequents also local cycads. In New-Guinea, Szent-Iwany *et al.* (1956) has been the first to mention *Lilioceris clarki* (Baly) on the new fronds of *Cycas circinnalis*. Later on, Hawkeswood (1992) recorded *Lilioceris nigripes* (Fabricius) in Queensland on the forest dwelling species *Bowenia spectabilis* Hook, a Zamiaceae. There were similar captures in Vietnam, and Shepard (1997) has reported an undetermined species of *Lilioceris* on the fronds of *Cycas siamensis* Miquel in Thailand in a *Dipterocarpus* forest. Larvae were localized under leaflets, and were browsing the abaxial epidermis and a part of the mesophyll. These larvae, as also the adults, were red, very prominent over the dark greeen foliage. *Cycas celebica* Braun, the unique and rare cycad in New Caledonia, does not seem to harbour any criocerine, and the local beetles of this leaf beetle subfamily have been captured there on orchids only.

Aulacoscelis spp. (Chrysomelidae, Aulacoscelinae) also rasp young and new tender green fronds of several *Zamia* species, to suck up sap. They are mostly common in Central America, after the spring rains. Adults migrate over the mountains of Panama (El Cope), probably looking for new plants. In Central America, they are often in company of the caterpillars of *Eumaeus minyas* and *E. godarti* (Lycaenidae) and the langurid, *Nomotus lateralis*. Langurids and *Aulacoscelis* seem to rasp the leaves, partly for pharmacophagy, as toxicity of the cycads protects them from predators. Being very toxic they are never attacked by ants or other predators. *Nomotus* is black and *Aulacoscelis* is orange-red and both are aposematic. The *Eumaeus,* in contrast to many Lycaenids, are not associated with ants. Their own acquired toxicity protects them very well. The larva of *Aulacoscelis* has been recently described by Cox and Windsor (1999). Its biology is unknown, but with what we know at present of *Janbechynea,* a big aulacosceline, we could suspect a development inside the seeds in the cones. This aspect is actually under study.

It seems very probable that during the Jurassic the Protoscelinae were feeding on Cycadales or Bennetitales. The remains of those plants are contemporaries of these insects in the geological layers in Siberia. All first observations on aulacoscelines were done in Panama and Costa-Rica (Jolivet, 1998; Windsor and Jolivet, 1997; Windsor *et al.*, 1999). There exist a dozen of species of *Aulacoscelis* in America and five species of *Janbechynea*. When fed in laboratory, they accept fruit juices, like mangoes, which means that juice sucking is part of their normal diet. Very probably *Janbechynea* feeds on cycads in Bolivia, and there is a high possibility that the larvae live inside seeds.

— 2. **Toxicity**

Most of the insects feeding on fronds or cones of Cycads are aposematic. The toxicity of the plant, of the cones and the seeds is very high, and, though many reptiles, birds, and mammals seem to eat with impunity their cones and their contents, livestock in New-Guinea, Australia, South Africa is gravely and definitely poisoned when feeding on the cones. PJ has seen very often, in New Guinea, the cows sick after having eaten young cones. They turn and turn over themselves like mad cows before dying. In Cycads, toxins are numerous, cycasine, neocycasin, macrozamine and methylamino-L-alanine and are probably sequestred in some specialized cells of the cones and leaf tissue, the idioblasts (Schneider *et al.*, 2002; Norstog *et al.*, 1992).

Many lycaenids (Lepidoptera) are specialized for feeding on cycad fronds, as *Catochrysops pandava* Horsfield in Indonesia and *Chilades cleotas kaiphas* Frühstorfer in New Guinea, various species of *Eumaeus* in Florida, Central America, etc. Those butterflies borrow their toxicity from their host-plant. Miriam Rothschild (Rothschild, 1992; Rothschild *et al.*, 1986) has specially studied *Eumaeus atala* and its gregarious caterpillars, brightly coloured, and containing cycasin, a violent poison. The lycaeanid, despite its toxicity, seemed once endangered in Florida, but PJ saw plenty of them on cycads in Miami botanical gardens.

Some seeds from coastal species of cycads contain a spongy tissue and they float. The sarcotesta or external envelop of *Macrozamia* seeds contains a high concentration of macrozamine, a very efficient toxin. These seeds are often brightly coloured to attract local animals, naturally immune to the poison. The seeds are often red, scarlet, orange or yellow and most of the time bright. Some cones are often orange, red or yellow (*Encephalartos*), sometimes even green, contrasting then with the seed colour.

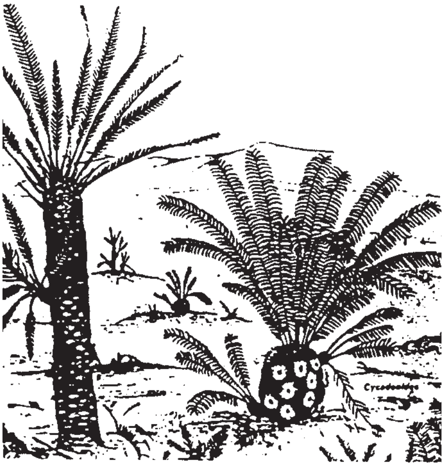
It may be noted that some *Cycas* seeds, after cooking, are eaten by Australian aborigines. The stem of other species is a minor source of sago in the Philippines, the fronds and even the fruits are sometimes eaten in Malaysia. As for the cassava, precautions should be taken by those who want to get a taste of it for the first time because the toxicity of the plant. *Zamia* extracts are sometimes also used as a poison, though they are edible only after a special treatment of the roots. It is the same in Africa with *Encephalartos*. *Aulacoscelis* when offered to chickens kill them instantaneously. The chamorro aborigines in Guam eat flying foxes (*Pterotus marianus*), and the bats eat the seeds of cycas trees (*Cycas micronesia*). That causes a degenerative brain disease among humans. Toxicity of the cycads could be due to cyanobacteria associated with the roots.

The toxicity of the leaves and of the fruits is so strong that the beetles, which feed on them are very toxic themselves, and are thus protected from predators. Weevils, which feed on the parenchymatic tissue, avoid partially the toxins by keeping clear of the epidermic trichomes. Brain dementia in Guam has been attributed to the consumption of bats feeding on cycads, as has been mentioned above.

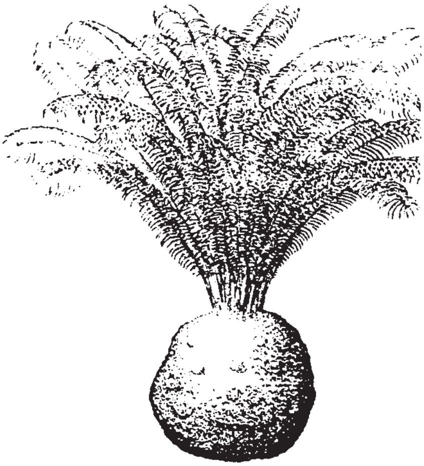
— Conclusion

We are indebted to Crowson (1991), who made an extensive study of beetles associated with cycads. The observations, made and recorded in Panama and elsewhere in Central America, have provided further information. Pollination among aberrant gymnosperms like Gnetales is done by Lepidoptera and Diptera (Kato *et al.*, 1995). It is not the same for cycads, on which caterpillars feed only on the leaves. Entomophily seems predominant among the cycads, but it is not the exclusive mode of pollination. It seems that entomophily is mainly due to the odour produced by the strobilas, which also produce nectar. Among the *Araucaria* (Coniferae), Palophaginae (Chrysomelidae) and Nemonychidae (Curculionoidea) live within the male strobils, but do not seem to visit the female strobili, and they don't help in fertilization. What happens among the cycad cones? It seems that there is often passage from male strobilus to the female one, and thus the fertilization is helped by beetles. However, many are beetles, which only frequent the fronds and never visit male or female cones, such as *Lilioceris* and probably many langurids. It is possible that some of them, like the aulacoscelines, visit the female cones only to lay eggs there. The cycads or Bennetitales cones, during the Mesozoic, were bisexual and pollinated by borers, probably beetles, as suggested by fossil traces. They were of a protofloral type, probably protandrous, that is male organs maturing earlier, while the present cycads have separate sexes, which makes fertilization more difficult.

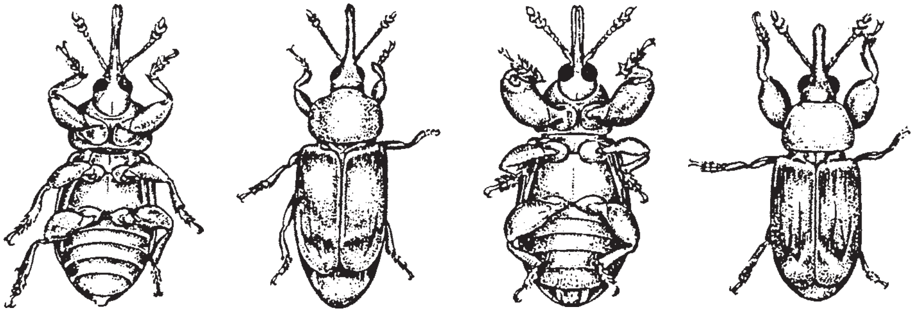
The associations of cycads with aulacoscelines, Boganidae, and some weevils, are very ancient. When PJ visited with Don Windsor the *Zamia* parks in Panama, they got the impression of visiting "Jurassic Park". Only dinosaurs were missing. Langurids and curculionids were also present on *Zamia floridana* cones in Florida. There the "Jurassic Park" impression was not complete, since the *Aulacoscelis,* so common in Mesoamerica, have not yet reached Florida. A recent capture of a larva of an aulacoscline in Florida inside a *Dioon* seed could prove the contrary.



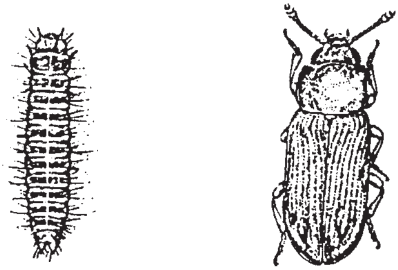
— Fig. 23.1. Cycad ancestors were certainly pollinated by beetles. A Jurassic *Williamsonia* and a Bennetitale (after Jolivet, 1998). Bennetitales had bisexual flowers. Not the cycads.



— Fig. 23.2. A correct representation of a Bennetitale, *Cycadeoiea* sp. The place of the flowers is still controversial (after Delevoryas, 1971).



— Fig. 23.3-23.6. *Rhopalotria mollis* Sharp (Col. Curculionidae), pollinator of *Zamia furfuracea* L. female and male, with swollen femora (after Norstog and Fawcett, 1989).



— Fig. 23.7-23.8. *Pharaxonota zamiae* Blake and Fabricius (Col., Languridae), which feed on male cones of *Zamia floridana*, larva and adult (after Norstog *et al.*, 1992). This insect does not feed on fronds of the host plant.

— Fig. 23.9. *Zamia fairchildiana* Gomez, in Parco Nacional de Chagres, Panama.
A: *Zamia fairchildiana* Gomez. The forest.
B: A head of *Zamia,* with tender leaves (fronds) to be attacked during spring time by *Aulacoscelis* spp.
C: *Aulacoscelis melanocera* Stal (Col. Chrysomelidae), adults feeding on the fronds.
D: *Nomotus lateralis* (Col. Languridae) feeding on *Zamia* leaves.
(All photos by Jolivet, 1998).

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— 24. The Lost World or the Tepuys of Venezuela and Insects there

It is after the exploration of Im Thurn in 1884 (one year after the explosion of Krakatau in Indonesia and the famous tsunami over Indonesian islands) that Sir Arthur Conan Doyle wrote that fascinating science-fiction novel “The Lost World”. In that the famous professor Challenger, surrounded by colleagues and journalists, discovered the dinosaurs, the pterodactyles, and the ape-men, without forgetting the saber-tooth tigers, and the plesiosaurs. During their expedition, the explorers even dined on a roasted iguanodon.

The forgotten plateaus were populated by the fertile imagination of the author with what we used to call “prehistory” beings, or more exactly Mesozoic animals with, however, several compromises with the truth; we mean here the facts of Palaeontology. At the end of Conan Doyle’s book, one pterodactyle was brought back to London with a lot of difficulty, fed during the trip with rotten fishes. It escaped during a conference at the Royal Society from its basket, and flew away to the sky under the eyes of the scientists dumbfounded. Several films and TV shows reproduced the adventures of Professor Challenger in the Lost World.

Conan Doyle very probably was basing his novel on the Mount Roraima, in the SE of Venezuela, but some people consider his story as on Serra Ricardo Franco, in Brazil, near the Bolivian border. It is evident that those very old environs from the Palaeozoic remained unchanged during the Mesozoic. That it seems encouraged the fertile imagination of some writers and even of some scientists. What was there over those mountains, isolated, inaccessible, with vertical walls and sometimes raised over 3000 m above the Amazonian forest? This question has haunted human mind.

Those dramatically isolated mountains in the middle of the jungle were named tepuys (Spanish plural tepuyes) in Spanish, in English tepuy, tepuys, borrowed from the Indian local language, and derived from the Carib linguistic stock. A tepuy signifies a montain, normally with a truncate summit, that is a table mountain. There are tabular sandstone formations (Steyermark, 1987), also referred as cerros in Venezuela or serras in Brazil. They extend over an area of approximately 1,200,000 km^2 in Venezuela, south of the Orinoco river, with also peripheral areas in western Guyana, southeastern Colombia, northern Brazil (Neblina) and a bit of Surinam. In Venezuela, there are hundreds of sandstone elevations but the prominent ones, the tepuys, are numbered around 50 or a little more. The Pico da Neblina, between Venezuela and Brazil reaches 3014 m, but most of the summits range between 1000-1300 to 2500 m (Steyermark, 1987; Jolivet 1991, 1993).

Many expeditions have been organized, generally annually during the only acceptable month with the minimum of rain, on the Venezuelan side of the main tepuyes. Recently, the Brazilians explored their side of the Neblina, but, due to political reasons, there is a tendency to stop periodically the expeditions in Venezuela. The National Geographic Society and the Missouri Botanical Garden contributed to the expeditions and to the knowledge, mostly of the original flora growing on those tepuys. In addition, the expeditions found original birds, specialized insects, some mammals like the tapirs, the pumas, black reptiles or frogs, homochromous with the black rocks, but definitely no dinosaurs, no pterodactyles, and no Mesozoic monsters. The flora, however is rich, endemic, and there is even an endemic plant family.

The flora seems very old but not really archaic, except perhaps for the *Heliamphora*, for instance, probable ancestors of North American *Sarracenia* and *Darlingtonia*. Working conditions there are difficult: repeated and violent storms, incessant rain, plant chaos with no paths and no way to walk, and strong winds. The helicopter has solved many problems. Thanks to it; people can go over those vertical cliffs and return safely. When PJ was collecting near the Auyan-Tepuy, a helicopter was daily transporting up and down Japanese film makers. Only Roraima, at the SE of Venezuela, is relatively accessible by foot, but the last steps are rather perilous. Those summits have much in common and some insects or plants are closely related. The endemism in tepuys is directly related to the altitude and to the superficy of the top. Small rises have only the flora of the surroundings.

Many books have been written on the tepuys, specially notable is the one by Charles Brewer, an odonatologist, a botanist and a great explorer. Klaus Jaffe, an entomologist and a professor at the Simon Bolivar University in Caracas studies the ants, which are very close systematically to a lowland species. Steyermark and his disciples studied mostly the flowering plants.

Old or modern flora have evolved there in a way somewhat similar to as in any insular area. Endemism is remarkable and the Lost World is rich in strange forms. Besides the archaic Sarraceniaceae*,* there are the *Brocchinia* (Bromeliaceae), the only protocarnivorous plants of the family, related to *Catopsis*, epiphytic in the Florida mangrove. There are two species of carnivorous *Brocchinia* on the tepuys and other species of Bromeliaceae are also there, but they don't catch insects. Peat-bogs with *Brocchinia* and *Heliamphora* remind one of the populations of *Darlingtonia* and *Sarracenia* in the west and east coasts in the USA.

The tepuys are generally abrupt, vertical cliffs, often impossible to climb. Those sandstone massifs were carved during past centuries by the Orenoque and Amazon tributaries. Don't forget that this area has been submitted to marine transgressions, and that, from 1.2 millions of km^2 of area, only 200,000 survived the erosion in the form of sandstone mountains. Only a few, however, are high enough to be of a botanical interest.

Continental sediments were deposited on the Guyana shield, equivalent to the Brazilian shield, probably during the upper Jurassic or the Cretaceous or sometime much before. Those deposits were not uniform. According to some authors, those sandstones are similar to the central and meridional Brazilian deposits. Then the plateau has been gradually broken, and those cuts have been the result of a slow elevation, together with climatic changes, mostly an increasing rainfall and probably temporary floods. Tate, quoting Auyan-Tepuy in Venezuela, thinks that the elevation may still be going on.

Tepuys sandstones are not datable. No fossils have been found and all pollen analyses, spores, sponge spicules, found, are doubtful, and may be the result of contaminations. According to Snelling, these sandstones were formed during Triassic or even far back in the Precambrian. Really, the tepuys are made of stratified sandstones, quartzites, jasps, shales, conglomerats, and pebbles, with some inclusions of eruptive material. Also there have been found inclusions of mica and dolerite, and the dolerites have been dated as 1.7 billion year old.

A great part of that sandstone cover has been eroded and carried over as sand along the sides of the rise. The rocks of the base have been exposed on all sides and mass of fallen earth and stones are visible around. The remains of those formations represent the mountains themselves or the sandstone plateaus. On the summits, flat or curved, the soil consists mainly in a layer of white or reddish sand mixed with a bit of humus. The rocks on the top are often black, due to lichens. Amphibians and reptiles on the top tend to adopt the black colour. Vegetation there is as on an open savannah, with humid depressions forming peatbogs or rockpools. Some tepuys are hollow, with deep caves and caverns.

The climate on the top shows a short dry season. It rains 270 days a year, and storms and fog are frequent. The wind is always very strong. Temperature varies from 1°C to 25°C.

The altitudes of the high tepuys vary from 1200 m (Yapacana, Antana) to 3014 m (Neblina). Floral density and endemicity vary in function of surface, orientation, humidity, and topography, but many species are common to the all mountains. Certain species, as *Drosera roraimae*, are found everywhere.

While Neblina, Sipapo, Duida, Marahuaca and Guanay show unequal summits, Roraima, Ptaritepuy, and Chimanta have flat and equal summits. That could be due to different tectonic movements.

It seems a bit premature to speak of tepuys vegetation before the finalization of the Flora of the Guyana Amazonia, which is actually in the making. Cerro de la Neblina, in itself, shows the biggest percentage of endemism (60%). Curiously, if we find many endemic species, there is practically no endemic family, with the exception of the Tepuianthaceae and also the genus *Tepuianthus*. The origin of that flora is very diverse and many species have migrated from the lowland forest to the summits. Other species come from the Andes or present Gondwanian affinities (African or Indo-malaysian). A great part of those plants are adapted to the biotope (according to Maguire: 75%). The endemism in general is a result of local differentiations, from a general flora, altitudinal or not, from tropical America, Mexico or Brazil. The botanical colonisation of the Guyana shield dates probably from the lower Cretaceous, but that presumption is hypothetical.

Rather curiously, this flora is largely xerophytic despite the high humidity and frequent bouts of fog. Perhaps the sun reverberation on the dry and fissured rocks of the summits is the main cause of this. Bizarre forms have evolved with sclerophyll, reduced, waxy, bright leaves, often in tufts or in rosette, such as the *Neblinaria celliae,* which reminds one of the arboreal *Senecio* of the Ruwenzori in central Africa. Those bushes reach a size of one meter and are special to the cerro of Neblina. They belong to the Theaceae family and show pink flowers on their top. Many of those sclerophyll plants are covered with a silky, greyish, white or brown down.

Specialists distinguish a low vegetation, practically similar to the neighbouring Amazonian forest, a vegetation of talus slope till 500 m altitude, with a mountain humid forest higher up, which show some relationships with Andean forests and a vegetation on the escarpments where naked rocks harbour specialized plants, such as Bromeliaceae (*Brocchinia*). On the vertical places, where water is running, there are certain species of Lenticulariaceae (*Utricularia*), carnivorous epiphytes, which grow also on the summits.

The vegetation on the summits is the most diversified. There are real forests of big and small trees (*Bonnetia*), epiphytes, savannah, crevices and acidic peatbog plants (pH 3 to 5). None among the epiphytic plants is endemic and the orchids are numerous, since it is the most important family over the tepuys.

Small tepuys, as the Ptari Tepuys, with its summit composed of naked rocks and savannah, has poor flora diversity, but the Sarisarinama, which shows a different topography with open cavities, has evidently an original flora. Also, on the Guyana side there existed hot and cold, humid and dry phases; the glaciations and the intervals must have influenced this flora, its repartition and its diversity. Isolation, edaphic conditions, and palaeoclimatology have been the main factors resulting in the floristic diversity of the tepuys.

We find on the summits myrmecophilic plants belonging to Cecropiaceae (2 species of *Cecropia* and one species of *Coussapoa*) and to Melastomataceae (51 species of *Clidemia,* 2 species of *Miconia* and one species of *Myrmedone* and one species of *Tococa*). How many among those plants are still myrmecophilic at that altitude? It remains to be found. In the Andes, *Cecropia* loses their relations with *Azteca* ants around 2200 m. *Cecropia santanderensis* from the Andes of Merida and *C. auyantepuiana* and *C. kavanayensis* from the tepuys are myrmecophobic species, i.e. free from ants. Some species of *Cecropia* are also myrmecophobic in the Amazon plain, and some species in central Brazil, as *C. hololeuca*. *C. santanderensis,* for instance, still has hollow stems, prostoma, trichilia, signs of a former occupation by *Azteca* ants. *C. hololeuca* has lost all those characters, except the hollow stem.

It is very probable that *Clidemia*, *Miconia* and *Myrmedone* have lost the ants at this altitude. The question remains for the *Tococa* from the mountains. Have they retained their relations with ants in the ant-pouches or have they lost them? Among the Melastomataceae are found mostly ants of the genera *Crematogaster, Azteca, Allomerus*, *Pheidole* and *Myrmelachista*. It seems probable that some still survive there since the altitudes are relatively moderate.

On the tepuys, carnivorous plants are numerous and diverse. The genus *Heliamphora*, as we have said that already, is endemic on all the summits. All those plants are Sarraceniaceae, but their leaves are not completely fused. There exists a split through which runs and overflows the accumulated liquid. Certain species possess even a drainage hole situated under the split and discovered by Tate during his first climbing. Among *Heliamphora,* Brewer has described a sort of siphon made of special hairs above the drainage hole. We have the impression that everything is "foreseen" to prevent, under those torrential rains, the complete filling of the pitcher, which would stop the digestion of the captured preys. In the pitcher water, mosquitoes breed and even a leech is present and the digestion of preys is entirely bacterial. No digestive enzyme has been so far detected.

Other carnivorous plants on the tepuys are *Drosera roraimae,* common everywhere, several species of *Utricularia* (*U. quelchi, U. humboldti, U. alpina, U. amethistina*) which often grow as epiphytes, so humid are the surroundings, between the leaves of *Brocchinia* and *Orectanthe*. There is also a *Genlisea,* and two Bromeliaceae, *Brocchinia reducta* and *B. hectioides.* Those *Brocchinia* grow generally in peat bogs or in isolated habitats over the rocks. They always like acidic, sandy, humid soil and grow in full sunlight. Inside the *Brocchinia* pitchers, mosquitoes breed, and they are not digested with the rest of insects.

To summarize, as mentioned by Steyermark, all these plants are adapted in the tepuys to a combination of an acidic soil, black waters, heavy rains, intense sunny radiations, violent wind, frequent fog, and sudden changes of temperature. Some of the results of these influences is the arrangement of leaves in rosettes, which is a frequent adaptation in the tropics, and the pitcher shape.

Fauna over the tepuys is relatively poor, but is very original. Unfortunately, despite the many expeditions and the frequent collections, it has not been thoroughly studied, mostly for the insects. The exploration of the zoologist Tate, in 1926, is interesting, since it gave a good review of the fauna of Roraima. The birds were well studied by specialists, and Mayr and Phelps, in agreement with the botanists, admit that the tepuys have formed a minor centre of dissemination, which contains also several relics of types formerly more widely distributed. Speciation among birds of the area has been studied by Haffer.

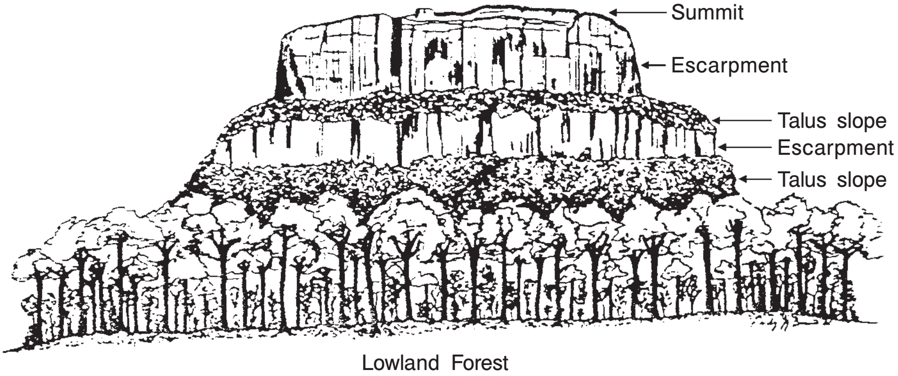
On the summits hummingbirds and parrots are found, several small mammals (mice, *Conolestes*), and also big animals like tapirs and pumas. Some small black toads (e.g. *Oreophrynella*) are homochromous with the rocks, and are found sometimes inside *Brocchinia* pitchers.

The insect world is rich and diverse. In the first description of Roraima insects, in 1895, Waterhouse mentions a dytiscid, a lucanid, an elaterid and a cryptocephaline, all new to science. Tate mentions also various arachnids (some spiders live inside the pitchers of the carnivorous plants where they capture their preys), myriapods, Collembola, Odonata, Trichoptera, Psocoptera, Homoptera, Hemiptera, Thysanoptera, Lepidoptera, Coleoptera, Diptera, and Hymenoptera. Most of the main insect groups are represented there. There are also ants studied by Klaus Jaffe in Caracas.

It is the same Klaus Jaffe and one of his students (Issa and Jaffe, 1999) who discovered aquatic grasshoppers in the bottom of the rock pools on various summits of the tepuys, namely *Hydrolutos roraimae* and 3 more species. They belong to the family Anostostomatidae. Those insects are nocturnal and stay during the day at the bottom of rock pools entirely submerged. They feed on algae and stay under water for periods of more than 20 minutes each time. They rise up to catch air from time to time. They swim very well, but are very frail and cannot survive in captivity for more than 10 days. They have been collected on Auyantepuy, Roraima, Kukenam and Aracamuni, and there must be more species elsewhere. Let us summarise that on Cerro do Cipo in Brazil, there are in the bottom of rock pools, on the mountain, Dynastinae (*Chalepides fuliginosus*), mimicking Dytiscidae, and feeding on detritus, aquatic plants and algae (Jolivet, 1993). They are preadapted to this aquatic life, due to having abundant hairs at the apex of elytra, stigmata invaginated below the general abdominal surface, fusiform body shape, and with air accumulation under the elytra. The lifestyle for the grasshopper is completely aberrant, and this suggests that in tepuys there is still a lot to be discovered.

Most of these insects are endemic in the tepuys, and many remain to be described. Most of the flea beetles, Alticinae, for instance, still remain undescribed, and also many other beetles. Since the expeditions are generally arranged during the better (dry) season, we see what remains of the insect fauna during the rest of the year. And still many of these summits have never been explored scientifically.

When we see what remarkable adaptations are shown by the plants to that hostile conditions, we can imagine what it can be with the insects in that humid, windy, hot and cold, sunny world, a world of extremes. A world, which lodges so many special, xerophytic, carnivorous, ultraspecialized plants should also have produced insects as specialized. Long expeditions are needed and it may be expected that many new visits by scientists will be organized in the near future.



— Fig. 24.1. A typical tepuy in Venezuela.

— Fig. 24.2. Major tepuys of Venezuela (after Steyermark, 1987).

— Fig. 24.3. Lowlands around the tepuys (photo Jolivet).

— Fig. 24.4. A tepuy, view from the forest (photo Jolivet).

— Fig. 24.5. Auyan-tepuy in Venezuela. From there you can see Angel fall during good weather, the highest fall in the world (photo Jolivet).

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— 25. **Insects and the Gondwana Hypothesis**

Before seeing how some insects provide support for the palaeogeological Gondwana Hypothesis, let us become familiar with the hypothesis. The hypothesis was suggested by Eduard Suess, an Austrian geologist. According to it, South America, Africa, Peninsular India, Australia and Antarctica were formed by breaking up of a large land mass or supercontinent in the southern hemisphere, and by subsequent drifting of the resulting land masses (continental drift). Suess gave the name Gondwanaland to the supercontinent of the south.

Even before Suess some elements of the hypothesis had been conceived by Alfred Wegener, a German geologist in 1912. He suggested that in the Palaeozoic era (about 255 million years back) there was a single huge land mass, which he called Pangea. About 245 million years ago it broke into two parts, a northern portion and a southern part, which subsequently moved away from each other. Later geologists named the northern continent Laurasia and the southern one Gondwanaland.

As per our present notion, by middle of the Jurassic period (about 160 million years ago) a huge sea, the Sea Tethys separated Laurasia in north from Gondwanaland in south. Later Laurasia broke up to form North America, Europe and Asia. Gondwanaland remained undivided up to Cretaceous (130 to 140 million years back), and then it fragmented to form South America, Africa, Madagascar, Peninsular India, Australia and Antarctica. Africa and Peninsular India became well separated from the southern land mass, and moved northward to become connected with the

Eurasian land mass. Madagascar, as an African satellite, remained in a splendid isolation. South America and Australia remained almost connected with Antarctica till about 75 million years back and, even later on, they maintained close proximity with the Antarctica.

The Gondwana Hypothesis, as outlined above, is well supported by geological evidence. Structure and stratigraphic sequences in Palaeozoic deposits match well in mountain ranges of eastern North America and northwestern Europe. Palaeozoic stratigraphic sequences are very similar in the southern continents and in the Peninsular India. In 1960s, shore lines on the two sides of the Atlantic at depth of 1000 m have been worked out through drilling and computer mapping, and they have been found to be quite fit for juxtaposition of the continents on the two sides, agreeing well with fragmentation of the old land masses, as suggested by the hypothesis.

The hypothesis receives convincing support from floral and faunal distribution too. Fossils of the seed fern *Glossopteris* are found in all the southern continents and in the Peninsular India. They are not met with anywhere else. McDaniel and Shaw (2003) have studied Australian and South American populations of the moss *Pyrrhobryum mnioides* using DNA analysis, and have inferred that the moss populations in the two geographical areas are monophyletic (i.e. having evolved from a common ancestral stock), and that there has been no intercontinental dispersal between them, which means the origin of the two sets of populations should be Gondwanian.

The Gondwana Hypothesis explains well the disjunct transpacific distribution as resulting from the sequential break-up of the supercontinent Gondwana, during the last 165 millions years. New Caledonia, New Guinea, New Zealand were still linked at the end of the Mesozoic (-65 myr) to what survived in the South of the great Gondwana continent, from Patagonia, via Antarctica and Australia. In that period, Antarctica was not tropical but it had a warm temperate climate, and that allowed migration of fauna and flora in both directions. During the mid-Cretaceous (-110 myr) South America and Africa began to drift away (Sanmartin, 2002; Sanmartin and Ronquist, 2004). Antarctica in the late Cretaceous (-65 myr) to early Eocene (-60 myr) was covered with an angiosperm-rich flora dominated by *Nothofagus*. Winteraceae, with *Taktajania* in Madagascar, Monimiaceae with *Hedycarya* and *Kibaropsis* in New Caledonia, Amborellaceae, with *Amborella* in New-Caledonia, Austrobaileyaceae with *Austrobaileya* in Queensland are remains of that period. Many gymnosperms, like *Araucaria* and related (missing in Madagascar) are also all witness of that time. Several gymnosperms have a subantarctic-pacific distribution: *Araucaria*, *Libocedrus*, *Prumnopitys* and *Retrophyllum*. In New-Caledonia many plants are true relics of an old Cretaceous distribution (Richier de Forges *et al.*, 1998). Among the angiosperms, Cunoniaceae, Proteaceae and many Myrtaceae also have had a Gondwanian origin. During most of the Paleogene (-70 myr), New Zealand and New Caledonia were progressively submerged, but some dry land remained and insect and plant relics survived there. It is probably in the Cretaceous that *Nothofagus* and Proteaceae colonized New Zealand and New Caledonia, from South America, following the antarctic northern margin of Gondwana (Richier de Forges *et al.*, 1998). Another opinion, however, is that *Nothofagus* came from Australia to South America. An interesting genus, *Gunnera* (Gunneraceae), the terrestrial plant with the biggest leaves has also had a Gondwanian distribution (Wanntorp and Wanntorp, 2003), but is missing in New Caledonia and in continental Australia, though represented in Tasmania and New Guinea. It is of some interest, since *Gunnera* is somewhat related to Myrtaceae, which has been reported as harbouring occcasionally the genus *Stenomela*, one of our archaic Gondwanian eumolpines. No wonder why archaic eumolpines (Jerez, 1996) are found at the two extremities of the Southern Gondwana, in Chile and in New-Caledonia.

There are several interesting instances in animal distribution supporting the Gondwana Hypothesis. Lung fishes (constituting the natural group Subclass Dipnoi) show a Gondwanian distribution. Among them *Ceratodus* is in Australia, *Protopterus* in Africa, and *Lepidosiren* in South America. The side-necked turtles (constituting the Suborder Pleurodira) are confined to the three southern continents. The flightless birds (constituting mostly the natural group Ratitae) are also almost confined to Australasia, Africa and South America. Among them ostriches are in North Africa, rhea in South America, emeus in Australia, cassowaries in New Guinea and Australia and kiwis in New Zealand. Some others are recently extinct (Moas, *Sylviornis, Aepyornis*), probably due to human interference, in New Zealand, Australia and Madagascar. Marsupials (that is mammals giving birth to immature young ones, which have to be kept in a special pocket on the belly of the mother for allowing them to develop further, constituting the Subclass Metatheria) are in Australia and South America. Their presence in Central America and south part of North America is due to their northward dispersal, just as ostriches extend their range into the Arabian countries. Survival of marsupials only in these two southern continents has been attributed to their long isolation from other land masses in geological history, and consequent absence of competition with higher and more successful forms in these continents.

Insects also provide some instances supporting the hypothesis, but such cases are not many, mainly because insects are mostly small and light bodied and are provided with wings. These attributes of insects are responsible for their great migratory capacity and wide dispersal possibility (see the chapter "Insect Migrations"). One illustrative example of how successfully an insect may reach a new area and readily establish itself is that of the small yellow ants (*Anoplolepis gracilipes*). This ant was unknown in the Christmas Islands, which are close to Australia, till about 70 years ago. It is a carnivorous ant species, and is now a threat to the original life on the islands. It has voraciously eaten away small animals of all descriptions, including insects, crabs and birds. In absence of animal pollinators forest flora is being lost at a fast pace (Anonymous, 2004). It seems that the ant has entered the islands with floating timber, and, on finding absence of competition, abundance of food and favourable climatic conditions, has multiplied fast. A chrysomelid beetle, *Chaetocnema confinis* is, through typhoons and hurricanes, conquering the whole of the tropics from a North American origin, invading Africa, Asia and Oceania. Its success is due to parthenogenetic females, which, on reaching a new area, multiply by themselves. The beetle is bisexual in North America, probably its country of origin.

Some primitive genera of leaf beetles, belonging to the subfamily Sagrinae (Family Chrysomelidae), are almost confined to the Australian region (Australia and New Guinea), but the genus *Megamerus* occurs in Brazil and Madagascar, besides Australia, and the genus *Sagra,* more advanced, occurs in tropical Africa, India, Indonesia and China (Jolivet, 1997; Jolivet and Verma, 2002). *Atalasis,* closely related to *Megamerus*, occurs in Argentina. A few fossil sagrines are known from the Northern hemisphere, but the living archaic genera are all from land masses of the southern Gondwanian origin. Sagrines went extinct in Europe and elsewhere. *Eosagra* from the Eocene of Germany seems to be a real sagrine, but others are doubtful. It should be noted that sagrines show a primitive way of feeding: they are borers into the stems or roots of young plants and their pupae are gallicolous (inducing formation of and living in plant galls). This brief account of life history holds for the sagrines, which have been studied. Practically nothing has been observed and recorded for the archaic sagrines of Australia, but they are expected to have a similar biology. There are no living sagrines in New-Zealand and New-Caledonia.

There are some primitive members of the subfamily Eumolpinae (Family Chrysomelidae) in Australia and South America, namely *Spilopyra* and *Macrolema* in Australia and New Guinea, *Richmondia* in Australia, *Bohumiljania* in New Caledonia, and *Hornius* and *Stenomela* in South America. It may be recalled that New Guinea and New Caledonia are in the Australian region, as is New-Zealand, which is devoid of these primitive eumolpines. Probably there they are extinct or they never reached the place. These primitive eumolpines have basic similarity among them (Verma and Jolivet, 2002; Jolivet, Verma and Mille, 2003; Verma and Jolivet, 2004); hence they have been regarded as monophyletic. *Bohumiljania* of New Caledonia and *Hornius* of South America are particularly close. Really, this is a good example of the Gondwanian distribution, as for many other beetles which are common between Australia and Patagonia, at least at the genus level due to close association between the Australian region and S. America through the Antarctica in the Gondwanian history. The recent discovery of an Australian species of *Sphaenognathus* in the mountains of Queensland, by Monteith (Moore and Monteith, 2004), is an event of considerable zoogeographical importance, this lucanid being known outside only from the neotropical region. It is another Gondwanian relic.

As has been pointed out earlier, it is known that till late Cretaceous (about 75 million years ago) Australia and South America were almost connected through Antarctica, while Africa, Madagascar, with the Seychelles plateau, and India had drifted away. Presence of the primitive eumolpines only in the Australian region and in South America and their absence in other land masses of the Gondwanian origin may be explained in the same way as for the marsupials, that is due to long isolation of South America and Australia from other land masses and consequent better survival of primitive forms in absence of competition with higher and more successful forms. That *Megamerus* is also present in Madagascar, in addition to South America and Australia, is another pointer to Gondwanian origin of the former.

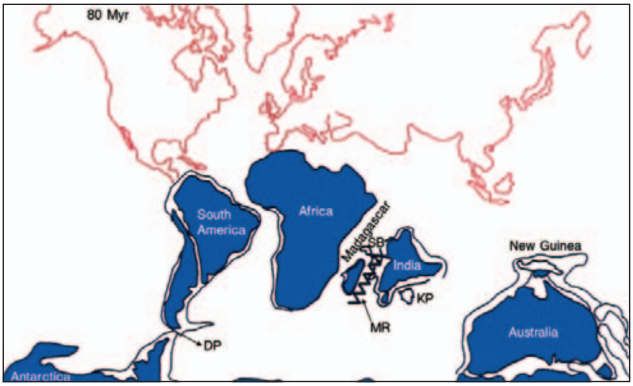
For reasons not clear to us leaf beetles of the subfamily Chrysomelinae, Paropsini are confined to Australia, New Guinea and some other neighbouring islands. Perhaps these chrysomelines evolved after separation of the Australian plate from other land masses of the Gondwanian origin, and then, finding a variety of vacant niches, they diversified into Paropsini. *Cratopus*, a colored weevil, originated in Madagascar and the Comores and invaded the Mascareignes, where it diversified explosively. It populated vacant niches on plants and trees, since it has the same habits as chrysomelid beetles, feeding openly on leaves.

Jeannel (1942) was an ardent supporter of the Gondwana Hypothesis. But he has been criticized by those who have studied the Madagascar fauna. That the fauna of this large island closely resembles the African fauna and shares not much with the fauna of other land masses of the Gondwanian origin is mainly because of its proximity with Africa. As Mahe (1972) has pointed out, there was a large peninsula shaped of relatively shallow sea between the western coast of Madagascar and Africa, and also that during the Pleistocene, when most water was locked up as ice, perhaps there was a chain of islands between Africa and Madagascar. Such stepping stones were the way, people believe, Galapagos islands were populated with big tortoises and endemic apterous insects. In spite of the comparatively recent invasion of the African fauna, relics of the Gondwanian origin are still there. Paulian (1972) has pointed out some such forms in the Madagascar fauna, for example: (a) "…Orphninae which have produced some very well differentiated Malagasy forms whose equivalent is found only in the Congo and the islands of the Gulf of Guinea or in South America.", (b) "…the Blepharocerid Edwardsininae are now found only in South America, Australia and Madagascar; their Malagasay representative, *Paulianina* Alex, is highly specialized and produces a long series of

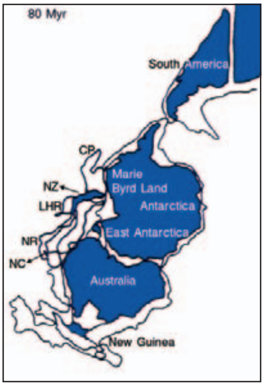
Malagasy species…”, and (c) “The Plecoptera with the genus *Madanemura* whose numerous species are related to the South African and New Zealand forms of primitive Neonemouridae…”. Endemism is specially pronounced in Madagascar due to its long isolation. There is quite a big quantity of common genera of beetles between South America and Australia.

It is easier to understand the presence of big fossil tortoises in Madagascar than in the Mascareignes, pure volcanic and relatively recenty emerged islands. However the historic presence of a *Hippopotamus* in the big island of Madagascar remains a dark mystery and no satisfying interpretation has been done until now.

— Fig. 25.1. Gondwana (-140 myr), when Africa and India started drifting to North (after Sanmartin, 2002).



— Fig. 25.2. Gondwana (-80 myr), during the Cretaceous, showing the Southern Gondwana continent, still linked with Patagonia, with Africa, Madagascar and India drifting to North (after Sanmartin, 2002).

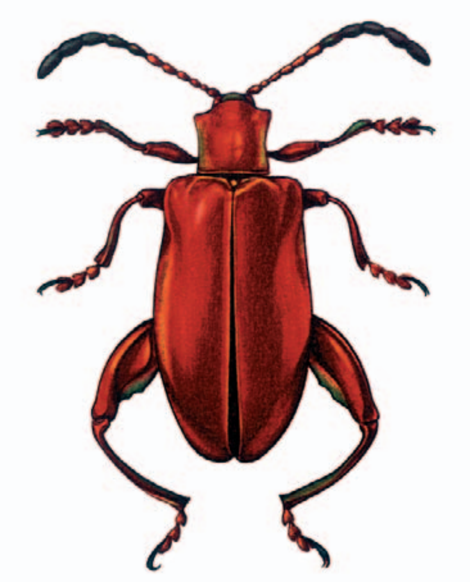


— Fig. 25.3. Antarctica (-80 myr). Still links with Patagonia and the Australian Plate persisted (after Sanmartin, 2002).

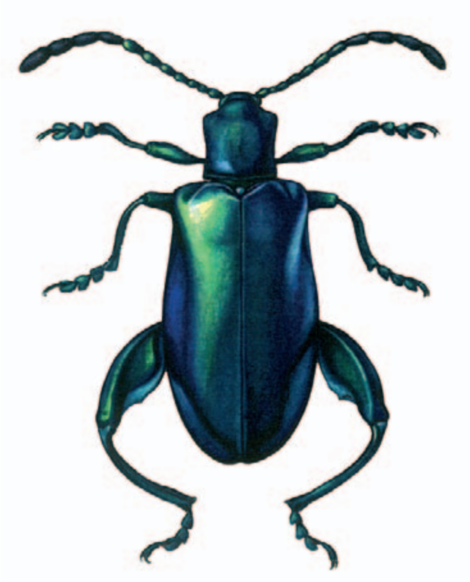
— Fig. 25.4. Antarctica (-60 myr). There are still links with Australia, New – Guinea but separation started from South America (after Sanmartin, 2002).

— Fig. 25.5. *Spilopyra sumptuosa* Baly (Eumolpinae). NSW Australia on *Cupaniopsis anacardioides* (Sapindaceae) (photo P. Jolivet).

— Fig. 25.6. *Bohumiljania caledonica* (Jolivet). New Caledonia on *Syzygium cumini* (Myrtaceae) (photo Christian Mille).



— Fig. 25.7. *Sagra femorata* Drury (Sagrinae), red form.



— Fig. 25.8. *Sagra femorata* Drury (Sagrinae), greenish form.

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— 26. **Love match!**

Sexual reproduction is almost a rule among animals, and mating between a male and a female is the initial step in it. But cases of parthenogenesis, budding, and scissiparity are also known among them. Parthenogenesis is common among insects, and even among such specialised insects as beetles. In case of snails, the two partners copulate mutually and both lay eggs, as either of them is provided with male as well as female gonads. A book was very famous during the war: “Die Sexualität” by Hartmann (1943). This book is entirely devoted to relative sexuality, mostly among Protozoa, where the size determines the sex, whether an individual will be a male or a female. The smaller one acts as a male. Homosexuality is known among many animals including beetles. A serious Hungarian journal (Rovart Lapok) had many years ago a paper entitled “About pederasty in beetles”. It is a fact that people have very often recorded, among weevils, leaf-beetles, and scarabeids, interspecific matings, matings between males, between females, between larvae and adults, between nymphs and adults, etc. There are sometimes “normal” cases of mating between nymphs and adults among insects, as males do not wait for the complete emergence of the female from the skin of the penultimate instar. There is a show of urgency among competitors for such matings.

Mating among insects is extremely diverse and complicated. It is really aberrant among the bedbugs (Cimicidae), Nabidae, Corixidae, Anthocoridae and some other families of Heteroptera or bugs. Also, Strepsiptera, outside the Hemiptera, show an extra-genital insemination. It is the haemocoelian or traumatic mating (Carayon, in Usinger, 1966; Carayon, 1977). Among the Cimicidae, insemination is never effected by the usual genital route. The male punctures the body wall of the female with its aedeagus and injects an abundance of sperms into the female abdomen, but outside the usual reproductive tract. Insemination is thus extragenital and traumatic, because it starts with making of an integumental wound. There are, in connection with this behaviour, special structural differentiations, which together constitute the "paragenital system" (Carayon, 1977; Jolivet, 1991). A specialized organ exists in *Cimex*, Ribaga organ to facilitate the haemocoelian copulation. Among Nabidae and Anthocoridae, there is a tissue specially adapted to drive the spermatozoa through the blood to reach the oviducts. In *Cimex*, males never introduce their copulatory organs into the vagina of females. The male straddles the back of the female obliquely, his abdomen strongly incurved against the right side of his partner's abdomen, so that its extremity reaches not the orifice of the genital duct but that of the organ of Berlese, which is a special integumental pocket, where the penis penetrates and injects the sperms. Parts of the spermatozoa cross the walls of this pocket, and through the hemocoele some reach the seminal receptacle, and others penetrate directly into the ovarioles. Another part of the spermatozoa seems to be digested by the amoeboid cells in the pocket, and the products of the digestion would contribute to the development of the ovaries. Those amoeboid cells also secrete a hormone activating the spermatozoa (Poisson, in Grassé, 1951). The paragenital system and its accompanying behaviour are extraordinarily complex among *Cimex* and several other bug families. *Afrocimex* males, unable to distinguish the sexes, frequently mate between themselves, and, less often, inject mutually the sperm (Carayon, 1977). It is not infrequent to see two males copulating. Among Corixidae, sexual behaviour seems linked to the size of the partners, the smallest mounting the biggest. Lesbian *Drosophila* exist, and the gene for it seems recessive. Male and female bipotentiality in mating is known in *Ceratitis capitata*. In cages, its sexual bahaviour depends on various conditions, like sun, light, chemicals etc. It should be emphasised that homosexuality has been observed in all cases in breeding cages and under artificial conditions.

A question remains: what could be the utility or the finality of this aberrant homosexual behaviour of the Cimicidae? According to a friend entomologist, this mating system would prevent a too big consanguinity (i.e. close inbreeding) in a restricted area, like a room. Two males copulating would mix up their spermatozoa in the hemocoele and the mixed sperms would be so reinjected to a female which would get that way a greater variety of gametes. The idea seems rather far-fetched, and it would be necessary to see if a male, so "fertilized" by another male, is capable of reinjecting, partly at least, into a female, the spermatozoa of another male.

In many insects there may be a violent conflict among competing males for a female for a successful mating. The size of the horns of a horned beetle gives them sometimes an advantage in the fight. Horny leaf beetles use them to fight, but hornless ones, such as the Colorado potato beetle and *Gastrophysa viridula*, also fight vigorously to get a female, and, when they get hold of one, the winner stays around to protect her.

Pseudocopulatory behaviour is known among the females of a weevil, *Otiorhynchus pupillatus*. A parthenogenetic female of this species, when ready to oviposit, searches actively another female and mates with it.

Some insects remain coupled all their life. An example is the love-bug, *Plecia nearctica*, in North America. Since 1965, this fly (Diptera, Bibionidae) has invaded Florida, from Mexico, and population explosions are known twice a year, in May and September. The flies are harmless, but they adhere to the windshield of cars during driving. Many times PJ was obliged to stop and to clean his windshield. Flight of the flies has been encountered by light airplanes at altitudes up to 500 m. Each female lays more than 300 eggs in decaying vegetation. Spattered remains of these insects can damage the car by clogging the radiators (Hetrick, 1970; Denmark and Mead, 1992). The small flies get crashed like scrambled eggs and the mixture slightly damages the paint on vehicles. The mating flies do not separate and remain connected for life.

More than two sexes have been recently attributed to some American ants. That fits science fiction where authors always try to invent new ways of reproduction on their ghosty planets. It has recently been found that certain ants of the genus *Pogonomyrmex* seem to possess three or four sexes: the queen must copulate first with a male of her proper genetic group to produce queens, and then with males of another genetic group to produce workers and soldiers (Parker, 2004). Caste differentiation in *Pogonomyrmex* ants is very complicated and results also from environmentally induced differences in gene expression (Gahan and Keller, 2003). Genetic basis is advocated for queen-worker dimorphism of *Pogonomyrmex* and this mode of caste determination has consequences in multiple mating by females for control of sex ratio (Volny and Gordon, 2002). Among other ants, the castes seem to be determined by environmental or nutritional factors. Certain fungi show some hundred different types of reproduction, but *Pogonomyrmex* is the only example known in the animal kingdom.

Many hymenopterans, in the temperate and tropical world, do make love with flowers. In Australia ants show this phenomenon, and we know how infrequently ants pollinate flowers. The fact was discovered in 1916, in Algeria, but has been restudied in detail by Kullenberg (Kullenberg, 1961) and the Scandinavian school after 1961 (Kullenberg and Bergstrom, 1976). Several orchids, without nectar, oil, or edible tissue, have got transformed into prostitutes, and have mimed morphologically and chemically an insect female, and thus have succeeded to get pollinated by various hymenopterans. Practically, in such cases a male insect masturbates itself on flowers. The fact was discovered among *Ophrys* species, which are European and mediterranean orchids, and which possess a labellum recalling by its shape, its colour, its velvetiness, an insect body. Similar cases have been found among the Australian *Cryptostylis*, the Neotropical *Paragymnomma* and several others. There are certainly many other examples over the planet awaiting a detailed study. These orchids are visited by wasps, flies, bees, ants, and several other insects, which also take care of the pollination in addition to their sexual satisfaction.

An opposite situation: the English *Ophrys apifera* pollinates itself, its own pollen gets the pistil fertilised, since it has lost its pollinator or its “sexual” partner through extinction.

The strange resemblance between the insect and the flower was already seen in 1831. Mating between insect and flower takes place generally with newly hatched males when the females are still uncommon.

In North Africa, it is *Scolia ciliata*, a wasp which pollinates *Ophrys speculum* during pseudo-copulation. In Northern Europe, *Ophrys muscifera* is pollinated by two species of wasps of the genus *Gorytes*. In the mediterranean region, several *Ophrys* species are pollinated by various hymenopteran insects, *Scolia*, *Eucera* and *Andrena*. Kullenberg has recorded bigeneric attractions of *Ophrys scolopax,* in Lebanon, which attracts *Eucera* and *Andrena* males. To facilitate the copulation, the labellum of the flower is relatively strong and the epidermal cells have very strong walls. The primary stimulation is essentially olfactory, and is followed by tactile and visual stimulations, the last one less important (Jolivet, 1998).

It is a fact that for a non-initiated insect male, the flower morphology of an *Ophrys* flower is close to the shape of an insect, mostly a hymenopteran, with pseudo-eyes, pseudo-antennae, and pseudo-wings, as well as with hairs similar in shape, colour, odour and texture to the ones of an insect female. A layman, with little experience, may behave as a finalist. Bernardin de Saint Pierre, an extreme eighteenth century finalist, maintained that if a melon had ribs, it was to be eaten in a family. La Fontaine, the fabulist but also another finalist, said, in one of his fables, that if a pumpkin was growing on the ground and acorns on a tree, that was to prevent them doing any harm in falling on living beings. La Fontaine did not know that there was a pumpkin tree (*Dendrosicyos socotrana*), the only cucurbitaceous tree, in Aldabra Island. These analogies have been mentioned to point out how an inexperienced individual may be confused. That is how an uninitiated male takes an orchid, with only a rough resemblance of a female, for its mating partner.

The insect seems mainly attracted by the odour, similar to the female of its own species. The plant secretes a real mimetic pheromone. This smell is so powerful that the males look for a flower, even wrapped in a paper. It has even been seen that, at least in one case, the males preferred the flower to their own females.

In addition to flower morphology and the odour it produces, there seems to be another factor for attracting male insects. To compensate for its immobility, the labellum, where lands the insect, is dark purple with clear marks and spots, mirror-like reflecting the UV rays. Among some flowers, the labellum moves also slightly with the wind.

Once landed on the orchid labellum, the insect finds the hairy curves, the projections, the hairs, which seem to persuade him to believe that he has really found the soul mate, and he immediately enters in pseudocopulation with length and vigour. The copulating organ is protruded and driven into the velvety parts of the labellum. The males, excited by the smell, may sometimes be seen fighting for the possession of a flower. However, the orchid does not seem comfortable with its loving partner, and though the penis is out and rubbed continuously, there seems to be no ejaculation at least in *Ophrys*. Sperms have been detected once on *Cryptostylis*, an Australian orchid, pollinated by ichneumonids.

Orchids have sometimes, for attraction of insects, extra-floral nectaries on the pedicels, the bracts or on the petioles. Their flowers are generally entomophile and pollination is done generally by bees and wasps, very little by beetles and very exceptionally by ants. Pseudocopulation is extremely rare among them. Examples are the cases of *Microtis parviflora* in Southern Australia or *Leporella fimbriata*, also in Australia (Peakall, 1989; Peakall *et al.*, 1987). Seeds are also exclusively anemophilic. *Leporella* is exclusively pollinated by the flying males of *Myrmecia urens*. Janzen once mentioned the extreme rarity of the plant pollination by ants, assuming that these insects were wingless (workers), that they possessed metapleural glands, which were pollen killing. As is true for many other Hymenoptera, such as *Scolia*, *Andrena*, *Gorytes*, *Eucera* and many others, the ant male also shows a real pseudo-copulation with the flower, resembling a smelly female, but without nectar. In the case of *Leporella*, an extraordinary case, the ant male lacks in metapleural glands, which in other ants are meant to destroy pollen (Jolivet, 1996). It was known that sometimes flies pollinate orchids. A recent paper (Blanco and Barboza, 2005) mentions a pseudocopulation in *Lepanthes glicensteinii*, an orchid from Costa-Rica, by fungus gnats (*Bradysia floribunda*, Diptera: Sciaridae). The species has a minuscule labellum adapted to the pollinator. The fly appears to ejaculate during pseudocopulation.

As was written by A. Huxley, "even so, the insect flies, full of hope from flower to flower, do again the semblance of copulation, and, we can hope, takes pleasure, but, with much efficacy, carries the pollen". It also happens that sometimes the labellum is violently bitten during the operation.

The copulating orchids vary very much in shape and pilosity according to their copulation partners in their geographical area, and in their botanical species. *Ophrys lutea* produces an inverted copulation because of its floral structure.

Anyhow, this "sexual" adaptation between a flower, lacking in any other device for attracting a pollinator, and an insect, which does not get any reward for its action, but for assumed sexual satisfaction, is extremely interesting. It must have been the result of a long evolution from a formerly nectariferous plant ancestor. For such orchids, this "sexual" solution seems their only chance of survival after losing their nectaries, since autopollination is not a desirable alternative.

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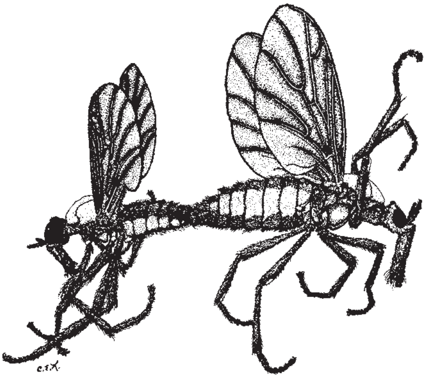
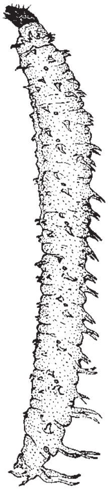
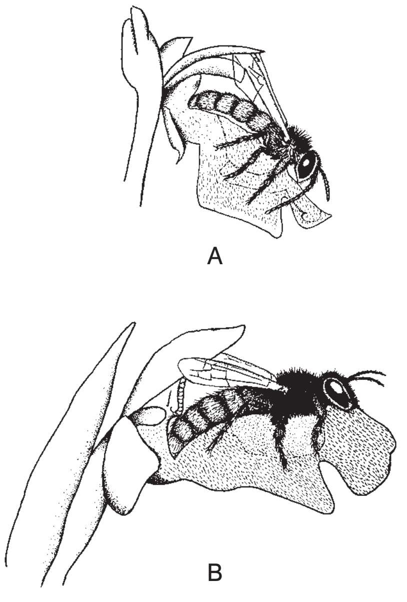


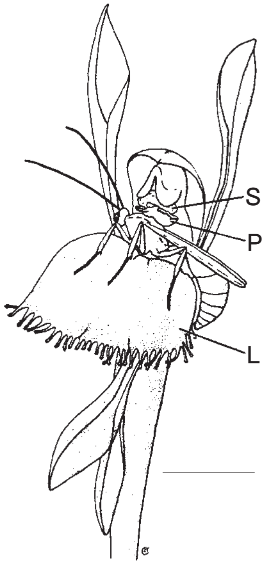
— Fig. 26.1. Mating pair of *Plecia nearctica* (Diptera: Bibionidae); female on right. 13-15 mm. Florida.



— Fig. 26.2. Larva of *Plecia nearctica*. 11-12 mm (after Hetrick, 1970).



— Fig. 26.3. Mating trials of A. *Andrena maculipes* with *Ophrys lutea*; B. *Andrena mactae* with *Ophrys fusca* (after Kullenberg, 1961; Jolivet, 1991).



— Fig. 26.4. Male of *Myrmecia urens* pseudocopulating on the labellum of the orchid, *Leporella fimbriata*. L: labellum; P: pollen accumulated on the vector; S: stigma (after Peakall, 1989: Jolivet, 1991).

— 27. **Damselflies, experts in ballistics**

During the Carboniferous (about 236 mya), there were giant dragonflies, or more exactly enormous species, to some extent related to the typical Odonata. The big *Meganeura monyi* was described by Brogniart in 1884; it measured more than 70 cm in wingspan. Carpenter (1992) places it under the Protodonata. Such a big insect had no predators, and probably was a great destructor of the already rich insect fauna, flying in the primitive forests, composed mostly of Ginkgoales, Equisetales, arborescent ferns, *Lepidodendron* and *Sigillaria*. Cycadales appeared in abundance later during the Mesozoic, and real flowering plants were absent until the Trias, when they appeared in very primitive forms, to evolve further during the Cretaceous. Those big Odonata-like insects disappeared during the Permian. There is no insect even now so big as Protodonata on our planet. The biggest moths *Thysania agrippina*, have a wingspan of 230 to 305 mm, *Attacus atlas* of 160-300 mm, and the longest phasmids in New Guinea are less than 400 mm. Two species of *Epiophlebia* from Japan and India have Mesozoic characters, combining the characteristics of both suborders, the dragonflies and the damselflies, but their size is average (Asahina, 1950, 1954).

There are, however, in South Africa and in Amazonia very big damselflies, which seem directly surviving from the prehistory, when you see them flying. PJ saw them often in Brazil. They belong to the Pseudostigmatidae in America and to the Megapodagrionidae in South Africa, Tanzania and Madagascar, families placed among the Zygoptera, i.e. the damselflies, a suborder under Odonata. They are delicate forms with forewings and hindwings similar, with the wing base narrow and petiolated. The larvae of *Mecistogaster modestus* breed in the water accumulated in the leaves of epiphytic bromeliads; others (*Microstigma* sp.) in the water of *Bertholletia* pods, fallen on the forest floor. The long abdomen of the females of *Mecistogaster* has been regarded as an adaptation for penetrating deeply into leaf axils of bromeliads during oviposition (Calvert, 1911). The argument does not explain why male abdomens should be longer than those of females (Fincke, 1984). Young (1980, 1981) has studied the biology of *Megaloprepus coerulatus* in Costa Rica.

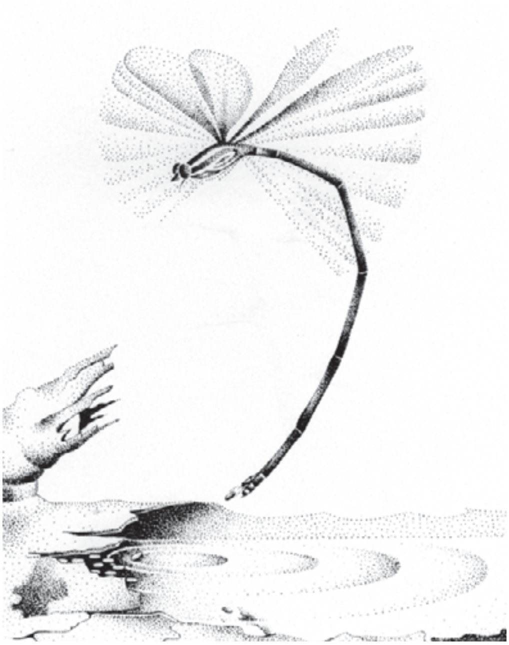
Normally Odonata eggs are laid close to the surface of water bodies, permanent or not. Many Zygoptera and a few Anisoptera (dragonflies) families insert their eggs into tissues of plants growing near or in water. Some Anisoptera attach their eggs to plant leaves or stems, but most of the genera lay their eggs in open water. The colour of these eggs is generally white or greyish, and can change to brown or dark grey later on. Among tropical species the eggs can be brilliantly coloured as blue, green, pink, and also change colour later. Most of the species from the two suborders, mentioned above, lay their eggs in phytotelmata, the natural reservoirs on tropical plants, such as tree holes, wrapped leaves of banana plants, *Heliconia* or epiphytic Bromeliaceae, etc. Those natural aquaria, often suspended on the trees, contain an abundant plant and animal life, including many insects: Odonata larvae, larvae of Diptera, belonging to many families, including chironomids, mosquitoes, Tipulidae, beetles, including Helodidae and Hispinae (like *Cephaloleia* in *Heliconia* water-filled bracts, Jolivet and Verma, 2002), Oligochaeta worms etc.; they devour each other voraciously. Frogs even sometimes join the group, but water bugs like Belostomatidae are missing. It seems, however, that dragonfly larvae eat each other, and they also devour rapidly the predator of mosquito larvae, *Toxorynchites*, to the great displeasure of the medical entomologists. But Odonata larvae in general help in mosquito control.

Forty-seven species of Odonata seem specific for breeding to phytotelmata, and among them only a few species, including some big Zygoptera, have been observed breeding in tree holes, for instance, one in Africa, one in Australia and one in the neotropical region. These big tropical damselflies, flying slowly and delicately, however show some punctual interruptions, like when capturing spiders or their preys, already wrapped into the net. This behaviour is different from that of most of the dragonflies or damselflies, which catch their prey when flying. Really very little is known of the behaviour of those big insects, and very few observations have been made in the tropics.

While the long wingspan is important among those big species, the abdomen is also very long, sometimes longer for the male (*Mecistogaster linearis*). The meaning of this lengthening of the abdomen has remained for long a mystery. It has been suggested that those long abdomens allow the females to deposit their eggs through the narrow openings of the water-tanks of Bromeliaceae, since to penetrate inside treehole or phytotelmata remains a very risky venture for a dragonfly, because a vertebrate predator, a toad, for instance, may be hidden inside. Moreover, the distribution of tree holes and phytotelmata through the forest requires a difficult search by the female of the damselfly. Sometimes, the males protect those holes against the trespassers, rival males for instance, and allow only the females with whom they had copulated, to lay eggs inside the holes. The larval habits of *Mecistogaster modestus* have been well known. It has been suggested that the unusually long abdomen of the adult is functionally correlated with the need to place the eggs in or near the water contained at the base of the bromeliad leaf (Corbet, 1983). However, this explanation is not fully satisfying, because, as has been pointed out before, it does not account for extra long abdomen in males. Fincke (1984, 1992) has reported the female's behaviour in searching for treeholes in Panama, and the behaviour varies much with species.

What is the use of the long abdomen in the large odonatans? It seems that Machado and Martinez (1982) have solved the problem, at least for one treehole breeding Bolivian species, *Mecistogaster jocaste*. The female of this species hovers above a tree hole and makes jerky movements with the curved abdomen, then she throws individual eggs at the water surface in the direction of the shaded area underneath the roof of a hole. The abdomen never touches the water, and the yellow eggs, after drifting horizontally, remain floating. The female always oviposits unattended by the male. Egg throwing for *Mecistogaster* is different from egg-dropping in several genera. It is probable that the system is efficient because of the extended abdomen. To be able to throw the eggs inside holes, a long abdomen is more useful; the longer it is, the greater would be the velocity of the egg at the time of its ejection. Roughly, the main advantage is to introduce the eggs into water contained in a deep hole with a small opening, without taking any risk for the female itself. The oviposition procedure of other big damselflies is not well known. It is probable that if some of them throw their eggs, others drop them only when in flight. Many Zygoptera lay eggs in aquatic plants (peduncles, leaves, stems). The egg development is endophytic. A North American damselfly, *Enallagma hageni*, is one of the species, the females of which submerge themselves completely before inserting their eggs into plant tissues (Fincke, 1985; Preston-Mafham *et al.*, 1993). Probably *Megaloprepus coerulatus* does oviposition by egg-throwing, but that remains to be verified (Young, 1980, 1981).

Machado has used mathematics to study the kinetic energy imparted to the egg by the length of the abdomen, and to study the parabolic pathways taken by the egg towards the surface of water. It has been inferred that a damselfly has to aim straight, and that the giant Odonata are experts in ballistics. The longer the abdomen, the higher the velocity of the egg at the moment of ejection. It is likely that the African



— Fig. 27.1. *Mecistogaster jocaste* female, a Bolivian damselfly, throwing its eggs inside a treehole full of water (after Machado and Martinez, 1982).

megapodagrionid, *Coryphagrion grandis*, lays its eggs through a strong ejection and perhaps also the Australian species, *Podopteryx selysi*, and the neotropical, *Megaloprepus coerulatus*. All are treehole breeders. *P. selysi* with 90 mm wingspan is the largest damselfly of Australia. However, the biology varies so much that no generalisations may be made before many more studies have been done on their habits and ways of life.

Recent papers (Uhia and Cordero Rivera, 2005) have shown that mating process is not simple among Odonata, particularily among damselflies. In Odonata, males remove sperm during copulation from the spermatheca or the bursa copulatrix. Sperm competition and cryptic female choice are both involved. More attention should be devoted on egg laying or throwing, mostly in the tropics.

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— 28. **Forest on the back**

Some beetles (Coleoptera), chiefly weevils (Family Curculionidae), are known to carry literally a forest on their back, that is on the dorsal surfaces of the pronotum and the elytra. Such beetles are known from forests on high mountains of New Guinea. The forest on the insect back is made up of algae including blue-green algae, mosses, hepatica, fungi, lichens, and prothalli of small ferns; the forest is inhabited by minute animals, e.g. psocids, mites, nematodes and rotifers, and the forest denizens also include various Protozoa, diatoms, unicellular algae, and bacteria. Some Psocoptera feed occasionally on algae and fungi. It would be interesting to work out food chains among the components of the forest on the back. This discovery was made by J. L. Gressitt with his assistant J. Sedlacek (Gressitt *et al.*, 1965). They named the phenomenon epizoic symbiosis. Such gardens are found only from 1500 to 3600 m, and are unknown on big weevils with smooth elytra on the lowlands, even if they belong to the same genera. See also Jolivet (1986).

Among the insects in the mountains of New Guinea why such tiny forests are found mainly on weevils? Probably it is because of relatively long life of weevils (5 years or more), rather long for an adult insect. Besides, the elytra and the pronotum of the weevils present on their surface engravings and pits, in which a mucoid epidermal secretion collects. Mites and spores, disseminated by wind, get caught in these tiny collections of mucus, and other organisms follow them.

Some interesting facts about longevity of adult insects. According to Grassé (1949), the queen of termites may live for 80 years or more. Some queens of *Nasutitermes* may be, he wrote, 100 years old. But among beetles great adult longevity has been noted only in state of diapause; a dessicated diapausing beetle may survive for 10 years or more. Among arthropods only tardigrades may last for a longer period in a state of suspended animation or diapause. *Chrysolina* and other chrysomelids in the Arctic Circle may live quite long (about 6 years), entering into diapause repeatedly both in the larval as well as in the adult stage.

Another question in this context: Why are cases of forests on insect back known only from forests on mountains of New Guinea? They have not been reported from tropical forests on mountains elsewhere. There are high mountains, covered with forests, in Malaysia, Africa, Borneo and tropical America. These mountainous forests have high humidity and permanent fog or mist. Some of them have permanent glaciers. Thus climatically they are very similar to those in New Guinea. Why then do they not have forest carrying insects? One answer to this question is that such cases may be there in these forests, and they await discovery. The insect fauna of these forests have not yet been well investigated. It is also very difficult to see the lichens on dry insects in collections. The organisms on the body of an insect make a greyish crust almost invisible, when the insect has been dried and stored in museum collections. In New Guinea, this flora can be found commonly on the trunks of surrounding trees. These cryptogamous gardens have been discovered only on big apterous weevils with fused elytra, belonging to the subfamilies Leptopiinae, Brachyderinae, Cryptorhynchinae, Otiorrhynchinae and Baridinae and also on a species of *Drytops* (Colydiinae). Probably the gardens exist on the back of other beetles too, but only the Eastern side of New Guinea has been investigated by entomologists, and the higher summits are on the other side, that is on the Indonesian side or Irian Jaya, remaining to be explored. Gerson *et al.* (1977) mention also some other cases of simple epiphytic symbiosis on beetles and some other insects.

One of us (PJ), when in New Guinea, went to the top of Mount Kaindy, in Eastern New Guinea, near the tropical station of Wau, with J. L. Gressitt. The place harbours the tallest moss known. He collected some big weevils, a *Gymnopholus*, labelled on its back by Gressitt, as well as other weevils of the mountain, which after dissection showed a parasitic gregarine in its gut; this prorozoa is related to the one from a high central

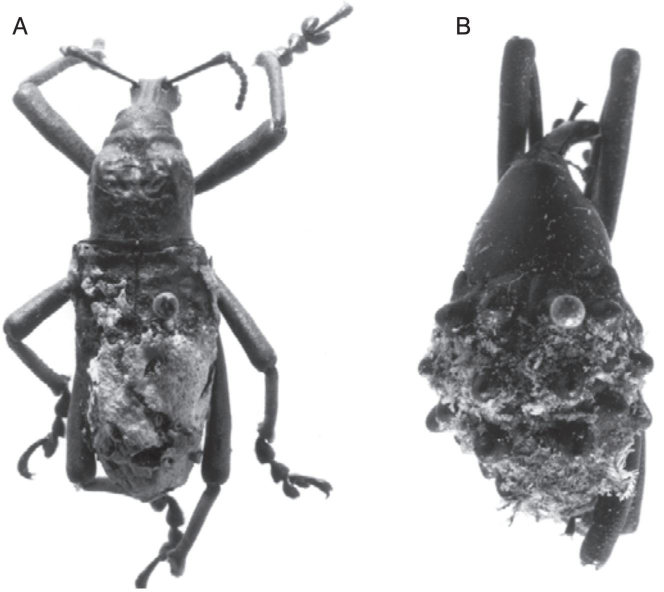
African mountain. No forests are known, however, on the back of beetles in Africa. PJ there, at 3,000 m in the Ruwenzori, found only galerucines as big beetles. All others, above that altitude, among plants like *Lobelia, Erica* or *Senecio*, were tiny specimens. Some middle sized weevils in the Panamean central chains have green algae on their integument, as also fresh water turtles and other aquatic reptiles, but no one shows the mixed presence of a number of organisms, which may be referred to as a forest. Some curculionids in Mt. Humboldt, New-Caledonia, look like covered with a lichen and algal crust. As for some weevils, in the neotropics, this lichen cover is only made of scales and is a case of homochromy with the surroundings.

It may be pointed out here that molluscs and turtles are known to carry a complex of organisms on their shell. Marine Turbellarian, *Convoluta roscoffensis*, is associated with algae. The giant molluscs of the genus *Tridacna* have algae on their gills. The gastropod *Elysia atroviridis* uses free chloroplasts from marine algae. Whales and marine iguanas may be covered with barnacles and vegetation. Fishes have algae infested gills. Fresh water *Hydra* has zoochlorellae in its body. Marine anemones and some sponges are with algal association. But they are all aquatic animals. Instances of terrestrial animals, carrying and transporting various organisms, with the exception of parasites, cyanobacteria, algae or fungi, on their body, are very rare. One rare instance is that of the South American sloths living on trees. Their fur lodges blue-green algae and some fungi, and also some pyralid moths. The algae give these dark animals a greyish-greenish colour, and thus the advantage of camouflage through homochromy with their surroundings. The adult moths seem to feed on the algae. They lay eggs on the sloth excreta, from which their caterpillars seem to derive their nourishment. Among terrestrial animals with vegetation, we may mention the giant Galapagos tortoises which carry lichens on their shell. These lichens on the female tortoise eventually get worn because of the friction during copulation. In the same way old New Guinean weevils loose their scales when getting old and also some part of their flora, mostly lichens, by rubbing against each other or against the leaves. Another case of vegetation on a vertebrate is the growing of bryophytes on the head of a Mexican lizard (Gradstein and Equihua, 1995). A Chinese geometrid moth is also known to lodge algae on its body, also some grasshoppers and an Australian spider. In southern

Brazil, in the Cardoso island, in the rain forest, there were found cyanobacteria and two liverwort species (Hepaticae) growing epizoically on the dorsal scute of the harvestman, *Neosadocus,* near *variabilis* (Machado and Vital, 2001).

It is likely that many insects host microscopic flora/fauna on their body, but we have failed to detect them. Generally, insect specimens are studied in a dry preserved condition, and in this condition it is very difficult to detect and make out microscopic organisms, if they were there on their body.

Do the New Guinean weevils get any advantage from this forest on its back? Most probably the advantage is of camouflage through homochromy with the surrounding foliage and mosses. It has been noted by naturalists that the forest carrying weevils are nontoxic and quite edible to predators. The only defensive device with the insect seems to be the little forest carried on its back. The weevils show only small mobility. The relative sedentary habit also appears to be a part of their defensive strategy. The predators in those altitudes are birds of paradise, and several marsupials, like *Antechinus*, *Petaurus* and *Eudromicia*. Really, the weevils are



— Fig. 28.1. A-B: Two giant New-Guinean weevils carrying lichens, algae, and mosses over their elytra (after Jolivet, 1986). Wau, New Guinea.

difficult to see. PJ's students detected some during mountain climbing, which PJ himself did not even see.

In Ohio, in 1976, a neuropteran larva (*Nodina pavida*), which is a chrysopid, was discovered carrying an accumulation of cryptogamic vegetation somewhat comparable to that on the back of the New Guinean weevils (Skorepa and Sharp, 1971). It was composed of lichen soredia and thalli, pieces of bark, parts of moss gametophytes, pollen grains, fungus spores and other debris from plants and insects. This too is a case of symbiosis, because the lichens are dispersed by the insect. There is also a larva of a Colombian lacewing, a *Chrysopa*, covered by soredia of several lichens. Thus the forest carrying phenomenon does not seem confined to the New Guinean weevils. An analogous situation is in nymphs of some reduviid bugs and some beetle larvae carrying a trash on their body for purpose of camouflage. The trash consists of dead insects, cast skins, feces and other debris.

It appears that chill, constant high humidity in the environment, longevity of the insect and its relative immobility and big size are prerequisites for the insect to have a flora on its body. All the terrestrial cases of animals carrying flora are known to occur in moist situations.

A recent study on two algal symbionts, found in the sea anemone *Anthopleura elegantissima* (Lewis and Muller-Parker, 2004), suggests the directions in which the New Guinean weevil tiny forests may be investigated with likelihood of getting interesting and significant results.

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— 29. **Scorpion beetles and lantern beetles**

Everybody is familiar with the beetles or scarabs. They are so many that the great biologist Haldane said once that God, when he created the world, showed "an inordinate fondness for beetles". He created so many of them. There are about 600,000 described species, but probably there are 2 to 3 million species still alive, and mostly undescribed. Majority of unrecorded ones are among staphylinids, weevils, leaf-beetles, and several small genera, some not measuring more than 1 mm, others, the better known ones through collections and merchandises, measure several millimeters, centimetres, even 20 cm or more. Whether small or large, all of them need to be protected from extinction, including described and undescribed fauna. In the Permian, and later on after the Trias, probably they were hundreds of thousands, and probably non-existent at present. They are *beetles* in English, *Käfer* in German, *biller* in Danish, and most of the languages have given them a common name, except in France. In France beetles are referred to as scarabees, carabes, bousiers, crache-sangs, taupins, coccinelles etc., there being no common name for the entire group of beetles. They are called « bilulus » in Zaire and « binatang » in Papua-New Guinea. In Zaire, during his youth, PJ got a nickname: "bwana biloulou", "Mister beetle", a memorable title. He was also Mr. Binatang in New Guinea, as Gressitt was, and all the beetle men there. Papuans and Congolese were good observers, and they always gave a nickname to the newcomers in their kingdom.

As for all insects, their body is wrapped in a hard shell, made of chitin, but in the beetles this shell is particularily strong and thick. Beetles are chiefly characterized by the first pair of wings, which are very tough and thick;

they are called elytra or wing covers, as they cover the membranous hind wings, carefully folded below the elytra in repose. Special rugosities on the wings and on the underside of the elytra help the folding process and keep the folded wings in place. Generally these insects are totally inoffensive to man, although some of them are provided with sharp and acute spines, which may prick the catcher.

Some beetles are poisonous and secrete a strong irritant, e.g. cantharidin by meloids or oedemerids. Some others are naturally poisonous due to presence of strong poisons in their body, like Melyridae (*Choresine* spp.). In New Guinea, they render birds or frogs, feeding on them, deadly poisonous. Batrachotoxins are neurotoxic steroidal alkaloids first isolated from a Colombian poison-dart frog (*Phyllobates*) and later found also in certain passerine birds of New Guinea. These frogs and birds do not produce the toxins *de novo.* Melyrids are also suspected in Colombia to be the source of the batrachotoxins in these vertebrates (Dumbacher *et al.*, 2004). Poisonous frogs, birds and beetles have bright warning colours: orange and blue elytra in *Choresine*, bright orange belly in the birds (*Pitohui* and *Ifrita*).

Generally longhorned beetles (Family Cerambycidae), when they are grabbed, extend their antennae, which are sensitive and delicate receptor organs. Some neotropical cerambycids of the tribe Anisocerini and subfamily Lamiinae violently strike your hand with their antennae, if you seize them, and inflict serious wounds, which get infected rapidly in the tropics. They throw their antennae backward and upward, with a strong jerk, and then strike with the scorpion-like terminal joint. In fact the apical antennal segment in those beetles looks like a recurved scorpion sting. Fabricius gave this beetle the name *Lamia scorpio*. Common name for the beetle is scorpion beetle. All scorpion beetles belong to the subfamily Lamiinae of the Family Cerambycidae. The scorpion-beetles are big, nearly 3 cm long. They are crepuscular or nocturnal in their activity, clinging to rough bark covered logs during the day. They have rugose forms, and mostly have white scales over their body. They mimic lichens on the bark of the trees and are difficult to locate (Alvaranga Julio and Monné, 2001).

Scorpion beetles (Tribe Anisocerini, Subfamily Lamiinae) belong to several genera, including *Onychocerus* and *Hoplitocerus*, the former name meaning "horn with nails" and the latter "provided with horns". That the swollen terminal joint of the feeler encloses a poison gland has been suspected. But Smith (1884) has doubted it, and Costa-Lima (1955) has denied it. But on basis of a study of sections, Wandolleck (1896) inferred that there was such a gland. Zikan (in Costa Lima, *loc. cit.*) considered the antennae as venomous, as well as Gahan (1899). For Kirby (in Wandolleck, 1896), the ending claw was used only to lay hold of surfaces. More careful studies are needed to confirm presence of a gland in the terminal antennal joint. It is really strange how books on beetles (Crowson, 1981; Paulian, 1988) and all encyclopedia of entomology have totally ignored these peculiar beetles. Miguel Monné reported (1982, pers. com.) that he had been many times attacked by scorpion beetles, around Rio-de-Janeiro, by using their antennae, when normally beetles use their mandibles or legs for inflicting wounds. The feeler wounds look like mosquito bites and they show gradual reddening. Hequet (1996) mentions and figures the *Onychocerus* in her book on Guyana longhorn bettles.

Among the Anisocerini, some, like *Onychocerus scorpio*, *O. concentricus*, *O. aculeicornis*, *O. albitarsis*, *O. crassus*, *Cyclopeplus batesi*, *C. batesi*, *Hoplistocerus dives*, *H. dichrous*, *H. gemmatus* have a more or less well defined scorpion sting-like ending antennae. Some more, among the many species found in the Neotropics, may also have such antennae, but other species of the same genera or of different genera, like *Taurolema*, *Xylotribus, Acanthotritus,* do not show sting-carrying feelers.

Many other beetles have long and sharp spines, but situated elsewhere and not on the terminal sting-like feeler joint. Femoral spines of certain species form efficient defensive weapons, as well as the thoracic spines of certain beetles. Femoral spines of some big moths, cephalic and thoracic horns of scarabaeids among beetles, and on many other organs have defensive value. Spines and pointed structures are also known on the antennae of some male Hymenoptera, but only in some Anisocerini, both sexes have the scorpion-like ending antennae.

Chemical defense exists among many cerambycid beetles. Toluene and o-cresol have been identified as the main volatile components in the defensive secretions of two species of Australian longhorn beetles, *Stenocentrus ostricilla* and *Syllitus grammicus* (Moore and Brown, 1971). The chemicals are produced in paired mandibular glands and emitted through pores on each side of the frons, via specialized frontal organs. So, it would not be surprising if antennae of some Anisocerini dispense chemical irritants.

After the scorpion-beetles let us have a quick look at the lantern-beetles, that is those which emanate light, e.g. glowworms (Lampyridae) and some click beetles (Elateridae). Oxygen, an enzyme called luciferase, and a compound called luciferin are involved in a complex chemical reaction to produce light, and adenosine triphosphate (ATP) provides energy for the reaction. The colour of the light produced may vary from red, yellow, blue, green to violet. The light thus produced is sometimes referred to as cold light, because of minimum heat production in the process. Fireflies convert 98% of the energy produced into light. Man is far away from achieving this result. With his bulbs and neon lights he transforms a much smaller percentage of energy into light, and the rest is lost as heat. Members of four or five beetle families are light producing. In *Phengodes* (Phengodidae), the photophores or light emanating organs of the anterior part of the body give out red light and the abdominal organs produce green. Bioluminescence is best known among fireflies, which are toxic, and that their luminosity has a warning (aposematic) function is a possible explanation (Lloyd and Gentry, in Resh and Cardé, 2003). Light in fireflies like *Photinus* spp. is also a mating signal for the males. The code varies according to the species. Some predacious firefly females of the genus *Photuris* mimic the flash response of other species, attract males of those species and eat them. There is also a case of luminosity under water: the larvae of the firefly, *Luciola,* in India, Japan and Indonesia; they emit a blue light. In the Indo-Australian region, the males of *Pteroptyx*, which is a lampyrid, on trees, emit synchronized signals each half second. The exact meaning of this firework and the mechanism of this synchronisation have not been understood. Maybe it is for giving equal mating chance to all the females involved.

In fields of Central America, bright bi-coloured elaterids (*Pyrophorus*) fly very fast between the trees. The twin spots on their thorax produce a glow of such an intensity that there appears a long, golden red path of light during the flight (Klausnitzer, 1981). One of us (PJ) failed very often to capture them with a net in Nicaragua and Panama. It has luminous organs at the posterior angles of the pronotum and at the base of the abdomen.

These organs emit simultaneously red and yellow-green light. The *Pyrophorus* larvae are also luminescent and feed on scarab larvae. So strong is their luminescence that Humboldt is said to make with them a reading lamp. Missionaries during colonial times, as we are told, read their breviary with the help of the elaterids inside a glass bottle. Some Staphylinidae and Phengodidae are also luminous, even spiders in Burma. Many insects show light signals, often to capture preys in their webs, like *Arachnocampa luminosa* (Diptera, Family Mycetophilidae) in New Zealand caves and several Collembola. The ceiling of the caves in Waitomo, near Aukland, with millions of glowworms and their prey capturing threads, looks like a star-studded night sky. Several other Mycetophilidae are luminous in Australia and America. Light production, among beetles, which is not polarized and produces chlorophyllian assimilation, serves several functions: sex attraction, lighting of the soil when the insects land, trapping other insects, and warning about toxicity. However, there are some disadvantages too, like an easy location by predators such as bats.

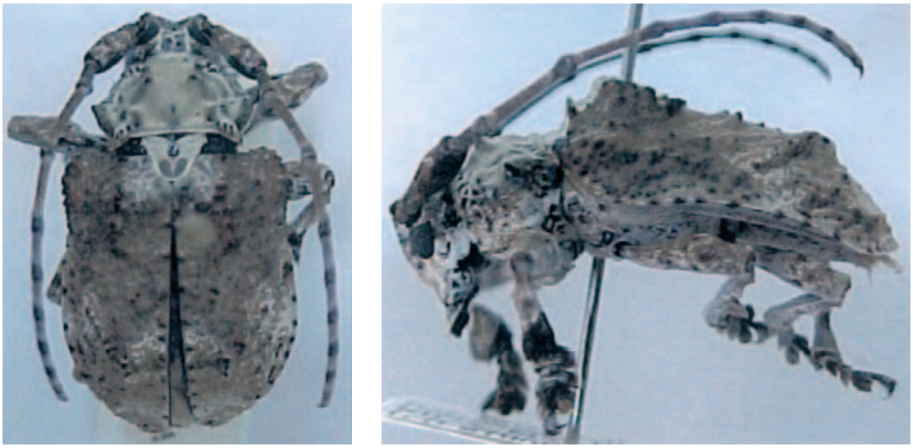
It is difficult to explain why some longhorn beetles (Cerambycidae), having no close relationships with lampyrids, mimick the fireflies. They copy their external appearance and possess under the belly several segments clothed with whitish pubescence, in pure imitation of the luminous organ of the Lampyridae. Of course they are not real photophores; the resemblance is only in colouration, appearance and location of the hairy areas. These beetles have been given suggestive names, *Alampyris*. *Alampyris photinoides*, *A. planipennis*, *A. mimetica* are typical members of the genus. Early in the last century Bates mentioned their similarity with fireflies. Some *Alampyris* (*A. nigra*, etc.), however do not show the pseudo-luminous spots. *Alampyris* is a Lamiinae. Many species of *Alampyris* are known from Mexico, Guatemala, Brasil, etc. Some species of *Alampyris*, like *A. planipennis*, have two yellow-green spots under the abdomen (segments 3-4), made of scales. It possible that they shine in ultra-violet radiation and be perceived radiating by potential predators.

Now there is a question. What is the reason of this similarity with lampyrids and why the copy of their photophore? The copy is nearly perfect. What is the use of these pseudo-luminous organs? Those cerambycids, of which the biology is a little known, seem entirely diurnal and the lampyrids are nocturnal. Why copy a nocturnal species, which certainly are very toxic? If they are active also during the night, this aspect could be a batesian protection against predators. They could this way copy the toxic and well protected lampyrids. Also, if the spot is shown in UV during the day, that could give the explanation. The Indo-Australian *Pteroptyx* offer extraordinary male nocturnal ballets, but no mimetic cerambycid is known there. Why is this phenomenon localized to Brazil and the countries around?

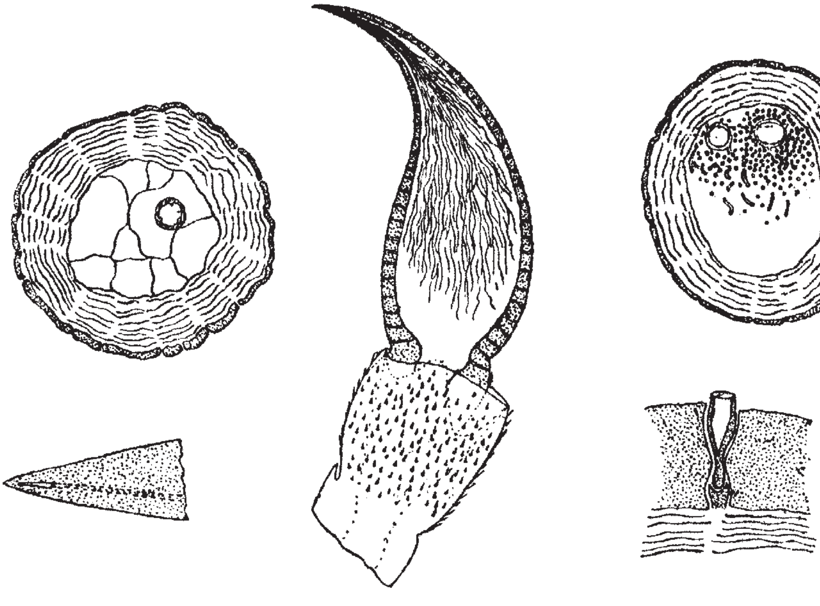
We have a nearly perfect case of mimicry among the Indo-Malaysian butterfly, *Kallima*, imitating a folded leaf, with false veins, false caterpillar bites, false fungus spots, and even a false petiole formed by the base of the hind wings, when resting on a branch. In that case the perfection could be understood. But why do S. American cerambycids go that far?

The uniform morphology of the photophores of the lampyrids has been inferred on the basis of their shape and their position. It is a possibility that these luminous organs act as do the eye-spot of so many Lepidoptera. These spots of butterflies suggest the presence of head there. It is well known that among certain butterflies, like the *Caligo*, in Brazil, these spots are protective against birds. The butterfly turns over on its back, when it is about to be attacked by an approaching bird. The bird is surprised and stops a few seconds. In many cases the bird attacks the false head, suggested by the eye-spots, and the butterfly flies away with a small bit of wings missing. One often meets a butterfly with a bit of its hind wing torn and lost.

The explanation of the eye-spot is valid for the butterflies. Perhaps it is true also for the lampyrids and for the pseudo-lampyrids. But to have the end of the abdomen bitten away is not good for survival. Or as, said Rabaud, there is no explanation in the phenomenon and that it is pure chance, but as said one scientist “a non-adaptative character is a character not properly understood”. We hope someone will understand and explain one day the *Alampyris* mystery.



— Fig. 29.1-29.2. *Onychocerus crassus* (Cerambycidae). Costa-Rica. The antenna is Showing, at the end, the scorpion tail. Among other species, the "tail" is more realistic (photo Jean-Michel Maes).



— Fig. 29.3. *Onychocerus albitarsis* from Brazil, showing in cross-section, longitudinally and transversally the "scorpion-tail" organ. The supposed venom orifices are said to be visible (after Wandolleck, 1896).

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— 30. **Timarcha, a blood spitting magistrate**

Timarcha is a leaf beetle (Chrysomelidae), doubtfully placed under the subfamily Chrysomelinae. In view of its peculiar and primitive features, some chrysomelidologists prefer to place in a subfamily of its own, Timarchinae.

Why is this large black beetle given the name *Timarcha*? The name is in view of its shape, its deliberate and noble walk, and its majestic bearing. *Timarcha* is generally black, sometimes bluish or cupreous, and a very archaic beetle, with very primitive characters, such as an old style aedeagus and tegmen, a very simple and primitive nervous system, besides some apomorphic characters (i.e. of recent origin), like fused elytra. It is totally apterous, and this character seems ancient, as its pupa is also without developing wings; very few beetles, as *Meloe* spp., share that characteristic. Loss of wings, early in its evolutionary history, has given it features like a small metasternum, loss of wing muscles and nerves, and other related changes.

Once in Greece, in Athens, on the side of the Acropolis, PJ saw in a café, a painting representing a man followed by a lot of kids. He asked what the meaning of the picture was, and he learnt that it was an early last century painting, showing a man, who used to walk two steps forward and one step behind. The boys, following him, used to imitate his way of walking. *Timarcha* is a beetle, not walking like the gentleman of Athens, but slowly, peacefully, majestically, and constantly looking around as if searching for something of value.

Timarque, in Greek *Timarchos*, was, as is said, an Athenian politician, from the fourth century BC. In 347 BC he tried to stop the selling of arms to Philippos, the father of Alexander the Great, and he repaired the Athens wall. Pushed by Demosthene, he became the main accuser of Eschyne, during the embassy affairs in 346 BC. Unfortunately, his dissolute morals, even at that time, offered to Eschyne a good way to counter attack. Due to the seriousness of the revelations, Demosthene could not defend Timarque, who was then deprived of his civilian and political rights. After this trial, Timarque is said to have commited suicide. It is also said that "timarchia" is used to characterize a government founded on the love of honours. In Roma, later on, Timarchia became the name of the Censure or Judiciary. It is said by the etymologists that the slow and majestic walking of the *Timarcha* beetles reminded Latreille, the French entomologist, of the nobility of the Athenian judges, and thus he coined the generic name for the beetle.

The genus *Timarcha* comprises four subgenera, two of them not much different, *Timarcha* s. str. and *Timarchostoma*, and two others well separated: *Metallotimarcha* and *Americanotimarcha*. There are around 125 species and 30 subspecies, spread in eastern North America and around the Mediterranean basin (Jolivet, in Capinera, 2004). *Timarcha* species are present in central Anatolia, but they are missing in Syria, Lebanon, Israel, and Egypt where they have been probably eradicated during the Pleistocene desertification. They are missing also in Sinai, and, in Lybia; they survive along the coast on the western side and in Cyrenaica. In Lybia they occur also in certain oases, 80 km south. *Timarcha* did not survive in Hoggar, in the middle of Sahara, where some species of *Chrysolina* still live. When Sahara was green, not more than 5,000 years ago, probably *Timarcha*'s distribution was much wider than today, but it never crossed totally the desert since it did not reach Mauritania and Senegal in the west, extreme south of Algeria, and south of Tunisia in the east. Some Moroccan species were shared with Spain once, in the Betico-Riffan massif, before the opening of Gibraltar strait. Western islands of the Mediterranean were, most of them, colonized, except for instance Iviça and Malta, and *Timarcha* never reached the eastern islands: Creta, Corfu, Rhodos and Cyprus. Iviça seems to have a different geological history than the rest of the Baleares. Malta must have had its *Timarcha*, but they were probably lost with the intense urbanization, dating from the Greeks and the Romans.

Fossil *Timarcha*, before the Peistocene, are unknown, but *Timarcha* is a very ancient genus, probably related to the Upper Jurassic *Timarchopsis*, a fossil from Siberia. It is very probable that the genus originated in Central Asia, where it could have been eradicated by the glaciations. From there it migrated to Europe, where it adapted to cold in Europe, due to a complex cycle of egg and adult diapauses, and to North Africa, where it became a steppic species or it adapted to local mountains. It also migrated to North America, probably through North-Atlantis, but a trans-Beringhian migration has also been seriously envisaged (Poinar and Jolivet, 2004; Poinar *et al.*, 2002). Strange enough, for supporting the hypothesis, no traces of the beetle are there in Japan, in Russian mountains, like the Altai, or in southern China. The subgenus *Metallotimarcha* has adapted to mountain life, but, as are the American species, it is entirely nocturnal. Several species in Morocco seem to be crepuscular, a way to escape the heat or the luminosity in the Atlas mountains. The steppic species remain totally diurnal. It is a fact that in America, as in Europe, the northern distribution of *Timarcha* coincides with the meridional extension of the quaternary glaciers: south of Baltic states, Denmark, Southern Scotland, island of Vancouver, in Canada, Montana in USA.

Apterism and fused elytra, with a subelytral cavity below, is a form of protection against heat and water loss in steppic areas, and also a protection against the cold in middle Europe. These modifications reduce transpiration and compensate the loss of liquid through reflex bleeding. *Timarcha* ejects actual blood through prebuccal openings and femoral articulations, and was nicknamed the bloody nose beetle in England. Its blood is very toxic, being rich in anthraquinones, and, as a result, practically there are no vertebrate predators, birds or lizards. Their colour, generally black, is aposematic and contrast with the green of the food-plants. Let us note that the nocturnal species have lost partly (*Metallotimarcha*) or totally (*Americanotimarcha*) the reflex bleeding, and even the fusion between the two elytra becomes rather loose. Protection against big predators seems unnecessary during the night. Normally *Timarcha* species are totally black, but a Balearic species, *T. balearica*, several Spanish ones, show a bluish color, and the nocturnal *Metallotimarcha* spp. are cupreous, a colour possibly detected during night by potential predators like birds and others, which learn to avoid them. It seems that in North Africa, where *Timarcha* and *Pimelia* (Tenebrionidae) cohabit, there is a Müllerian mimicry between both, since *Pimelia* regurgitates liquid when disturbed.

Timarcha has no predators, and also few parasites. There are, however, several parasitoids (Hymenoptera chiefly) and intestinal commensals (Gregarines) and phoretic mites under the elytra, in the subelytral cavity (Canestriniidae).

Timarcha feed mostly in Europe, on Rubiaceae (*Galium*, *Rubia*, *Crucianella*, *Asperula*, *Sherardia*) and in North Africa on Rubiaceae and Plantaginaceae (*Plantago*). However, *Plantago* selection starts in Southern Europe, with several other plant families, mostly in Spain and North Africa, e.g. *Veronica* (Scrophulariaceae), *Scabiosa*, *Knautia* (Dipsacaceae), *Launea* (Asteraceae), *Carrichtera*, *Iberis*, *Alyssum* (Brassicaceae). *Metallotimarcha* species feed on *Vaccinium* (Ericaceae) and *Asperula* (Rubiaceae) and *Americanotimarcha* species feed on *Rosa*, *Rubus* and *Fragaria* (Rosaceae) and on *Vaccinium*, *Gaultheria* and *Rhododendron* (Ericaceae). Perhaps it is correct to regard *Vaccinium* as its original food-plant, as this plant is widely distributed in the Holarctis.

Size of *Timarcha* varies from 5 mm (*T. cerdo*) to 23 mm (*T. tangeriana*). The chromosomal meioformula varies slightly among its species, but remains in average as 2n = 12 in Europe and 2n = 44 in America.

Finally the bloody nose beetle remains rather enigmatic, and, more or less, a living fossil among the leaf-beetles. It varies enormously in the Pyrenees and along the Moroccan coast. It seems to be still in continued evolution, probably due to some interbreeding between the races. Otherwise, there is no crossing between the species, or, if that happens accidentally, it does not produce viable offspring.

Extinction of this beetle is fast approaching; it is being caused by urbanization, fragmentation of the habitat, use of insecticides and herbicides, general pollution and many other reasons. Being wingless, the beetle cannot recolonize new habitats.

There is a folkloric aspect of the bloody-nosed beetle. Kids in western Europe used to play with them frequently as with coccinellids. They were abundant everywhere during PJ's youth, but they are no more common now, except perhaps along the dunes, on halophytic plants. One wonders how long they are going to survive. When we build a golf or a racing course, a bungalow, they just disappear in that area forever. It is a Jurassic survivor which is vanishing away and needs protection.

— Fig. 30.1. *Timarcha tenebricosa* Fabricius, male on *Galium verum* L. (Rubiaceae). Normandy.

— Fig. 30.2. *Timarcha tenebricosa* larva, 3rd instar on *Knautia arvensis* Coult. (Dipsacaceae). Aveyron, 850 m (photos Jolivet).

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— 31. Rotation of the male copulatory organ in insects and biased chirality

In many insects the male copulatory or the intromittent organ or the aedeagus undergoes a rotation around its longitudinal axis through 180 degrees (in some flies or Diptera through 360 degrees) during development. It is believed that this change of orientation of the organ facilitates a particular mode of copulation, the riding mode, in which the male climbs over the back of the female, and then brings about intromission (Jeannel, 1955). The riding mode is believed to be the more advanced mode, and end-to-end copulation, in which the male and the female, resting on the same surface, face opposite directions, and bring their abdominal ends together for intromission, is believed to have preceded the riding mode in insect evolution.

This rotation is known in Phytophaga (=Cerambycidae + Chrysomelidae + Bruchidae), Staphylinidae and Silphidae among Coleoptera or beetles (Jeannel, 1955; Verma, 1994). Hypopygium inversum and hypopygium circumversum of lower and higher Diptera involve rotation of the copulatory apparatus through 180 degrees and 360 degrees respectively (Emden, 1951).

There is an important difference between the rotation of the aedeagus in Coleoptera and that in Diptera. In beetles the rotation is due to asymmetric development of a pair of corresponding muscles, connected with the aedeagal apparatus. These muscles arise from the ventral body wall (or a tubular invaginated part of it), and find attachment on the dorsal face of the developing copulatory tube. During development one of the muscles degenerates, while the surviving one exerts a one sided pull, making the copulatory organ rotate through 180 degrees. In Diptera rotation of the copulatory apparatus is due to some terminal abdominal segments rotating through varying degree on preceding segments, so that the enclosed aedeagal apparatus is made to rotate through 180 or 360 degrees. In beetles rotation of the aedeagus occurs without affecting the original symmetry of terminal abdominal segments.

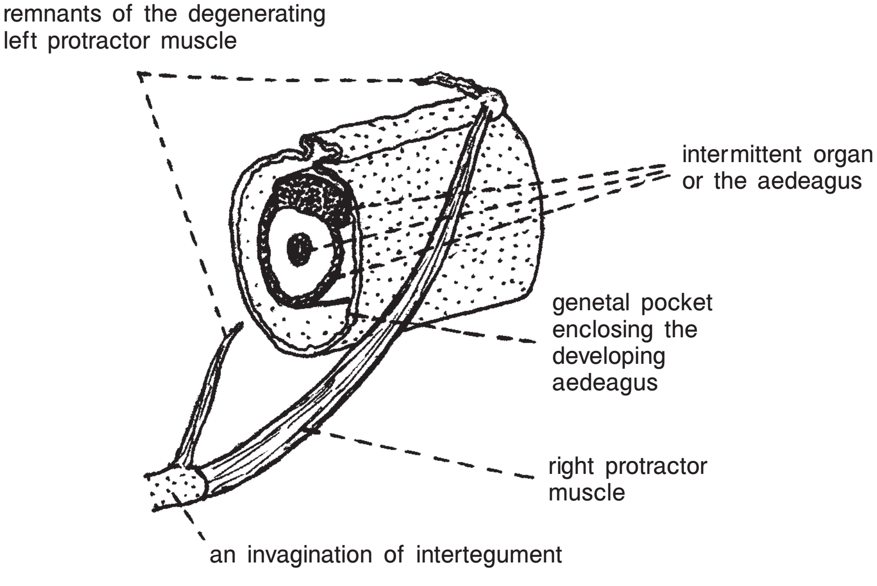
Among Coleoptera the aedeagal rotation is clockwise, when seen from behind, and only rarely anticlockwise. Interestingly in Diptera too the rotation is mostly clockwise, though the mechanism of rotation is very different from that in beetles. There is enough reason to believe that rotation of the aedeagus has evolved independently in Coleoptera and Diptera, but clear bias for clockwise rotation is found in both the insect groups.

If an object or a phenomenon is identical with its mirror image, it is called chiral, or it is described as showing chirality. The symmetry of human body is chiral, as in our mirror image the right hand appears left. It has been realized that most objects and phenomena in the universe show chirality (Hegstrom *et al.*, 1990). One surprising situation with chirality is that generally it is associated with bias in favour of one variant or the other. Human individuals may be right handed or left handed, but lefties are comparatively rare, though a left handed person does not have any intrinsic disadvantage. In this instance, there is an obvious bias in favour of the right handedness. Gastropods present clockwise coiling in the shell, if we look at the shell with its apex towards us; such shells are called dextral. Some shells may be sinistral, as they show anticlockwise coiling. In any gastropod species dextral shells are much more common than sinistral ones. Thus in this case chirality shows bias in favour of dextrality. Most plants, which helically coil round a support, for example *Convolvulus arvensis*, present generally a right handed spiral. A recent example is found with the study of New Caledonian crows, the ones which manufacture tools from *Pandanus* leaves (*Corvus moneduloides*). Weir *et al.* (2004) studied laterality of tool use in captive birds: five were left lateralized and five were right-lateralized. All subjects show near-exclusive individual laterality. The predominance of right-handedness in humans is not general, but all, including non-human primates, show strong individul laterization for tool use.

Bias in chirality is not confined to anatomy; it is even at the molecular and atomic levels. Amino acids, which polymerize to form proteins, present chirality in their molecular structure, but for glycine. They may be in dextro- or levo- form (D- or L-), which rotate the plane of polarization of a polarized beam of light in clockwise and anticlockwise directions respectively. Surprisingly, in natural proteins all amino acids are with the L-form; only very rarely D-amino acid molecules may be included. DNA and RNA molecules almost always present right handed helixes. Beta rays, produced in radioactive decay, also show biased chirality; they include mostly left handed electrons.

It is not understood whether and how biased chirality at the atomic or molecular level is related to lack of parity in chirality in anatomy.

As has been pointed out earlier, rotation of the copulatory organ in insects is a phenomenon with biased chirality, bias in favour of clockwise rotation. About the mechanism of this phenomenon, it has been mentioned that in beetles the rotation occurs due to one member of a pair



— Fig. 31.1. Developing male genitalia of a leaf-beetle. The genitalia have been cut across, and have been looked at from behind.

of corresponding muscles degenerating, and the surviving muscle making the organ rotate. Usually it is the left member of the pair that degenerates; as a result the rotation is clockwise in most cases. The two muscles in the pair are very similar; they are laterally corresponding and homologous. Then how is it that generally it is the left member of the pair which undergoes degenration? One of us (KKV), with his coworkers, through experimentation, have inferred that, if there is normal release of the juvenile hormone (JH) after the last moult, it is followed by degeneration of the left muscle, and consequent clockwise rotation of the copulatory organ, while a delayed release of the hormone seemingly leads to degeneration of the right muscle and anticlockwise rotation. The two muscles in the pair are identical in appearance. Why are they differently affected by the time of release of JH after the imaginal moult? Are the two muscles differently programmed for cell death? Is the biased chirality at the atomic/molecular level in some way responsible for this differential programming? These questions remain wholly unanswered, and the biased chirality in rotation of the male copulatory organ remains an unsolved puzzle.

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— 32. **Carnivorous Plants – Insect enemies or friends?**

On the planet earth around 530 plants are carnivorous, i.e. specially adapted to capture and digest insects and other invertebrates. They only represent almost 0.2 % of the total of 250,000 flowering plants, so far described. It is a small portion, but this adaptation to carnivorous life has permitted those plants to colonize soils poor in organic matter, often peat bogs. Such plants occur at all latitudes. Certain carnivorous plants are epiphytic, that is growing on other plants, like *Nepenthes*, and others live in mountains (*Heliamphora*, *Brocchinia*). We may mention here also carnivorous fungi, but they only catch small nematodes and not insects. Myrmecophilous or ant loving plants are in about the same number, but their number is still increasing, with new discoveries, while the carnivorous ones seem to have reached more or less their final number. Botanists have tried to find relationship between all the real carnivorous plants. Recent phylogenetic analyses of nucleotide sequences indicate that stereotyped trap forms, leading to carnivorous habit, have evolved independently in different lineages of angiosperms (Albert *et al*., 1992).

Most of such plants show strange adaptations for insect capture and digestion (bright colours, nectar glands, digestive glands). They all live in selected biotopes, as mentioned earlier. *Heliamphora* species are found only on Venezuela mountains (the tepuys), as the protocarnivorous *Brocchinia,* and the truly carnivorous *Dionaea muscipula,* “one of the most wonderful plants in the world” (Darwin), is restricted to a small endangered area, wetland planted with pine trees, between North and South Carolina in the USA. Droseraceae family contains, however, also two ubiquitous genera, *Drosera* and *Utricularia*. The rapid closure of the Venus flytrap (*Dionaea muscipula*) leaf in about 100 ms is one of the fastest movements in the plant kingdom (Forterre *et al.*, 2005). The fast closure of the trap results from a snap-buckling instability controlled by the plant.

The carnivorous aspect of those plants is not at all exaggerated, and we know cases of gluttony. When these plants rot, the plant stomach digests itself by an excess secretion of pepsins. *Genlisea,* an aquatic plant, is a real living stomach in itself, very sophisticated, with only an anus missing, reducing similarity with our digestive system. It is the eeltrap of Darwin.

Carnivorous plants not only attract insects to eat them, but also to pollinate their flowers. In the latter case evidently they don't catch them. This is the case of a certain species of *Nepenthes* from Borneo, of which the flowers are pollinated by insects, and it maintains ants in their hollow petioles. The ants feed with impunity on the plant's extrafloral nectaries. The plant captures insects through their pitchers, but spares ants and the pollinating insects. It is a rare case of carnivory coupled with myrmecophily. This *Nepenthes bicalcarata* has been recently studied by an Australian team, after the old researches by Beccari in 1884 (Jolivet, 1887; Hölldobler and Wilson, 1990). The Australians confirmed the old observations. In *Nepenthes,* the ant guests are protected by their behaviour and by their physical adaptations to the leaf trap and the surrounding slippery mucus. Several insects, like mosquitoes breeding inside the pitchers of carnivorous plants, are resistant to plant enzymes, particularly when the contents are diluted. Spiders and other predators fish with impunity the preys of *Paepelanthus bromeloides* (Eriocaulaceae), a protocarnivorous plant, in Serra do Cipo, Brazil. Several predators, as some Hemiptera, live on the leaves of *Roridula*, among the glutinous hairs, without any harm. The digestive urns become diluted rapidly, when they open, and they quickly turn into phytotelmata, as in *Nepenthes* and other pitcher plants. Predators of the preys, caught by carnivorous plants are very diverse, from spiders to bugs and even beetles, and there are also slugs in Spain for one species of *Pinguicula* (Zamora and Gomez, 1996). Kleptoparasitic (or stealing of the preys) behaviour is risk-free for the slugs in most carnivorous plants, because they are able to crawl on the leaves without being trapped. Recent researches on the trapping system among pitcher plants reveal a very sophisticated mechanism to attract preys and to induce the slipping of the prey.

Until recently carnivorous plants have been considered generally as insect killers, with only one objective, namely to improve their nitrogen supply, as they get a meagre natural diet in a poor soil. Now some of them are seen also as users of insects for pollination, offering, as a reward, the flower nectar.

Recently some new theories have been proposed (Juniper, Robins and Joel, 1989), mostly for pitcher plants, Sarraceniaceae and Bromeliaceae in America, Nepenthaceae in tropical Asia, the Seychelles and Madagascar, and Cephalotaceae in Australia, and some kind of mutualism between these plants and insects has been suggested. All are passive traps.

This theory could eventually be extended to other groups of carnivorous plants, but not to active traps, which actively catch their victims, while very few escape. Let us remind here that active traps are the ones as *Drosera, Dionaea,* which catch themselves the preys with their glutinous hairs or closing leaves, and passive traps are the ones such as pitchers plants which receive the preys which fall down by themselves.

Pitcher plants according to this theory seem to have developed attractive and efficient traps similar to those of many flowers to attract pollinators. Surely, insects do not visit those plants by mistake, and those plants do not resemble other flowers and are not able to attract the same insects. Also, the nectar from their pitchers, a real reward, is provided to insects visiting those plants. Of course, we cannot say that those traps do not resemble grossly the bright flowers of noncarnivorous plants, but they do not exactly copy any one of the latter in particular. They are only traps producing a sweet smell for their prospective preys.

On comparing, in the book on carnivorous plants (Jolivet, 1987), ant plants (myrmecophilic) and carnivorous plants, PJ referred to the first relationship, that is in myrmecophily, as mutualism and the second as antagonism. Now, Joel (1988) suggests that carnivorous plants are also mutualists, at least the pitcher plants. He assumes that their relationships with the insect communities in their surroundings are not deceptive. According to him the insects benefit from the nectar, which is provided by the pitchers and which is nutritive and valuable in areas where other sources of nectar are rare, even absent. At the same time, the insects pay the plants thanks by offering a part of their population as prey to those plants growing on soils deficient in organic supply.

This opinion has been adopted in the book by Juniper, Robins and Joel (1989). The correctness of this view may be doubted, but when we observe attentively a pitcher plant, we can see that, after catching some prey, few insects are trapped, and many insects feed on nectar and fly away without being captured. Thus, at the insect population level, there seems to be an effective exchange of benefit between plants and insects.

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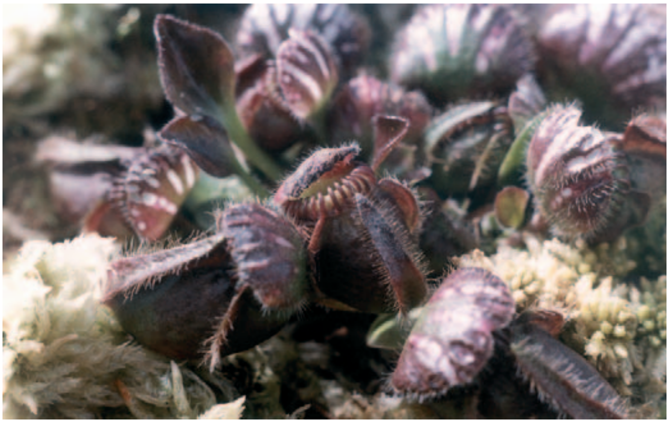


— Fig. 32.1. *Cephalotus follicularis* (Cephalotaceae). From the SW of Australia (photo Jolivet).

— Fig. 32.2. *Dionaea muscipula* (Droseraceae). From the peat-bogs of the South of North Carolina (photo Jolivet).

— Fig. 32.3. The same as Fig 32.2. Flies trapped into the leaves (photo Jolivet).

— Fig. 32.4. *Heliamphora nutans* (Sarraceniaceae) from Mts. Roraima, Venezuela. All *Heliamphora* species are found only on the tepuys (photo Jolivet).

— Fig. 32.5. *Sarracenia* sp. (Sarraceniaceae). Eastern USA (photo Jolivet).

— Fig. 32.6. *Darlingtonia californica* (Sarraceniaceae). California (photo Jolivet).

— 33. **Parental care in insects**

Parental care, as seen in mammals, specially in man, has little to compare with in insects. But some different protection strategies for progeny are seen among insects. After all, survival of offspring for continuity of the race is an important factor in their selection too.

One simple offspring protection strategy among insects is production of a large number of eggs, so that at least some complete their development and reach adulthood. Many insects show high fecundity, a single female producing hundreds to a few thousand eggs in her life time. Many insects, for example some leaf beetles (Family Chrysomelidae), lay eggs in the form of aggregates or egg clusters. *Timarcha* (Chrysomelinae) glues their eggs together to form an aggregate, using their secretions. Eggs, laid in groups, have defensive value in several different ways, namely:

(i) If eggs are in an aggregate, some of them are able to survive a parasitic attack, either because some eggs in the mass are shielded by others, or because the attacking parasite has a limited egg laying capacity. It has been observed by Becker and Frieiro-Costa (1988) that some eggs in an egg collection in an ootheca of a tortoise beetle remain unparasitised.

(ii) In some insects the female provides a protective cover for laid eggs, or an ootheca. If eggs are in an aggregate, a single ootheca affords protection to a number of eggs, and the mother is able to provide the protection to several eggs in a single operation.

(iii) In some species, larvae are gregarious, and they take to a group defence strategy, like round defence or cycloalexy (see the chapter on "Round defence"). If eggs are in an aggregate, formation of a larval group is facilitated.

(iv) In some New World tortoise beetles (Family Chrysomelidae, Subfamily Cassidinae) the mother remains close to her developing progeny, protecting them. Laying eggs in a group helps to make parental care available to a number of developing individuals at the same time.

The ootheca, or the protective cover around eggs provided by the mother, is made up mainly of a hardened secretion from some glands associated with the last part of the oviduct in the mother. It may be a simple parchment-like dome around one or a few eggs, or it may be a complex structure, enclosing a fairly large number of eggs, as in case of mantids and some tortoise beetles. The ootheca of the tortoise beetle *Aspidomorpha miliaris* is a series of parchment like leaflets, arranged serially, partly fused at the edges, and enclosing between them several transverse rows of four eggs each (Kalaichelvan and Verma, 2002).

Many tortoise beetles make a simple ootheca, enclosing one or a few eggs, and place over it a fecal discharge. The fecal deposit not only conceals the eggs, it is believed that it also provides physical and chemical protection to them (Kalaichelvan and Verma, 2000). As has been said in the chapter "Chemical defence in beetles and moths", the fecal discharge may be mixed up with toxic secretion of some exocrine glands, or some toxic compounds, present in mother's food, may have passed out with the fecal discharge.

Golden eyes (neuropterous family Chrysopidae) have taken to a peculiar way to protect their eggs. The eggs are attached to long, slender and flexible stalks, and may be laid singly or in groups. The stalks readily bend, and thus the eggs are difficult to reach by a parasite or a predator. A similar egg protection strategy is seen in some tortoise beetles, e.g. *Chelymorpha* and *Omaspides* (Olmstead, 1996) and also in some Clytrinae, a chrysomelid subfamily.

Generally insects lay their eggs on or close to the food of the future larvae, e.g. on leaves, stems, grains etc.. In this context specially notable is the case of ambrosia beetles (Family Platypodidae). The wood boring female of these beetles makes a burrow in a tree trunk or a freshly fallen log, extending deep into the sap wood. She releases from a special pocket on her thorax spores of a fungus. The fungus grows on walls of the burrow, and stains them black. The tunnel has side pouches or "niches". One egg is laid in each "niche". Larvae, on hatching, feed on the fungus. Such special care for providing food to their larvae appears to have evolved independently in nearly a dozen of families, especially those that exploit decomposing wood, dung or fungus (e.g. in Passalidae, Platypodidae, Scolytidae, Erotylidae, Tenebrionidae, Staphylinidae, Silphidae, Scarabeidae). Hydrophilidae and Chrysomelidae, not specially connected with dung, wood and fungus, show also, among some subfamiles and genera, maternal care.

Some solitary wasps (hymenopterous families Sphecidae and Eumenidae) make mud nests on rocks, walls of buildings and trees. They provision their nests, before egg laying and sealing of the nest, so that their larvae on hatching find themselves surrounded with food. The provision in the mud nest is stung and paralysed spiders in case sphecid wasps, and paralysed caterpillars in nests of eumenid wasps.

Maximum parental care is seen among social insects (ants, bees, wasps and termites). Their developmental stages are lodged in the nest of the colony, taken care of by constant presence of adults, and their larvae are given regular feed by workers, which also actively defend and protect the colony.

In some tortoise beetles of South America the female, after laying her eggs in a cluster, remains close to them and to the resulting larvae and pupae, actively defending them against predators, like ants. This association between parents and their offspring has been referred to as "subsociality" (Wilson, 1971; Jolivet, 1988, 1997; Windsor and Choe, 1994), as it shows one significant feature of the typical insect social life, namely presence of adults around the developmental stages, throughout their development, to protect them. Windsor and Choe (1994) tried to make out a parallel between classification of and maternal care among South American Cassidinae. Membracid bugs (Homoptera) and many other insects maintain feeding aggregations of adults and developing offspring, until the latter reach adulthood. In case of the membracids, the presence of ants adds to the protection of the eggs and then of the offspring. Recently, Lin *et al.* (2004) tried to compare phylogenetics with evolution of maternal care among membracine treehoppers. They conclude that there is a strong phylogenetic component in the evolution of the subsociality of the bugs. In some cases, among some rare insects, the male parent remains close to the female and the progeny, apparently helping the female to protect the latter. Some female fungus beetles, like *Pselaphicus giganteus* (Erotylidae) in Trinidad, gather their young larvae into a pile before going in search for a fungus for them to eat (Preston-Mafham *et al.*, 1993). It is rather strange that subsociality seems confined to cassidines only in tropical America. Guarding can last three to four weeks in some American cassidines. Among Chrysomelinae, some species of *Gonioctena* show in the Palaearctic Region larval cycloalexy combined with maternal care, and sometimes also ovoviviparity (Kudo and Hasegawa, 2003). In *Labidomera suturella*, another chrysomeline, females in Costa-Rica exhibit guarding their larvae by their presence (Choe, 1989). *Platyphora* in tropical America lay eggs or larvae according to the species. They are brightly colored and very toxic. The larvae generally go on cycloalexy, but the parents do not seem to watch them.

It is paternal care in some water bugs, as male carries the eggs on its back, and also in a spider-hunting wasp, *Trypoxylon superbum*, in which male remains close to its nest to guard its progeny against parasitoids and ants. Some male assasin bugs in Africa (Reduviidae) guard the eggs, and protect them from parasitoids. Pelissier Scot (in Resh and Cardé, 2003), mentions, as an advanced paternal care, in the cases of the arctiid moth, *Utetheisa ornatrix*, and in some katydids, in which the male transfers toxins to the female during mating, so that the eggs, laid by the female, are toxic. Paternal care was once suspected in some cycloalexic tortoise-beetles of South America, but has never been proved.

Biparental care is rarer and limited to some beetles, earwigs, termites and some cockroaches. It is known in the beetle *Necrophorus* spp. (not *Nicrophorus*, a typographic mistake, by someone ignorant of Greek) and in many Scarabeidae, e.g. *Cephalodesmius* (Monteith and Storey, 1981). Here, there is utilization of plant material and progressive provisioning for the growing larvae. In the last case, the male is closely involved. There is some task distribution between the two sexes. An exceptional case of biparental cooperation has been studied by Rasa (1998), in the Kalahari desert, with the tenebrionid *Parastizopus armaticeps*. Males dig and extend breeding burrows, while the female forages on the ground surface at night for the larval food.

Some insects, for protection of their offspring, have taken to viviparity, that is eggs develop within the body of the mother, and young larvae are laid. The chrysomeline *Chrysolina* shows viviparity in the Arctic in order to shorten the developmental period in hostile conditions outside mother's body, and *Platyphora*, in the neotropics, as a protection against hymenopterous egg parasitoids. It has been mentioned above that larvae of *Platyphora* show cycloalexy for their protection. Some cockroaches are also viviparous, and may show a complex situation in this context. Eggs of the cockroach *Diploptera punctata* are very small, and there are complex "milk glands" opening into the female genital tract. Secretion of these glands provides nourishment to the developing stages within mother's body.

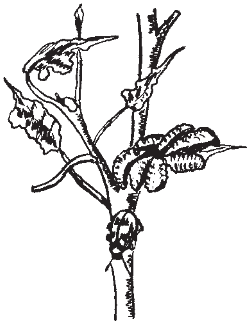
According to E. O. Wilson (1971), four ecological pressures result in selection for parental care in insects: 1) stable environment, 2) stressful environment, 3) the need for unpredictable resources, such as carrion or dung; 4) high predation pressure. It is definite that chrysomelids, which protect their offspring by their presence, are under pressure of heavy predation (by ants and bugs) and strong parasitoid pressure.

Providing protection to the offspring is quite widespread among insects. Parental care in insects, as defined by Michelle Pelissier Scott (in Resh and Cardé, 2003), ranges from covering eggs with a protective coating to remaining to feed and protect young to forming eusocial societies with life-long association of parents and offspring. Parental care is most developed in Isoptera (termites), Hemiptera, Homoptera, Dermaptera, Thysanoptera, Embioptera, Coleoptera and Hymenoptera, also in some Orthoptera, Psocoptera, and Diplura (Choe, 1989). It is exceptional among Lepidoptera; it is so far known in a single butterfly genus, *Hypolimnas,* in Guam and in the Philippines. Care of eggs is also rare among Diptera and is restricted to some genera and families and to some mosquitoes. Only a dozen, among thousands of Dermaptera, exhibit parental care. Among Dermaptera and *Gryllotalpa* (Orthoptera) , females protect their eggs by holding them in their mouth-parts and licking them regularly, thus using anti-fungal properties of their saliva. Embioptera are also known to pick up their eggs in their mouth-parts and to coat them with wood, silk and chewed-up food. Hemiptera often resort to wing-fanning to repel the parasites or predators. Some females add their eggs to a cluster already being guarded by another female. The female of some reduviid hemipteran, like *Ghilianella*, even carries her nymphs on her back. Embioptera, in their silk tunnels, cover carefully their eggs with macerated bark to repel hymenopterous parasites.

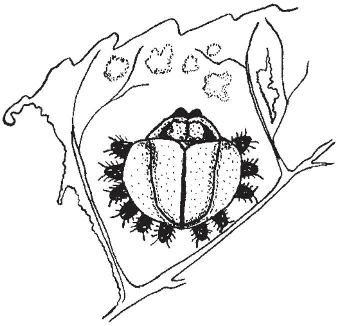
Half a dozen of books and many articles have been written on the topic of parental care in insects, and several encyclopedia have tried to summarize this rather complex problem (Preston-Mafham, R. and K. 1993; Resh and Cardé, 2003; Capinera, 2004). Reference is given here to the excellent review of parental care among insects done by Hinton (1981) in his trilogy on insect eggs.

— Fig. 33.1. *Omaspides* (*Paromaspides*) *sobrina* Boheman (Coleoptera: Cassidinae), female protecting its pupae. Viçosa, MG, Brazil (photo Jolivet).

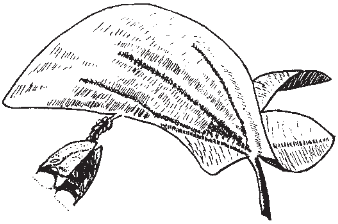
— Fig. 33.2. The same as Fig. 33.1. Parental care (photo Jolivet).



— Fig. 33.3. *Gonioctena rufipes* DeGeer (Chrysomelinae), female, protecting its young larvae. Germany.

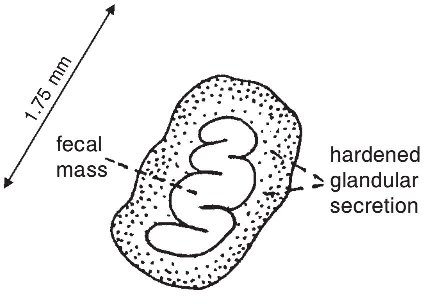


— Fig. 33.4. *Omaspides pallidipennis* Boheman (Cassidinae), female, covering its young, as a hen. The abdomen of the larvae are outside the mother's elytra. Brazil.

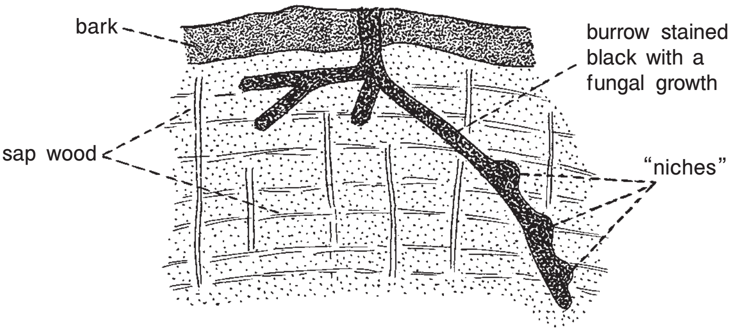


— Fig. 33.5. *Acromis spinifex* Linne (Cassidinae), with its eggs (after Jolivet, 1988). Brazil.

— Fig. 33.6. Female of *Eugenysa cascaroni* (Cassidinae) guarding her progeny, a group of pupae (after Jolivet, 1997). Brazil.

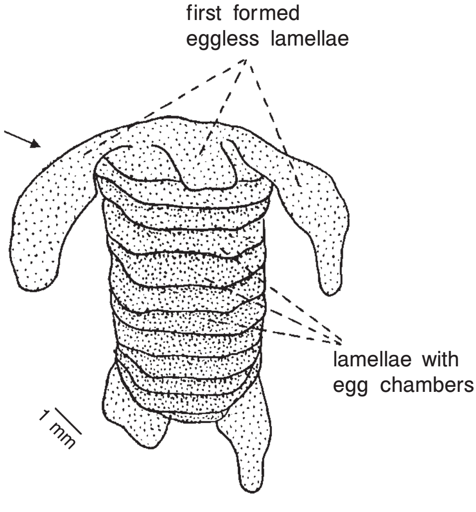


— Fig. 33.7. Ootheca of *Chiridopsis promiscua* (Cassidinae) (from Kalaichelvan and Verma, 2000). India.



— Fig. 33.8. Burrows of an ambrosia beetle (based on a photograph in Batra and Batra, 1967).

— Fig. 33.9. Eggs of a golden eye (*Chrysopa* sp.) held on flexible stalks.



— Fig. 33.10. Ootheca of *Aspidomorpha miliaris* (Cassidinae). The arrow indicates the end attached to the leaf surface
(from Kalaichelvan and Verma, 2002).

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— 34. **Pheromones**

Years ago one early morning my (KKV's) elder daughter, then a child, approaching my bed, asked me to get up and see a large moth resting on the mosquito net. Hazy appearance of the insect, as seen across the net, suggested that it was a saturniid moth. Sleepily I asked the child to see if the feelers of the moth had long side branches with a comb like arrangement on either side. She said she could see such side branches, but they were not quite long. I prophesied that soon there would be another moth with long side branches on its feelers. In a short while the foretelling turned out to be correct. Female saturniid moths have short side branches on their antennae, while males have long ones. Females of some moths are known to produce a sex attractant, which is a very volatile chemical and which attracts males from long distances. The prophecy was based on this information. Such chemical messengers, produced and released by an individual into the environment and producing an effect in conspecific individuals (that is individuals belonging to the same species) even in very low concentrations, have been called pheromones. Such observations were already made in 1870 by the French naturalist, Jean-Henri Fabre with *Saturnia pyri*, the great peacock moth. Forty male moths arrived at Fabre's home, the Serignan harmas, "eager to pay their respects to their marriageable bride born that morning" (Fabre, 1989, reissue). After that it took 90 years to identify the chemicals involved.

"Pheromone" is quite a meaningful term. It is akin to "hormone". They are chemical messengers that induce a behavioural reaction or developmental effects among individuals of same species (Cardé and Millar, in Resh and Cardé, 2003). In fact pheromones have also been called ectohormones and they are also referred to as semiochemicals or chemicals that are involved in communication. External secretions by an insect, which produce such changes/effects in individuals of other species, have been called kairomones or allomones. As E. O. Wilson (1963) has said, "…hormones are…secreted internally to regulate the organism's own physiology, or internal environment, pheromones are secreted externally and help to regulate the organism's external environment by influencing other animals." The regulation of the external environment is brought about by influencing and modifying the behaviour and/or development of other individuals of a conspecific group or population.

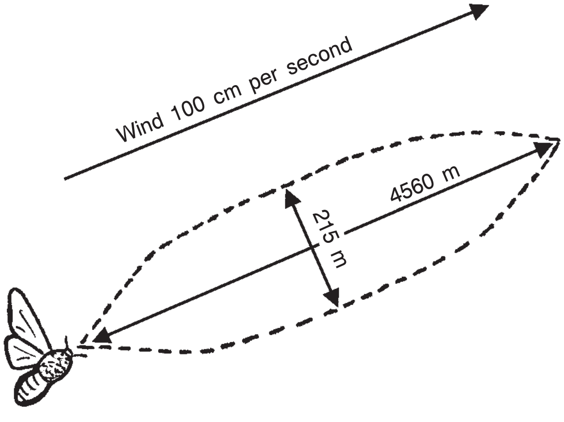
Bossart and Wilson have worked on the sex pheromone of the female gypsy moth. Taking into account diffusion properties of the pheromone, they have made mathematical models, from which they have inferred that, when a mild wind is blowing, the space, with effective concentration of the sex pheromone, will be ellipsoidal, with length of several thousand metres, and horizontal width, where it is the broadest, of about 200 metres (Wilson, 1963). Butenandt has reported that the female sex pheromone of the emperor moth may attract a male from a distance of eleven kilometers (Tembhare, 1984). On perceiving an effective concentration of the female pheromone, the male flies upwind to reach the pheromone source.

In addition to the gypsy moth (*Porthetria dispar*), the female sex pheromone has been extensively studied in the silk worm (*Bombyx mori*) and the American cockroach (*Periplaneta americana*). *Bombyx mori* pheromone was isolated in 1959 and was the first to be isolated.

In some insects male sex pheromones are known, for example in the butterfly *Lycorea ceres* (Danaiinae) and in the giant water bug *Belostoma indica* (Tembhare, 1984). Male moths can become, in some species, attractive to the opposite sex and may succeed in recruiting females through their pheromone. Some male butterflies have specialized paired brushes at the tip of the abdomen, disseminating an aphrodisiac scent from them. The scent of Danaiinae has an odor that ranges from sweet to rancid. Once in Nicaragua, PJ captured a danaiine butterfly (*Lycorea cleobaea*) with a tiny galerucine (*Monolepta* sp.), attached to its hairbrushes. Probably, the beetle was attracted by the scent and remained there during the flight of the butterfly (Jolivet and Maes, 1995). Thus in this case the male pheromone of the butterfly behaved also as a kairomone. However, butterflies rely more on visual clues for mate finding. Bark beetles (Scolytidae) use pheromones to colonize host trees and to attract mates.

Another well known example of a pheromone, inducing a certain behavioural change in conspecific individuals around, is the trail marker of ants. It is a common observation that ants are seen moving in a train like row to a feeding source. The trail is formed through guidance offered by a pheromone, the trail marker. The scout ant, going out in search of food, may locate a good source of nourishment. Then during return to its colony or nest she protrudes her functionless egg laying shaft or "sting", and with its help marks a line with the trail marker. The trail marker is a secretion of the Dufour's gland, associated with her sting apparatus. The workers of the colony, intending to collect food, move along the line of the trail marker to reach the feeding source. If the Dufour's gland of an ant is dissected out, crushed, the released contents are taken on a needle tip and the needle tip is used to draw a line on a surface, the ants from the conspecific colony nearby will be seen moving along the line.

The trail markers of ants are highly species specific, that is the pheromone of a particular species will not elicit trail making response in ants of another species. Another notable feature of the trail marker of ants is that its effect is short lived. In some seconds the pheromone evaporates away.



— Fig. 34.1. Diagram to show length and horizontal spread of the space with effective concentration of the female sex pheromone of the gypsy moth, when a mild wind is blowing. Not drawn to scale (Based on a diagram by Wilson, 1963).

The advantage of this is obvious. If the trails are not ephemeral, there will be a confusing maze of trails around an ant colony. If a "train" of ants continues to move along a certain trail for quite some time, it means the feeding source is rich, and the returning ants are repeatedly applying trail marker along the path. Cycloalexic larvae (see chapter on Round defense) make their round formation with the help of an aggregation pheromone. Procession forming saturniid larvae are known to produce a trail marker.

Another ant pheromone, evoking immediate behavioural response in fellow workers, is the alarm substance (which in fact is a mixture of chemical messengers). The alarm substance ("substances" should be more correct) is produced by the mandibular glands and certain glands associated with the sting apparatus. These glands store their secretions in reservoirs. If an ant is disturbed, say by an approaching predator, she releases the alarm substance. Ants in vicinity rush towards the disturbed fellow, and show panicky movements, including use of their sting apparatus. Such movements are believed to be of a defensive value. Like the trail marker, the alarm substance is effective for a short period, so that, after small crises have been dealt with, turmoil and excitement in the group are over. Cycloalexic larvae are also known to produce an alarm substance, when a predator is approaching the group.

The classical observations of the Austrian naturalist Karl von Frisch on language in the honey bee, verified by other bee specialists, have firmly established that worker bees, after feeding on a good source of food, communicate to the fellow workers in the colony presence, richness, distance and in some cases also direction of the feeding station by performing some rhythmic movements or "dances". It is also known that a dancing bee releases a sweet smelling substance, which conveys richness of the food source.

In addition to those insect pheromones, which produce immediate behavioural response in the recipient, such pheromones are known, which evoke developmental changes in the recipient, and these changes may eventually produce some behavioural effects. Hence the behavioural response is a consequence of the developmental changes, and is not seen immediately after reception of the pheromone. The queen in a honey bee colony produces, through her mandibular glands, a pheromone, the queen substance. This secretion is ingested by workers, and it suppresses development of ovaries in them; as a result the workers are sterile. The queen substance also prevents the workers from constructing a queen cell in the hive and from rearing a new queen. The pheromone also evokes worker like behaviour in the sterile females. In a termite colony individuals of the reproductive and soldier castes are known to produce pheromones, which prevent the juvenile workers from moulting into reproductives and soldiers. Queen ant has also been found to produce a pheromone, which prevents development of sexual maturity in workers.

In fact we have only begun to understand pheromones and their effects. There must be many more insect pheromones, producing special effects singly or in combinations. Releaser pheromones in ants, according to E. O. Wilson, are responsible for alarm, aggregation, attraction, colony formation, territory making etc. In the mandibular glands of the weaver ant (*Oecophylla longinoda*) there are 30 different chemicals. The sting chamber of honey bee produces about 20 different pheromones. These external secretions must be acting as means of chemical communication in insect populations and societies. How else the various activities in an ant or a wasp or honey bee colony take place in a very well regulated and organized manner in the almost total darkness of their nests? Wilson points out that there are several glands in a worker ant's body, and there are at least 10 different pheromones produced by ants. Further work will reveal a number of interesting details of chemical language among insects.

Pheromones are useful in pest control either to detect pests and invaders or for mating disruption. Agriculturists are using in pheromone-baited traps synthetic copies of original chemicals.

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— 35. **Parasol ants**

Zoological parks exhibit mostly vertebrates, which in general are larger animals. But of late they have been trying to include invertebrates too among their exhibits. In 1984, during the 17th International Congress of Entomology at Hamburg, we visited the zoo there, Carl Hagenbecks Tierpark, where we saw a remarkable exhibit of parasol ants. In a glass covered enclosure a log, looking like a limb of a tree, was placed nearly horizontally. At one end of the log was an earth mound, enclosing an ant nest, and at the other end were twigs with fresh leaves. Ants were seen swiftly moving on the log towards the leaves, and there was another stream of ants moving on the log from the leafy branches towards the nest. Movements in the latter group were cautious and disciplined. Ants in this stream were moving in a single file, each ant carrying a cut away piece of leaf, caught between her mandibles, swaying over her head and looking like a parasol. The serene and orderly procession of seemingly parasol carrying little ladies was an interesting and a comical sight. At the Museum of Natural History, in Geneva, in the same period was a similar exhibit, and the ants were "fed" with bramble (*Rubus*) leaves, available all the year round in that area. In the streets of Brasilia, you see them along the side-walks, going their way and transporting their leaves or bits of flowers, while the street is full of passing cars. In the Viçosa University, in Brazil, they used to "feed" them with *Hibiscus* flowers, an Asiatic plant which they specially like. Normally they don't feed on *Cecropia* trees, inhabited by the ants *Azteca*, and there are other exceptions, and certain trees, the myrmecophobic ones, which are toxic, are excluded in their menu. PJ has seen that in Panama an *Acacia* tree was defoliated in less than one day by the *Atta* ants, which are parasol ants. When some trees have been defoliated in an area, they attack different plants the next day. Those *Atta* seem to be ecologically minded. Some genera of these ants are specialized for feeding on flowers and grasses, which they prefer to trees.

On returning, the ants enter the nest with their leafy trophy. But they are not leaf feeders. They use the leaf pieces for growing a fungus, and they are fungus feeders. There are some chambers in the nest, which are large and are used for developing fungus gardens, and the leaf pieces provide an organic base for growing the fungus. The relationship between fungi and ants have been recently extensively studied. The discovery of fungus feeding is due to Belt, an engineer, in Nicaragua during the XIX century.

Leaf-cutter ants live exclusively in the tropical or subtropical parts of the New World. In the Old world, termites fill their niche and cultivate fungi. Fungi, associated with ants, decompose cellulose of the plant tissues for them, and termites manage that with the help of endosymbiotic Protozoa in their intestine.

New colonies of parasol ants are started in much the same way as in case of other ants. Occasionally winged queen ants are produced in the colony. A queen ant, which has freshly emerged from the pupal skin, makes a pellet of fungal filaments or mycelia in a fungal garden, puts the pellet in a small pocket at the base of her mouth parts, and flies away. After mating with a winged male during her flight, she settles down at a suitable spot, sheds her wings, and makes a small chamber in soil, which is the beginning of a new nest. She lays a large number of eggs, deposits her excreta and places over it the fungal pellet. The excreta provide the first fertilizer for the fungal growth.

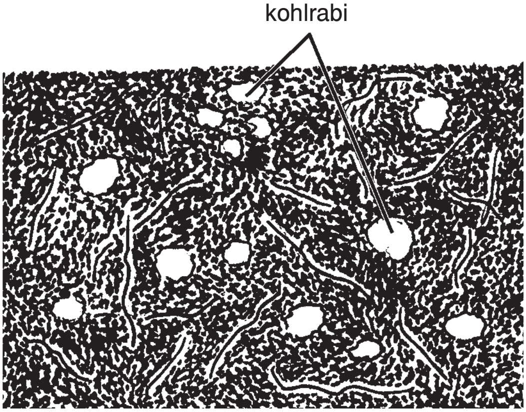
The female, laying the foundations of a new colony, is markedly ovivorous, that is she eats most of her own eggs (Poole *et al.*, 1963). The main reason for this is that she has to produce more excreta for growing the fungal mass, and at this stage worker ants are not available for bringing in leaf pieces for the fungus garden in making. As soon as the first batch of workers have completed their development, collection of leaf pieces will start, and the mother queen will confine her activity to egg laying.

While larger workers collect leaf pieces, smaller workers, the minimes, remain within the nest, and, receiving those pieces, they bite them into a pulp, adding their saliva to it. The pulp is added to the fungal garden. Inmates of the colony also deposit their excreta on the growing fungal masses.

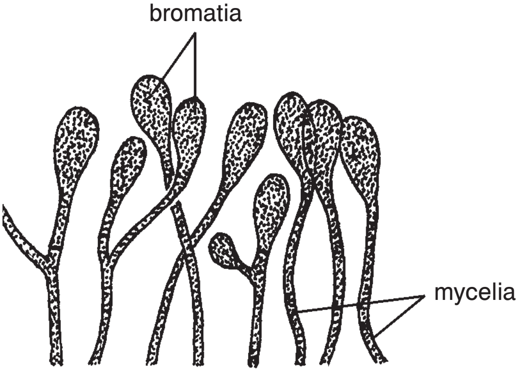
A fungal garden of parasol ants looks like a greenish grey felt with some rounded whitish spots. The spots are called kohlrabi. They are collections of terminal filaments of the fungus presenting bulbous swellings, which are named bromatia (Batra *et al.*, 1967). Adults and larvae feed on the bromatia. The bromatia are sweet tasting, and rich in sugars, proteins and vitamins. Adults in the colony not only eat bromatia but also often just lick them.

One interesting fact about the fungus, associated with a parasol ant colony, is that it does not give out spore producing fruiting bodies or mushrooms. But the fungus in an abandoned nest is known in some cases to produce mushrooms. Perhaps some activity of the ants prevents the fungus from producing spores. One possibility is that the worker ants "prune" the fungal growth to prevent formation of fruiting bodies. It may also be that the ant excretion and saliva contain some substances, which prevent formation of spore producing parts, and induce development of bromatia. Whatever it be, this association of parasol ants and a fungus is a remarkable example of mutualistic or symbiotic living. While the fungus provides prepared food to the ants, the ants give to the fungus the advantage of wide dispersal without production of spores, and also a readily available substratum for its growth. A bacterium, which grows on the ant's bodies, produces antibiotics to kill a parasite that may infect their fungal crop (Schultz, 1999).

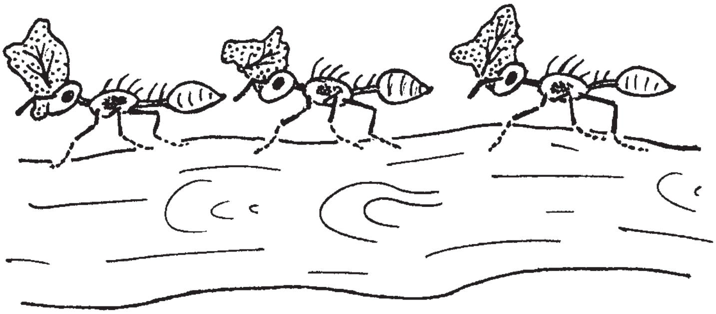
Cultivation of fungi for food by fungus-growing ants or Attini originated 50-65 million years ago (Mueller *et al.*, 1998). The ants succeeded at domesticating multiple cultivars (553 cultivars have been isolated) and the mycelium cultivation has had a single evolutionary origin (Mueller *et al.*, 2001). Relationships between the fungus and the ants are extremely specific and not yet properly understood.



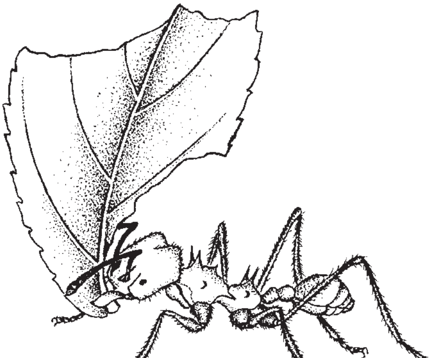
— Fig. 35.1. Fungal garden of a parasol ant.



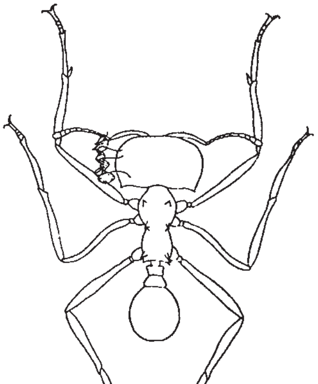
— Fig. 35.2. Structure of bromatia under magnification.



— Fig. 35.3. A part of an orderly procession of parasol ants, moving on a tree limb, returning to the nest with pieces of leaves (after Batra and Batra, 1967).



— Fig. 35.4. A leaf-cutting ant of the genus *Atta,* carrying a bit of leaf. (after Linsemayer, 1973).



— Fig. 35.5. A dwarf worker (minime) cleaning an *Atta* soldier (after Weber, 1966).

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— 36. **Do ants make slaves?**

In the recorded natural history of ants there are several cases of some ants taking "slaves" from neighbouring ant colonies. Let us see a few examples.

The blood red ants (*Formica sanguinea*), so named because of their red body colour, occur in Europe and North America. Scout workers of this species locate colonies of other ant species in neighbourhood, such as *Formica fusca*. An army of workers of the *sanguinea* colony then launches an attack on a chosen neighbouring colony. If the attacked colony workers offer resistance, they are killed. Developing stages, specially pupae, are removed by the *sanguinea* workers, and are taken to their own colony. Some of the pupae, brought in as trophies, are eaten, and some others are reared to their adulthood (Poole and Poole, 1963). The alien workers, thus produced in the *sanguinea* colony, are "slaves", and they serve the colony as if it is their own. *Formica sanguinea* queen is quite capable of living without its helper ants. So why this "slavery"? It seems that it is done mostly in the search of food. Only pupae when they are maturing, and never eggs, larvae or sexual ants are stolen.

While many *Lasius* species found their colony in the usual way independently, others may take to "slavery". The females of *Lasius reginae*, in Austria, founds its colony with the help of the common *Lasius alienus*. It is a small ant, which often penetrates into the human dwellings in Europe. The *reginae* female is smaller than the host *L. alienus* queen and even smaller than her own workers. She, however, manages to enter an *alienus* colony and to turn the legitimate queen on her back and kill her, tearing the skin between her head and chest with mandibles. The *reginae* queen does not have enough reserve nourishment in her body for initiating her own colony independently. After that the new invading queen begins to lay eggs (Dumpert, 1981). The queen of *Lasius carniolicus*, also smaller than her workers, founds her colony with the help of *Lasius flavus*. A large European species, *Lasius fuliginosus* also practices "slavery" at the cost of *Lasius umbratus*.

A specially interesting case, in this context, is that of the ant *Bothriomyrmex decapitans*. A newly emerged queen of this species proceeds on a nuptial flight, as is common among ants. After mating she sheds her wings and enters an ant colony of another species. Moving stealthily, avoiding attention of the workers of this colony, she reaches the queen chamber of the nest. Here she climbs over the back of the reigning queen, and waits there. In this position the workers of the colony pay no heed to her. This foreign queen gradually acquires the odour of the host colony. Now she bites away the head of the queen "on throne", and kills her. The workers accept the intruder queen as their own, and remove and throw out the dead body of the original queen (Poole and Poole, 1963). The *Bothriomyrmex* queen starts laying her eggs at a fast pace, and the eggs are taken care of by the host workers. Individuals of the original colony gradually die, and the *Bothriomyrmex* progeny take their place. Thus, after sometime the invaded colony gets transformed into a *Bothriomyrmex* colony.

The European ant *Anergates atratulus* shows the climax of specialization for the "slave" making habit. A queen of this species enters the nest of another species, a species of *Tetramorium*, and kills the queen of the host colony. Workers of the host colony help the foreign queen rear her progeny. It is specially notable that *Anergates atratulus* never makes its own nest, and is not known to produce its own workers. In contrast, in the case of *Bothriomyrmex* enslaving a colony of another species is facultative, that is a mated female may enter a colony of another species, or establish its own colony from the start. Another interesting situation: The Amazon ants, *Polyergus rufescens*, a French ant is entirely dependent on a *Serviformica* species. Without the latter, they are unable to obtain any food for themselves. In their colonies the "slaves" are five times more numerous than the "slave-makers".

A question, which comes up in this context: Why do those ant species, which suffer from the "slave" making habit of another species, not develop their own defences? When searching for an answer to this question, it has to be realized that to ascribe slavery to these instances is an anthropocentric thinking. In fact these are cases of social parasitism. Slavery is intraspecific, whereas the so called "slavery" among ants is mostly between different species. In cases of parasitism it is known that, when a parasite is freshly introduced into a host population, for sometime there are deep fluctuations in the host as well as in parasite population sizes. Increase in parasite population reduces the host population. Decreased host population results in a decrease in the parasite population. When the parasite population touches a certain low, host population begins to increase, and the cycle is repeated. The resulting oscillations in the sizes of the host and parasite populations are deep for some generations, and they dampen after some length of the association (Ananthakrisnan and Viswarathan, 1976), as a sort of equilibrium between the two is reached. It seems that it is this state of equilibrium between "slave" provider and "slave" maker species in the instances, described in this chapter.

Such social parasitism among ants, in which ants from one colony invade another colony and "enslave" the invaded colony, has been called "dulosis" (Holldobler and Wilson, 1990). According to Holldobler and Wilson (1990) "dulosis" in some cases may be intraspecific, that is invaders and invaded colony belong to the same species, a situation which may be seen, for example in the honey storing ant species, *Myrmecocystus mimicus* in USA. In this species, workers from a stronger colony drag out all pupae, larvae, and workers, including honey pots, from a weaker colony to be included in their own colony. This also may happen that a queen, unaccompanied by workers, may seek shelter in a helper colony.

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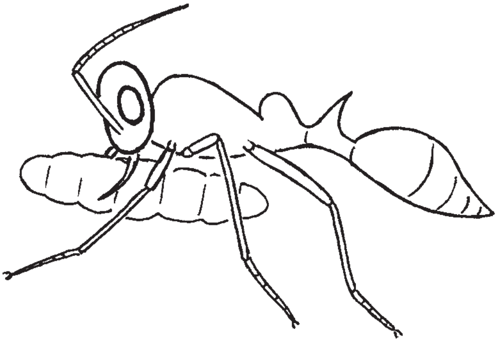
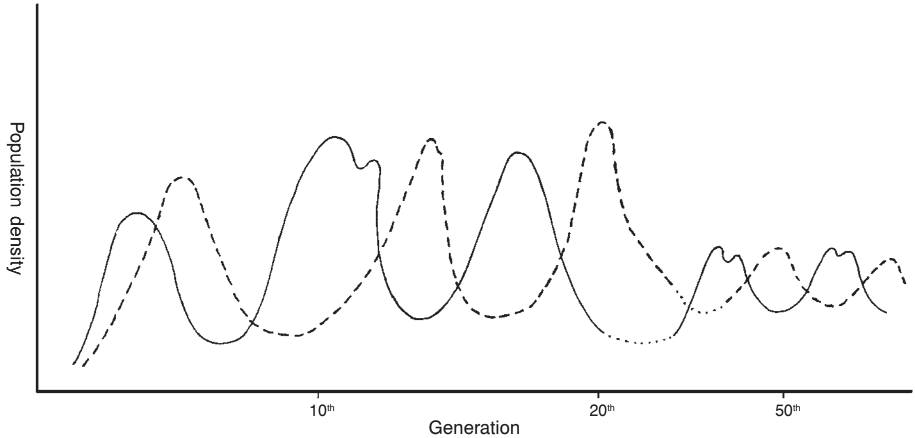


— Fig. 36.1. A blood red ant carrying a pupa from an invaded ant colony.



— Fig. 36.2. Oscillations in host's (*Callosobruchus chinensis*) population density (solid line) and that of the parasite (*Heterospilus prosopidis*) (broken line) (dots indicate break in the curves) (simplified from Utida, 1967).

— 37. **Do insects feel pain?**

It is a question raised sometime ago by Eisemann and six other scientists (Eisemann *et al*. 1984), and also a question that PJ raised himself (Jolivet, 1999, 2002). Really the question is rather perplexing and has been discussed by Berembaum (2000) and earlier by Wiggleworth (1980). It is very difficult to answer satisfactorily, because, if a reptile brain is so difficult to understand, the invertebrate brain, being much smaller and complex, seems to belong to another world. Darwin, who had recognized the complexity of invertebrate brains, used to say that the ant brain gave him a headache. The complexity of the eye and its evolution was also a headache for the patriarch of Downes. The ants did not exist during the early Cambrian, and they appeared during the Jurassic, but, much earlier in the history of the organic world, trilobites and other invertebrates already had very complex eyes and a complex nervous system. They had predators and enemies and probably even they felt pain. Not only ants have sophisticated eyes, they also have a brain capable of memory, learning, and complex adaptations required for strict instinctive behaviour. If we say so for the ants, what can we say about the bee, the earwig, the beetle, the cockroach and so many insects and invertebrates, capable of extremely complex behaviour, parental care and "intelligent" discrimination in labyrinths? Contrary to what Fabre and Bergson believed, the insect behaviour is not all instinctive. Learning also has a place in their behaviour. The question of pain among the insects induces ethical implications for the biologists, who often manipulate live insect material. Even very simple mobile organisms, such as bacteria, show evident avoidance and escape responses, when subjected to traumatic stimuli, such as heat, chemicals, electricity, pressure, etc. (Berg, 1975). The problem becomes more complex with higher organisms, and seems proportional to the degree of complexity (Gould and Gould, 1982). We can feel sympathy for a dog or a cat in distress, but we feel little compassion for a worm or a snail facing a traumatic situation. Perhaps our mental response, on seeing a suffering organism and realization of its pain, are proportionate to our evolutionary closeness with the organism.

Pain is subjective. The reality of pain, apart the imagination of Descartes, who crucified his dog to show that it was a machine, is deduced from the physiological and behavioural responses, shown by the organism, such as flexor reflexes, blood pressure increase, vocalization (screams), and hasty respiration (tachypnoea). Sensation of pain in an animal is deduced from the observations of reactions similar to those shown by a suffering human being. According to Wiggleworth, stimuli, such as high temperature and electric shocks, are perceived by the insects, as if they are feeling pain, while other manipulations do not seem to affect them much. Among mammals, pain induces reactions such as withdrawal, protraction, aggression, learnt avoidance etc. Mammals, especially, man, have limited preprogramming of their behaviour patterns, and they learn from pain and pleasure experiences (Elzack, 1973).

In contrast, most insect behaviour patterns are to a large extent preprogrammed (instinctive). There is, however, a capacity for learning (including avoidance) in both intact and decapitated insects. Some of the receptors present among the vertebrates seem missing among the insects, but we cannot imagine that reflex avoidance of a traumatic situation can exist without the implication of a sensation of pain. The discovery of receptors of opioid peptides among the invertebrates could implicate that these animals feel pain, but that is not fully convincing (Eisemann *et al.*, 1984). Insects go on with their activities after a traumatism or the removal of essential parts of their body such as the head or the legs. Hyperexcitability, ataxia and convulsions, shown by insects after insecticide poisoning, sound production, secretion of alarm pheromones after an attack can be considered as an instinctive response, and not as a reaction to pain.

In conclusion, it seems impossible to say at present if insects really suffer pain like us or only by reflex respond to external stimuli. It is evident that the problem can be totally different with mollusks, like Cephalopoda, with a very complex nervous system. Eisemann *et al.* (1984) advise, as also Wiggleworth (1980), that, in the state of uncertainty, it is necessary to anaesthetize the insects before start of traumatizing laboratory manipulations. The method not only facilitates the manipulations, but also avoids pain to animals, physiology of which is only imperfectly understood.

Berenbaum (2000) recounts her experience in Cornell with a dissected cockroach, emptied of its visceral mass, beheaded and legless, and still trying to swim after experiments on the water in the dissection dish. She too does not know if the insects feel pain, but she also advises to anaesthetize them before all experiments. Pain is probably universal among all the living beings, since the origin of life, but we do not know to what extent lower form of life have consciousness to feel it.

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— 38. **Pocket Mites**

Mites or acari are small arachnids, close to spiders and scorpions, but much more numerous in species and in individuals (Baker and Wharton, 1952). They are to be found in almost every habitat available to animal life. Some are free in the soil, forest litter, on plants, in fresh or sea waters. Others are parasitic or symbiotic on plants and animals or transmit diseases like tsutsugamushi, the scrub typhus etc. Some are floating in the air, with air currents, with the dust, and can cause allergies. Their variety is immense, perhaps millions, and a large number of them remain to be discovered and described, mostly in tropical forests and in the soil. In achieving biodiversity they have surpassed even their cousins, the insects. Ticks, which are big mites, are mostly blood suckers, and get inflated after a blood meal. They transmit diseases to man and domestic animals, like piroplasmosis and many bacterial and viral diseases. Lyme fever, caused by a spirochaete, is an important disease, and, in the US, deer are the main reservoir of the pathogen. The Erythraeidae are reddish, predacious mites, with legs adapted for running. *Dinothrombium*, the dinosaurs of mites, are very big mites running on the ground in the African tropics. They look like big reddish silken balls continuously agitated on wet grounds.

Mites, though having generally eight legs in the adult stage, have many things in common, mostly in biology, with the insects. For instance, they have six legs in the larval instars, which situation has led to some serious errors; for instance, during a congress of entomology, a specialist described a new order of insects, which turned out to be larval mites.

Among mites, there are some blind species, like *Amblyserus*; they have an extra-ocular vision, the receptors for which could not yet be located.

Mites are close to Solifugae, the camel-spiders, a kind of big arachnids, quite disgusting in appearance, and have two pairs of forceps (chelicerae). They are efficient predators, but quite harmless to man. They look like insects and walk on six legs, as the first pair of legs act as feelers and grab food. They are common in America, North Africa and Middle East. They fight and eat insects, rodents, lizards, small snakes, and even small birds. Their bite is ferocious. They tear their victim's integument and regurgitate a digestive liquid, which liquefies the organs of the prey, and then they suck up the liquid contents into their stomach. Female Solifugae are good mothers and they protect their eggs and their young ones, but the offspring are also ferocious and young ones are often cannibals. The Solifugae did cleaning of the house of PJ in Ethiopia, and in the morning not a vermin remained in the rooms. They were coming from outside under the doors and were leaving in the morning, having accomplished their work. They were the famous *Galeodes arabs*.

Mite life style is so complex that a book of more than even 1000 pages will not adequately cover it. They live as parasites in the lungs of birds and reptiles, in bee tracheae, and inside the skin of mammals. They are responsible for human scabies and for the galls in plants. *Demodex folliculorum* is a mite parasitic in the bases of human and animal hairs.

What is extraordinary, and relatively little known, is that several living beings (plants, lizards, bugs, bees, wasps, moths and probably some others) have acquired, during their evolution, special pockets to lodge the mites. In fact, as plant galls have evolved to limit the damage done to the plant body by insects and other gall producing organisms, it seems that these pockets in animals have evolved in order to neutralize the parasite presence. In several cases, it appears that the mites have occupied preexisting natural cavities (glands, typanic organs, cavities in plant stems etc.). In exchange of the lodging, and sometimes of food, plant mites are useful to their host. They prevent epiphyte growth, which affect photosynthesis efficiency of the host. They also serve to keep the leaf laminae of the host clean.

The transportation of mites, scorpions, insects and even plants by insects or arthropods is a phenomenon called "phoresy", provided it is only transportation and no parasitism. In the cases, we have cited above, the transportation is life long for the animal host, and, therefore, we may use the term of ectoparasitism or epizoitic symbiosis for such cases. For an example of such an association see the chapter "Forest on back".

Very distinct from insect, mite and bacterial galls (cecidia) are acarodomatia, which are gall like swellings lodging small mites, called pocket mites. The acarodomatia or pockets lodging mites preexist the entry of pocket mites into them in many plants. It has been suggested that the plant genome induces formation of acarodomatia to invite mites. A similar symbiotic association is known between ants and plants. Plants develop cavities and crevices (myrmecodomatia) to lodge and invite ants. (For this symbiotic association between plants and ants see the chapter "Omnipresent ants".) It has sometimes been doubted that the ant or mite lodgings are purposely genome guided. But it cannot be doubted that such associations are symbiotic, that is useful to the plant as well as to the ants/mites. Feeding habits of mites associated with plants has been detailed by Evans *et al.* (1961).

Acarocecidia should be carefully distinguished from acarodomatia, which preexist the entry of mites. Acarocecidia, on the other hand, are developed after entry into the plant body; they are in fact mite induced galls.

The mite pouches are mostly found along the axis of the leaf veins of certain plants. They are known even in 42 million-year-old fossils in Australia (O'Dowd *et al.*,1991; O'Dowd and Willson, 1991; O'Dowd and Willson, 1991-1992). It seems that the plant associated mites (the herbivorous ones) clean the leaf surface by removing epiphylls, fungi, lichens, algae, spores, pollen etc., and carnivorous ones by eating the herbivorous mites, insect eggs, small insects. Many mites are serious agricultural pests. Some are free, i.e. not exactly agricultural pests. But many of this last mentioned category induce the formation of acarocecidia and are not lodged in acarodomatia. The pocket mites seem to be really efficient in cleaning the leaves and increasing the photosynthesis efficiency. In the tropics, organic growth on the leaf surface is a serious problem, and the pocket mites solve this problem effectively.

Similar pockets exist on bodies of wasps, bees, lizards and moths, and also in certain bugs. In the last case, there are secretory glands regularly invaded by mites. Are those acari really cleaners of these pockets? It has not yet been proven. The best explanation, that we can give at present, is that those pockets diminish the damages to the host body by keeping the mites in a specially conditioned place. In view of what we know about plant galls, this explanation seems to be acceptable. Let us now learn more about such pockets in animal bodies.

Professor Fain, in Belgium, has described (1970) a new genus of acari parasitic in the vestibules of a pair odoriferous glands of certain Coreidae bugs (*Coreitarsonemus*). Those vestibules were full of small whitish tiny bodies, which were mites of the family Tarsonemidae. It seems that this parasite is very common among bugs of the family Coreidae. The glands, infested with the mites, certainly feed the mites and fix them at this precise place in the body of the host.

PJ was once in Southern Korea when an epidemic of conjunctivitis, due to a virus, struck the country. All the Koreans, one after another, carried a bandage over one eye, then over the other, while doctors appeared vexed. When PJ questioned one of them: "Why covering over only one eye?", he answered, not without logic, "Because if we were covering both of them, we could not see anything". It is exactly what is going on with some night flying American moths. Mites attack and paralyze one tympanic organ, and always one and never both (Coineau and Kresling, 1974; Treat, 1975, 1983). If the two organs were attacked, the insect would be completely deaf and it would be in danger, and with it the parasitic mites. Tympanic organs in the moth are necessary to avoid radar using bats. Normally this mite, studied by Aslar Treat, settles in only one "ear", which can contain one hundred individuals, and not the other, and this situation ensures preservation of both the species (mite and moth). Either species has to choose the lesser of two evils. The moth can survive with only one ear, and with it the acari.

Among the females of certain Indo-Malaysian bees, close to our *Xylocopa* (the big blue bee of our areas), belonging to the genus *Koptorthosoma*, have mite pockets between the posterior part of the thorax and the base of the abdomen. Many ectoparasitic or phoretic mites are found in these pockets, and generally the mites live upon the females only. The males don't go back to the nest after copulating, which takes place always outside the nest. Is this the reason why they do not have mites? Answer to this question we do not know. Among the males of these Indo-malaysian bees, the mite pocket exists, but is always empty and remains in a rudimentary stage. Among the females of the *Odynerus* wasps from Arizona and Mexico also there is a cavity between the first and the second abdominal segments, and the cavity in females is full of small acari which do not interfere with the movements of the abdominal segments. *Odynerus* males do not have this pocket and do not carry mites. Mites are also present, as phoretic, among sweat bees (Halictidae) and on many other Hymenoptera (Eickwort, 1979).

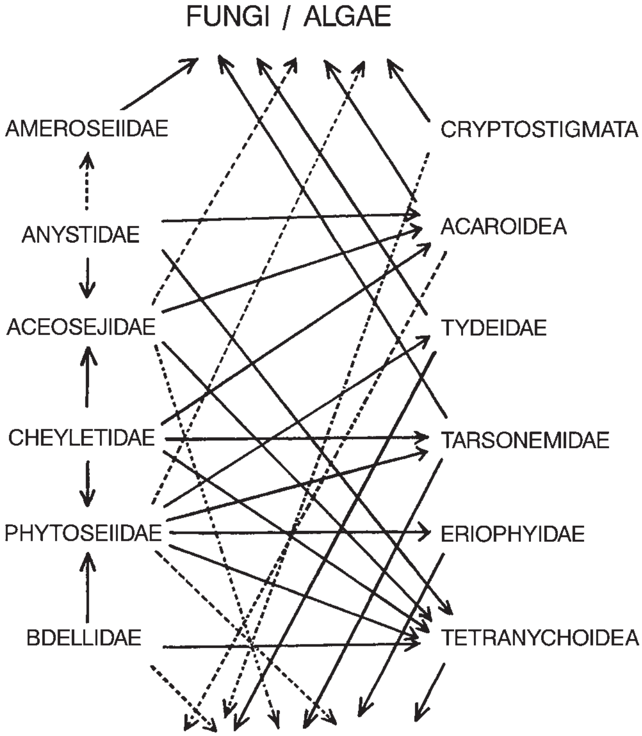
Many lizards, iguanas, chameleons, geckos, possess small skin invaginations. Those invaginations or folds are situated on the neck, in the groin, in the postfemoral region etc., and are sometimes used in taxonomy. Those pockets contain acarian larvae, mostly Trombiculidae, and are met with among members of five lizard families (Arnold, 1986).

This phenomenon seems linked with the humid tropics. These pockets are already present in lizard embryos; this fact suggests that they are genetically fixed. Similarly, the callosities of the ostriches, and of the warthogs in Africa are also genetically fixed (Baldwin effect). These pre-existing pockets in lizards are colonised by mites very early. The epidermis of these pockets is adapted to mite bites and repairs itself quickly. The mites are protected and, at the same time, the host minimizes the damage, which would be extensive if the mites spread all over the body.

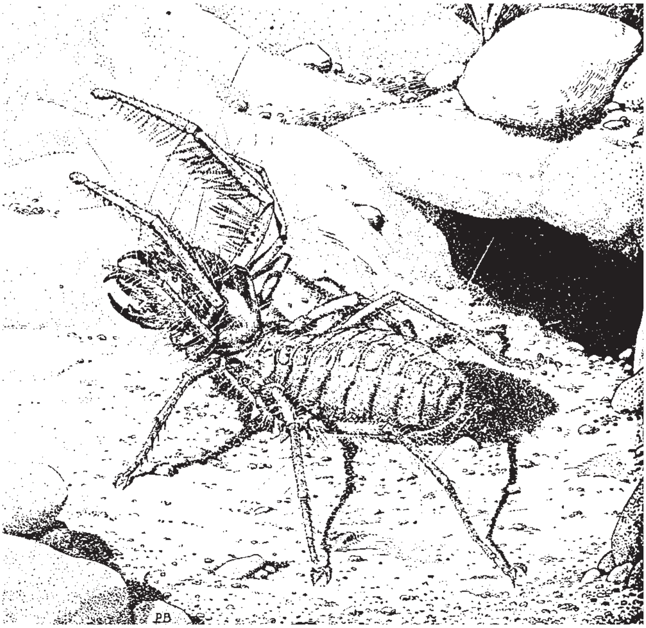
A special mite family was discovered in the cloaca of two aquatic North American tortoises (Camin *et al.*, 1967). This mite family, Cloacaridae, was described in 1967. They are very much modified morphologically and specially adapted to their strange habitat. They have been referred to as turtle crabs, and their transmission occurs venereally. Perhaps they are there in all tropical tortoises.

In conclusion it may be said that mite pockets exist in many plants and animals. These infoldings develop early, they preexist, and are colonised by mites at the earliest opportunity. Hence they seem to develop under influence of heredity. Among Hymenoptera the pocket mites infest only females. Evolution of these pockets seems to be an adaptation to minimize damage to the body by the parasitic mites. As the British say: “they keep the mites out of mischief”. About association of mites with plants, it is generally accepted that it is symbiotic.

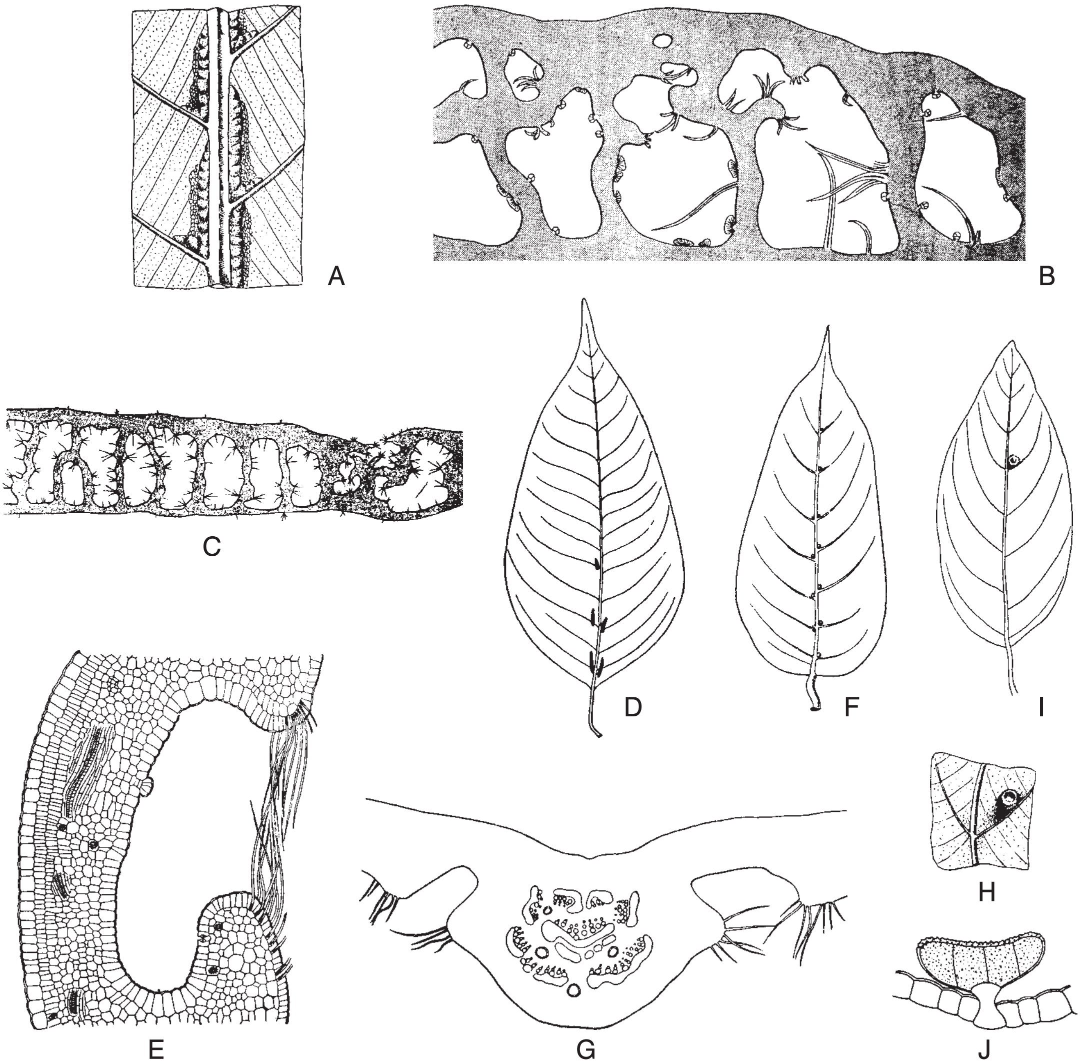
As the pocket mites are studied further, it is likely that we come to discover many more interesting facts. For example, some mites of the family Canestriniidae and some others perhaps show an inverted copulation pattern. The females penetrates the male to pick up the sperm, as among some rare butterflies and beetles.



— Fig. 38.1. Food habits of mites associated to plants. Solid lines mean main type of food and dotted lines substitute food (After Evans *et al.*, 1961).



— Fig. 38.2. *Galeodes arabs* (Solifuga). A night visitor in Ethiopia (after Jolivet, 1991).



— Fig. 38.3. A: Acarodomatia superposed on each side of the middle vein (x4). *Shorea maranti* Burck (Dipterocarpaceae).

B: *Shorea leprosula*. Cross-section perpendicular to the domatia area. The epidermis of the domatia has tector hairs and large hairs (x 55).

C: *Shorea maranti* Burck. Cross-section parallel to the middle vein, through the domatia. One pouch is seen opening to outside (x 20).

D: *Doona zeylanica* Burck (Dipterocarpaceae). Elongated domatia close to the middle vein (x 1).

E: *Doona zeylanica*. Cross-section of one domatium. Hairs are mixed up at the opening (x 150).

F: *Hopea nigra* Burck (Dipterocarpaceae). Many domatia, all at the bases of a secondary vein (x 1).

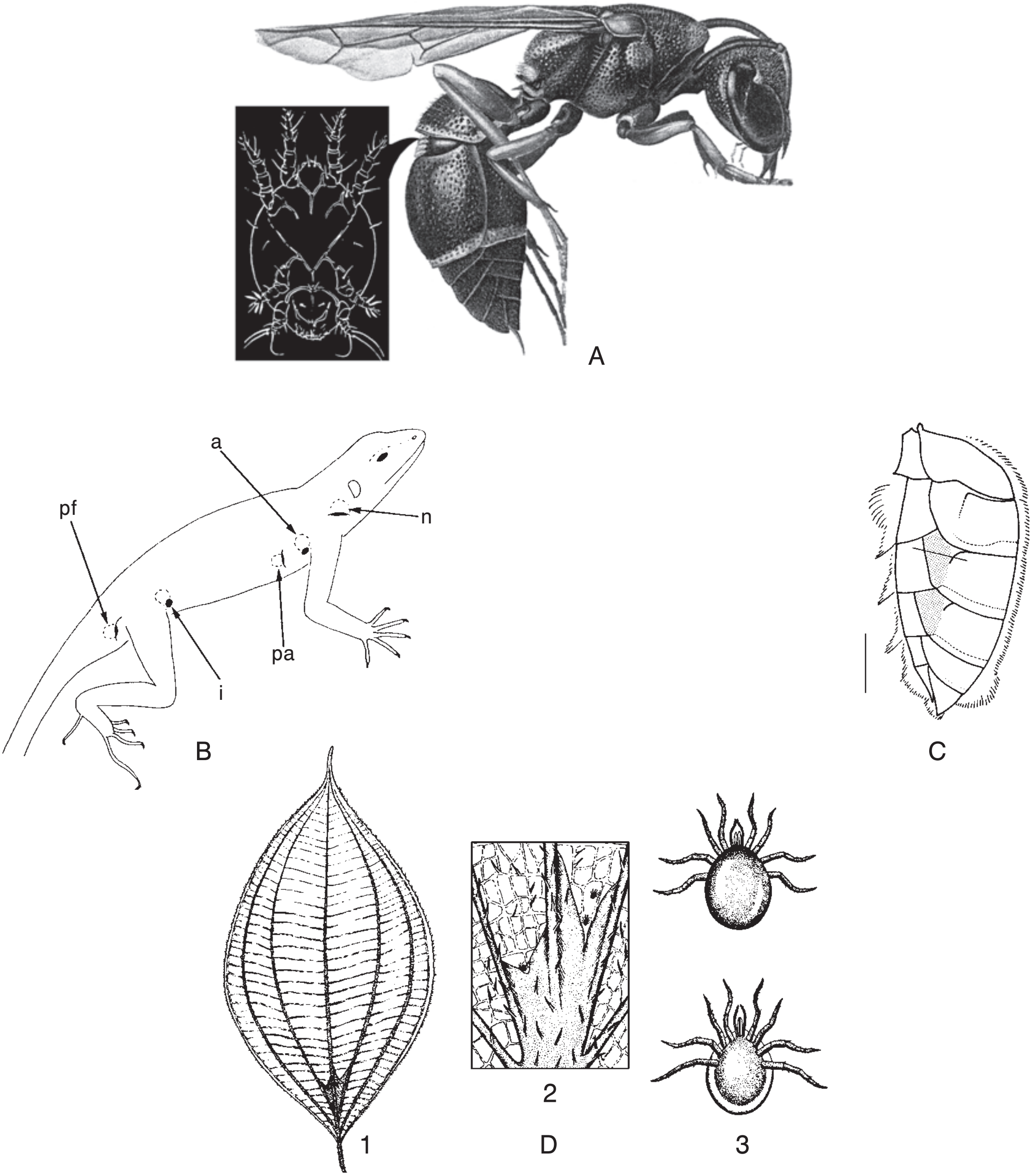
G: *Hopea nigra*. Cross-section of the leaf with two hairy domatia (x 300).

H: *Shorea* (=*Doona*) *odorata* (Burck) (Diperocarpaceae). Opening of a single domatium (x 4).

I: *Shorea odorata*. Leaf with a single domatium (x 1).

J: *Shorea marauti*. Epidermis of the domatium with verrucous shield hair (x 500).

(after Guérin, 1906-1907).



— Fig. 38.4. A: The wasp *Stenodynerus saecularis* with mites on the left side of the acarinarium at the base of the second abdominal segment.
B: Sites where are met frequently mite pockets among lizards: n= nuchal; pa: post-axillary; i= unguinal; and pf= post-femoral (after Arnold, 1986).
C: Abdomen of a female bee, *Ctenocolletes centralis*, showing the mite pockets (in dotted areas) on the side of the 3rd and 4th tergites (after Houston, 1987).
D: *Clidemia hummeli* Almeda (Melastomataceae). 1: typical leaf (abaxial surface); 2: enlargement of the inferior side showing the domatia; 3: the mite *Ololaelaps* sp., dorsal and ventral view (x 20) (after Almeda, 1989).

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— 39. **Aphids and ants**

Aphids are among the more familiar insects. They are small, wingless, soft, nearly oval bodied insects, green, yellow or dark in colour. They are seen adhering in groups to leaves, tender stems or fruits of plants. They have long needle like feeding organs or mouth parts, like those of a mosquito. These feeding needles are inserted into the plant tissues to suck plant juices, which constitute their food. They are quite sluggish, and change their position on the plant body of their own only rarely.

Though aphids are mostly wingless and idle feeders on plants, occasionally winged individuals appear among them. The winged aphids help dispersal of the species.

The long feeding needles, with a food channel between them, are penetrated deep into the plant tissues, and the tips of the needles reach a phloem cell. Phloem is the plant tissue made up of columns of dilated cells, through which products of photosynthesis, mainly a sugary solution, flow in the plant body, generally in the downward direction, that is away from the leaf bearing part of the plant. That aphids suck juices from the phloem is a statement not wholly correct. The turgor pressure in phloem cells actually forces fluid nourishment into the insect body through its feeding needles. Thus the idle insect gets its food without much efforts on its own part. There is a sucking pump in the head of an aphid, but, if using a sharp instrument the feeding organs are cut across at their base so that the feeding needles remain in situ penetrated into the plant body, while the rest of the insect including the sucking pump in its head is removed, plant sap is seen coming out from the cut end of the needle like mouth parts, and this continues for days (Zimmermann, 1963). Obviously the sluggish aphid gets its food effortlessly. In fact the constant flow of liquid nourishment into the aphid body brings in more food than is needed. Hence from time to time a drop of a sugary liquid appears at the anal end of the aphid. This sweet drop is called honey dew, and is readily grabbed by ants.

This ready availability of food keeps ants moving among aphid colonies, and this association of aphids and ants has evolved into a remarkable case of mutual benefit or symbiosis. Ants get advantage of getting nourishing food. Often ants are seen stroking the abdomens of aphids with their feelers. This makes aphids give out a larger droplet of the sugary liquid. This behaviour of ants does not seem to disturb or irritate the aphids in any way. The hind legs of the aphids resemble the ant feelers and the aphids frequently swing their hind legs, as if inviting ants for feeding.

Ants get advantage of easy availability of food through association with aphids. At the same time aphids get quite some advantage out of this association. Aphids, being wingless and sluggish, are an easy prey to insect parasites and predators. Ants actively defend aphid colonies from such invaders. Their defensive behaviour includes their quick and energetic movements around aphids, biting movements of their jaws and spurting a poisonous liquid through their anal end. If an attacker is not easily driven away, the ants may form a circle around a group of aphids. Some ants deposit debris or make a silken tent over an aphids aggregate. They may make their nest enclosing aphid colonies. The last defensive step is generally shown by ants associated with root feeding subterranean aphids. Pavilions are built by *Oecophylla* ants for the protection of their coccids, which also produce a sugary liquid, and *Pheidole* build them for their aphids and for the paths leading to the aphid groups. The *Hippeococcus* plant lice (Pseudococcidae) in Java, which are also honey dew producing hemipterans, are associated with *Dolichoderus* ants, and, if they are disturbed or menaced by predators, some of them climb on the back of the ants, whilst other lice are grasped between the ant mandibles (Reyne, 1954) and are thus protected.

Aphids from their association with ants reap another advantage. Perhaps company of ants has made aphids very sluggish. Even if the feeding source at one place has nearly dried up, they would not withdraw their feeding needles and move away. It is their tending ants which move them. The ants very carefully pull out the aphid feeding stylets, and then bodily carry away the aphids to a new site or to a new plant. Aphids do not resist this action; in fact they seem to enjoy this free ride (Poole and Poole, 1963).

In temperate parts ants do not leave aphids to die of cold in winter. When it is very cold and freezing outside, they lift their food providing associates, take them to their subterranean nests, and put them in warmth there against roots and rootlets. The aphids drill their feeding stylets into these parts of a plant, and are cosily lodged for the winter. They are again ready to produce sugary drops for the ants. When it is spring the aphids are removed to more exposed parts of the plant by their tenders (Poole and Poole, 1963).

Dying aphids are also a source of food for ants, as ants, associated with aphids, are carrion feeders too.

Thus ants protect and tend colonies of aphids as man looks after his cows, and aphids offer sugary liquid food to ants, as cows provide milk for human consumption. This symbiotic association has made aphids more helpless and dependent on ants, changes almost amounting to ‘domestication’. Aphids have been called ant cows, and aphid tending ants cow herders.

Certain other plant feeding insects are also known to offer sugary food or gland secretions to ants, and get the advantage of their defence in return, for example some lycaenid and riodinid caterpillars, sap feeding Homoptera (aphids, coccids, pseudococcids, membracids, etc.) and some weevils. But the extent of ‘domestication’ in their case is sometimes less than in aphids. Some of these honey dew producers, other than aphids, have been mentioned above.

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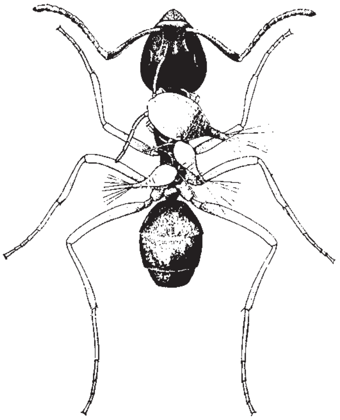
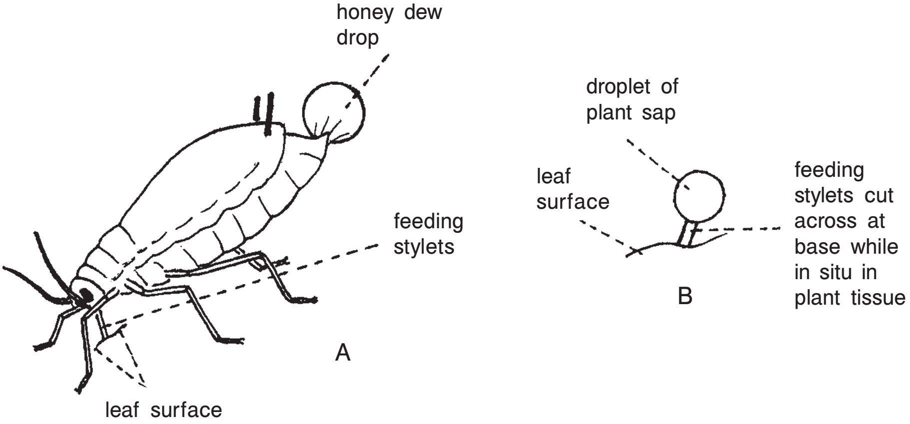
— Fig. 39.1. A wood ant milking an aphid (after von Frisch, 1974).



— Fig. 39.2. *Dolichoderus gibbifer* Emery, a worker running away with *Hippeococcus* on its back Central Java. (from Reyne, 1954).



— Fig. 39.3. A: An aphid feeding position; B: feeding stylets of an aphid, cut across their base, when the insect is feeding. Plant sap droplets keep on appearing for days (based on photographs in Zimmerman, 1963).

— 40. **Locusts**

Locust plagues have been recorded since very early in human history. In the Bible, there is reference to events which happened thousands years ago, viz. locust swarming as one of the ten plagues of Egypt. A locust plague is due to a big swarm of short antennae grasshoppers, called locusts, moving a long distance through several countries, denuding all vegetation of leaves and tender shoots in their way, and bringing in their wake famine, hunger and death in the countries covered. Such locust attacks may show an irregular periodicity, that is appearing every three, four or more years.

The grasshoppers around us may be minor or somewhat serious pests, but they do not form such devastating swarms. How do these grasshoppers differ from locusts? A major breakthrough in solving this problem was made by Uvarov (1928) and Uvarov and Zolotarevsky (1929). They gave what is known as the Phase Theory of Locusts. According to this theory, locusts are highly polymorphic (that is exhibiting two or more forms) grasshoppers. They exhibit two strikingly different forms or phases, a solitary or nonswarming form (phasis solitaria) and a gregarious or swarming phase (phasis gregaria). In addition, there are intermediate or transitory phases (phasis transiens). In the transitory phases are several intermediate forms, showing gradual changes from one extreme form to the other, i.e. from the solitary to the gregarious phase and vice versa. Locusts occur in three subfamilies of the family Acridiidae, Cyrtacanthacridinae, Oedipodinae and Gomphocerinae.

Locust swarms are formed in limited vegetation covered areas surrounded by arid stretches of land. Oases in deserts are favourable spots for rearing of swarms. In such a spot solitary locusts go on feeding and multiplying for some time. They quietly eat away the green food available in abundance. As their population density increases, individuals gradually acquire darker skin pigmentation, change in proportions of certain body parts, and tend to become more active; thus, they change in the direction of the swarming phase. Then in a certain climatically favourable year their population size increases so much that typical migratory phase adults are formed. Such migratory phase locusts look so different from solitary phase individuals that formerly they were regarded as distinct species or genus (e.g. *Pachytylus*). A situation, which may promote swarm formation in locusts: concentration, aggregation and gregarization are so often dependant of a drying out of the habitat, following good breeding conditions (Chapman, in Resh and Cardé, 2003).

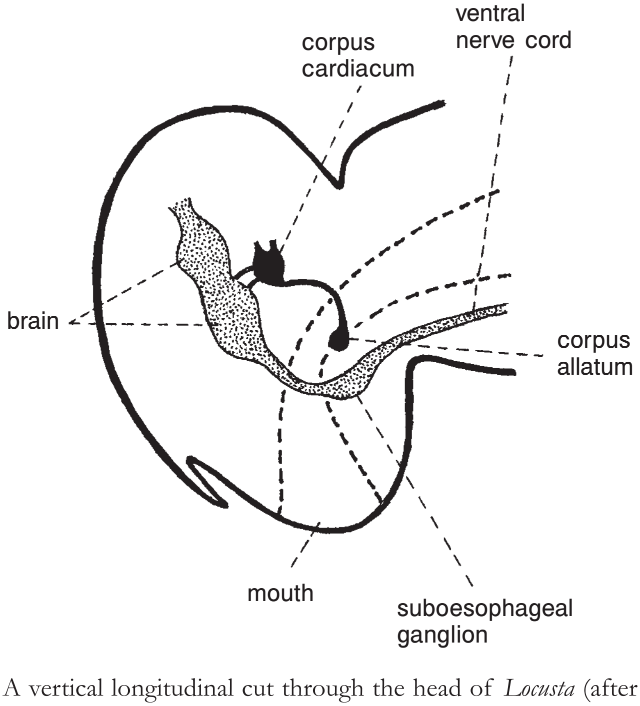
The migratory adults leave as a swarm, and this results in outbreak of a locust plague. Locusts are mostly daytime flyers, and the swarm has no directional movement and is carried downwind. Even if flights are generally downwind, there is, however evidence that the insects can maintain sometimes a particular direction. Night flights are known in the Australian plague locust, *Chorthoicetes terminifera*. In 1988, the swarms, coming from Africa, were carried with the wind to the Caribbean and the northern coast of South America, around 6000 km from their origin in West Africa. PJ still remembers the huge swarms passing through Ethiopia in 1961, devastating everything on their passage. He was once obliged to stop his land-rover since the sky was entirely black with insects.

When the swarm has departed, a number of individuals, which have still only partly changed in the direction of the migratory phase, remain in the habitat of swarm formation. Generation after generation they gradually change to the solitary phase. Population build up continues beyond this phase, and, when the population density has reached a certain incipient value, transition in the direction of the migratory phase again starts, and the cycle is repeated.

Typical solitary phase individuals are leafy green and not very active. But typical migratory phase adults have a pattern of orange and black pigmentation patches on their body, are very active, and have relatively longer femora of the third legs and longer fore wings or tegmina.

What is the mechanism of phase transformation? The problem remains to be solved in satisfying details. But some clues could be deduced from the studies made by a number of workers across the globe. It has been inferred that crowding leads to visual and tactile stimuli. How these stimuli, received by the nervous system, affect the effector organs is not very clear, but neuroendocrine integration (i.e. coordination between the nervous system and the system of hormone producing or endocrine glands) has an important role to play in this. Among the endocrine centres the glands, called corpora allata (singular: corpus allatum, abbr. CA) have a definite role in phase determination. These glands are small ovoid bodies, located in the head beneath the brain. They are connected by nerves with another pair of endocrine centers, corpora cardiaca (singular: corpus cardiacum, abbr. CC), situated a little higher up, closer to the undersurface of the brain. The CC are in turn connected to the middle part of the brain by nerves.

Joly (1955) was first to get definite indications of involvement of CA in phase determination in the locust (*Locusta*). He found that, on implantation



— Fig. 40.1. A vertical longitudinal cut through the head of *Locusta* (after Staal, 1961).

of additional CA from another hopper, a green pigment appeared in the blood of the recepient nymph, and, after the next moult, the pigment appeared in its integument. After some more moults completely green hoppers resulted even in crowded conditions. It may be recalled here that hoppers in the solitary phase have leafy green body colour. These observations have been repeated and confirmed by Staal (1961). In addition, Staal has found that, if CA are removed by microsurgery in the 4th nymph of *Locusta*, the next nymphal stage, i.e. the 5th nymph shows a pattern of yellow and dark pigmentation in the integument, which is characteristic of the gregarious phase, and shows almost adult like features. Staal has also found that, if CA are removed in the 4th nymph, in the 5th nymph the ratio F/C became reduced as compared to what it should be in a solitary phase 5th nymph. (F= length of femur of the third leg; C= width of the head where it the broadest). It may be pointed out here that the ratio F/C has a lower value in gregarious phase nymphs than in solitary phase ones at the same stage. Thus, it has been inferred that deficiency of the CA hormone is a necessary factor in the development of the gregarious phase.

Some other facts, which probably have relevance with the formation of the migratory phase in locusts: A peptide hormone induces the dark coloration of gregarious nymphs. Pheromones (phenylacetonitriles) accelerate maturation, and others are also involved in the maintenance of gregarization. Gregarious coloration has probably an aposematic value. Lizards avoid to eat insects, which have fed on toxic plants.

It seems that development of swarm forming and migratory tendency in locusts needs a genetic proclivity. This notion is supported by the fact that, when a swarm is leaving the breeding area, some individuals, which have not advanced so much towards the migratory phase, remain behind. Thus all individuals do not respond to the same extent to conditions, which tend to produce the gregarious phase. As Staal has pointed out, “It should be clearly understood that non-transient intermediates can also be produced in the laboratory under suitable conditions of intermediate density…” Another situation, supporting the notion of genetic basis for locust swarming: the advancing fronts of locust swarms have been sprayed with modern insecticides. Specially effective has been spraying from aircrafts. These operations have not only successfully checked the locust plague, they have also led to a great reduction in severity and frequency of locust swarming. It appears that the application of insecticides against moving swarms has brought about a Darwinian selection against the genes for swarming.

The devastating effect of locust migrations and swarms, and the largeness of the phenomenon may have led us to believe that this event is unique to locusts among insects. But it is not so. Similar changes in structure and behaviour in high population density may be seen in many other insects, though the changes involved may be much less marked. As pointed out by Staal, some grasshopper species, which do not show swarming, exhibit darkening of skin pigmentation and changes in bodily proportions in the state of crowding. Group stimulation is known to induce formation of well developed wings in book lice (Psocoptera) and aphids (Aphididae). The small winged grasshopper *Zonocerus* shows increase in wing length and short range migrations on crowding.

The legume weevils (members of the beetle family Bruchidae) of stored legumes are known to produce "normal" and "active" or "flight" phases, with several intermediate phases (Caswell, 1960; Utida, 1972; Tiwary and Verma, 1989a; George and Verma, 1994). There are many parallels between polymorphism in locust species and that in the stored legume infesting bruchids. The active bruchid individuals are, as the phase name suggests, more active than normal ones, have darker skin pigmentation and have longer wings (George and Verma, 1994). From experiments Tiwary and Verma (1989b) have inferred that deficiency of corpus allatum secretion promotes appearance of the active form in *Callosobruchus analis*. Both in locusts as well as in these bruchids crowding leads to production of some migratory or specially active individuals (for bruchids see Tiwary and Verma, 1989c). Tiwary and Verma (1989b) have performed various experimental crosses between different phases of *Callosobruchus analis*, and have reached the inference that for development into the active phase a genetic proclivity is needed.

Other examples may be cited to show that the locust phenomenon is not unique to locusts. Ronkin (1978) has described a migratory phase of the potato beetle *Leptinotarsa decemlineata*. The beetle *Chrysolina aurichalcea* is flightless, and has small wings. But Suzuki has described a population of this species with flying behaviour. This population shows some significant similarity with the active phase of *Callosobruchus maculatus* (see Verma and Kalaichelvan, 2004).

The swarming phenomenon of locusts stands quite apart from similar other examples of production of specially active individuals on crowding among insects because of largeness of locust swarms and the huge damage they do to things of human interest. The locust problem could be largely solved through extensive investigations on their biology, through use of modern insecticides and through international cooperation. When nations with swarm producing areas shared information about the phase status of breeding locusts with the nations likely to be covered in the forthcoming locust migration, the latter could forearm themselves to control the menace. But a lot of political conflict and instability in the Middle East and in the western part of the Indian subcontinent have greatly impaired the transnational antilocust efforts. We hear at times about small swarms still being formed. The year 2004 has seen new plague locust migrations over Africa. Slackness in these multinational efforts may encourage selection in favour of the genes for swarming and migratory tendencies in locust species, and the locust problem may return.

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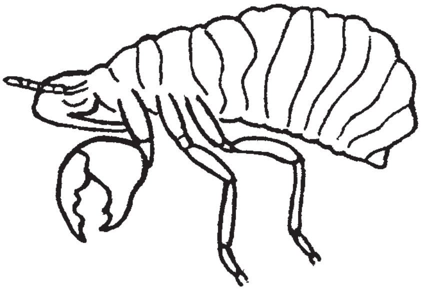
— 41. **Walking in Insects**

Insects are primarily terrestrial, though some have secondarily taken to life in water. The aquatic insects have adopted various methods of swimming or skating on water surface, but vast majority of insects walk on a solid surface. An insect has three pairs of legs; hence the class of insects is also referred to as Hexapoda.

How does an insect walk with six legs? At any moment during walking the insect rests on the substratum with minimum of three legs, a middle leg on one side and anterior and posterior legs on the opposite side. These three legs support the weight of the body like a tripod. The other three legs make the insect move; among them the front leg produces traction for the body or pulls it forward, the hind leg propels the body forward, and the middle leg mainly supports the weight of the body on its side. Cinematographic records reveal that the three legs, providing tripod like support at one moment, are lifted from the substratum at the next moment in the following order: first the front leg, next the middle leg of the other side, followed by the hind leg. Thus at any moment 3, 4, or 5 legs are on the ground. In fast moving there may be a change in the sequence of leg movements.

Some terrestrial insects show significant deviations from the general way of walking, described above. Nymphs of bugs, called cicadas, lead a subterranean life, sucking juices from rootlets of various trees. They make burrows in soil. Greatly enlarged tibia and femora of their fore leg form a sort of shovel for digging soil. Traction for movement in a burrow is provided by long middle legs, while long hind legs provide a crutch like



— Fig. 41.1. Nymph of a Cicada. Note its shovel-like front legs.

support and propel the body forward. Urine of the nymph cements soil particles and prevents caving in.

Preying mantis, with its front legs modified into raptorial organs for catching and holding preys, also moves on middle and hind pairs of legs. Insects jump (alticines, fleas, Orthoptera, etc.) with the help of enlarged hind legs. They even negotiate obstacles, walk up a vertical surface and even some, like flies, can walk on the ceilings without any problem (thanks to a combination of claws and pads, covered with oily secretions, as in coackroaches and leaf-beetles). Mole crickets (*Gryllotalpa*) dig deep in the soil using their huge and dentate forelegs.

In 1972, Bernadette Delage-Darchen discovered a new and interesting species of ants, *Melissotarsus weissi* (=*titubans*) in Ivory Coast. These tiny ants make and live in burrows in wood of trunks of various trees, and feed on cochineals (Diaspididae), which live and grow inside the burrows. Locomotion in these ants in the burrows is due to anterior and posterior pairs of legs, while the middle pair of legs is modified for palpating the ceiling of the burrow. The middle legs, besides being sensory, are provided with glands secreting a pheromone for marking the burrow, through which the ant moves. When kept on an open surface, with no ceiling above for palpating, the ants are unable to make normal and proper locomotion.

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— 42. **Coprophagy – insect brethren of the crowned pigs of Borneo**

Cuenot, the French biologist, trying to demonstrate the finality of the things of this world, once wrote in a humorous vein, "Excretion (he meant egestion) is pleasant!"

Horatius, the Latin poet, in his Satires, wrote one day the following verses:

> "*Mentior at si quid, merdis caput inquiner albis*
> *Corvorum ; atque in me veniant mictum atque cacatum…*
> (If I am lying in something, may my head be covered with the white
> shit of the crows, that come to me poo and pee).

This aspect of life has been touched in Latin or Greek more bluntly in writings of Suetonius, Petronius and Aristophane comedies. During that classical period a spade was called a spade.

This aspect of life, egestion, is generally considered a humiliating aspect, and we try to keep it in privacy, and do not talk about it. But as students of life, we should have no hesitation in discussing it boldly, here mainly in relation to insects.

Human and certain animal excreta provide food to Scarabeidae, the dung beetles. Those insects are however selective and pure gourmets. Some prefer human excreta, others monkey's shit, still others are found to live on bird droppings, or on antelope feces or elephant discharges. Under our climates, as under the tropics, the selection is strict and nearly as strict as is plant selection among the phytophagous insects. Certain species are specialized for feeding on semi-liquid excreta, like cow's dung, while others choose dry excreta as that from rabbit, marsupials, or horse. With the introduction of cattle, flies multiplied fast in Australia. It was the same in Hawaii with introduced mammals normally producing liquid feces, such as cattle. The problem was solved to some extent by Waterhouse in CSIRO in Canberra by introducing African and other tropical scarabs to feed on the liquid dung. This led to drastic reduction in the number of flies. However, PJ must say that there are still flies in the land of kangaroos, and they still are quite abundant. Somehow this introduction of dung beetles did not fully succeed. In New Guinea, the local scarabs (*Onthophagus*) are adapted naturally to feeding on horse excreta (Paulian, 1972), and they could never take to cow dung. In New Caledonia and Vuanatu (New Hebrides) also there were no big mammals in the past, except bats and a few rodents, and local scarabs fed normally, near Noumea, among others, on bird (cagoo) excreta. In Australia, New Guinea, New Zealand and New Caledonia no beetle has adapted to semi-liquid cow dung. An introduction of one Onthophagini, two Oniticellini and one Sisyphini, all scarabs, has brought to New-Caledonia and Vuanatu cow dung feeders (Gutierrez *et al.*, 1988). Three among the introduced species appear to be established on those islands. In Australia, there are dung beetles, which are adapted naturally to plant food as normal diet.

One day, in Ethiopia, in Ogaden valley, in a locality named Awash, one Ethiopian student of PJ observed big scarabeids, very busy around buffalo dung, feeding on it. He looked around and said: "It is their injera". Injera could be translated as bread. Injera in Ethiopia is the acid pancake made with teff flour. Teff is a peculiar Poaceae (Gramineae), *Agrostis teff*, with very small grains, cultivated in Ethiopia and in Eastern Sudan. It tastes a bit like sarracen (buckweed) flour. Yes, it was injera for those scarabs, who were eating it with delight. All we can say is that everyone has his own taste, even if that taste seems disgusting to us. This holds for the human species too. One man's joy is another man's sorrow (Jolivet, 1991).

It is a fact that nature has done well in adapting every species to search for and locate the source of suitable nourishment, and only exceptionally animals feed on their own excreta. An example of this is gorillas, which probably take to autocoprophagy to get vitamins. The smelly substance of excreta, the skatol (3-methylindol) is used, in small quantities, as a stabiliser of the flavour of vanilla in ice creams. Nature synthesizes skatol in Arum flowers (*Zantedeschia aethiopica)* to attract pollinating flies, and civet cats in Africa also have glands producing skatol. This chemical is widely used in perfume industry for giving long shelf life to odours. PJ remembers those civet cats in Ethiopia, which were expressing their hate when people were pressing their perfume glands to extract the precious molecules. The Abyssinian cheaters used to mix up sometimes child poo and that was why our perfumers in Paris used to pay the shipment only after analysis of the contents. After all, consistency and smell and even similar chemical formula, were present in the two, above mentioned, producers. Now an anonymous poem looks rather appropriate:

Why Your Offal Smell Awful.

Your body ejects poisons and things
It won't need,
And these are the things on which
You mustn'feed.

If your offal smelt tasty, like fresh
Cherry-pie,
Then you might eat it, and then you
Would die.

Your offal smells so bad that you kick
It off your plate
You then may survive and may
Procreate.

If ever an animal found its waste in
Good taste,
Evolution has cured that condition
Post-haste.

It would be necessary to ask gorillas why they behave that way. However, animals feed on other animal excreta, but practically never on their own.

Excreta are an excellent attraction not only for scarabs, but also for the splendid butterflies, often sensitive to smells, which to us seem nauseating. Around 50 years ago, one Belgian M.D., whom I want to keep anonymous, was the director of a hospital in Congo, and was also an ardent collector of butterflies. This medico-entomologist accumulated human excreta, with help of his boys, deposited over paw-paw leaves (*Carica papaya*), generally used in that country to tenderise the emaciated and leathery chickens living there. Those paw-paw leaves, so beautifully decorated with feces, were religiously deposited on the various shelves of the hospital refrigerator. Each morning the medico used to take one leaf, and place it on the garden lawn. Nearby a native, a green net in his hand, was trying to catch the beautiful *Charaxes* or other butterflies feeding on the decorated leaves.

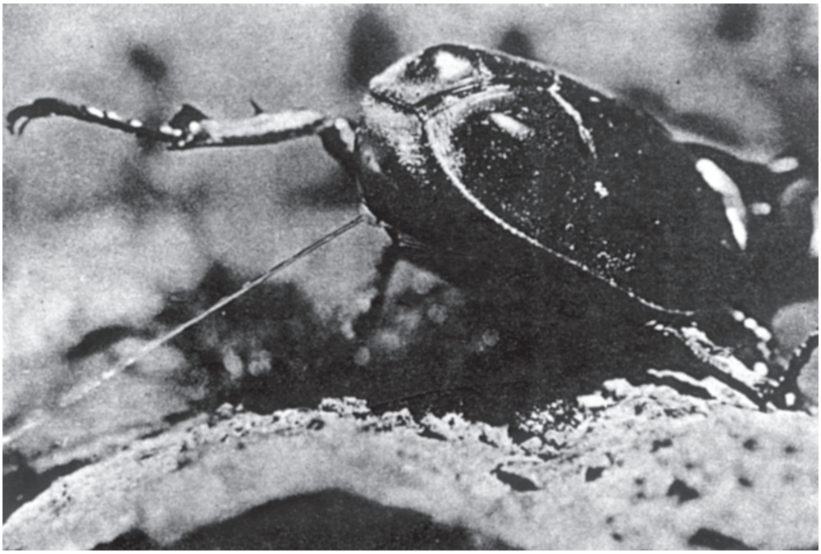
The truth is that with modern traps, suspended on trees, one can catch very easily these Lepidoptera, attracting them with rotten bananas and also human urine. Such secret recipes are also known to entomologists as making a cocktail of excreta, urine, rum and rotten fruits. I think that the good Belgian doctor was trying to do his best in his circumstances.

The splendid *Graphium weskei,* a Papilionidae, of which the host-plant remains unknown, gets down to drink in the middle altitude (1500 m) water falls in New Guinea. It is equally well sensitive to traps with organic matter and to pure water. It normally drinks on humid sand along the shores. Beetles, other than the dung beetles, may be also attracted by feces. In Florida, an American colleague, Bob Woodruff, found one day a chrysomelid (Lamprosomatinae) *Oomorphus floridanus*, feeding on rodent excreta. Normally that genus is an ardent feeder on Araliaceae plants. Is it an aberration? No, it is simply attraction towards a medium rich in water, salts and nitrogenous compounds (Jolivet and Verma, 2002).

Recently a good book has been written on this topic (Lewin, 1999). In this book not less than 22 paragraphs have been dedicated to insects. It is known that merdigerous, merdicolous, scatophagous, stercorarious, onthophagous flies and beetles are numerous. Merda in latin, skatos, stercos, onthos in Greek, all mean shit. These words show the richness of Latin and Greek languages. In this book, excretion is minutely studied and described, including its structure, its smell and its chemistry.

Lewin seems to assign partial production of greenhouse gases to the flatulence of cows. Termites also contribute gases in this process. In amber, when termites are caught, you can see the fossil traces, as tiny bubbles, of their palaeontological flatulence. He also mentions frequency of defecation among insects and vertebrates. He says that the Guatemala viper excretes once a month (practically it is the same for the sloth, but the ceremony involves also moths living in the sloth's fur) and that the rabbits do it once every three minutes. Termites feed on plant matter and fungi along with their intestinal fauna (Hypermastiginae). They produce gases abundantly. Their number compensates for their small body size. Americans have attributed yellow rain in Vietnam to the overabundant excreta of the bees.

It is certain that dung beetles help to clean our planet by feeding on animal excreta, while necrophores, like vultures and hyaenas also help by feeding on cadavers. Many books have been dedicated to the biology of the dung beetles (Hanski and Cambefort, 1991), and this significance of the scarabs has been well brought out by Lewin. Lewin is also a great oceanographer, and is married to a marine entomologist. He combines qualities of an eminent scatophile and a poet, celebrating plants and insects (Lewin, 2003).



— Fig. 42.1. Urinating posture of *Allomyrina dichotoma* (Linnaeus) (Scarabeidae, Dynastinae), in Japan (after Ohtani and Kuribayashi, 1985).

Human excreta are normally rich in salts, and the pigs in the Orient feed on them with relish. All tastes are in nature, but for the pig it is *Lucullus cenat apud Lucullum*. In South East Asia, thanks to pigs, everything is eaten and thus removed, and river banks are clean, unlike what we see in the Middle East. It is true that in Vietnam, for instance, the poor pigs have nothing else to eat, but for duckweed, which is collected dextrously by the women in ponds. One of PJ's former colleagues, Dr. Farinaud, eminent malarialogist with WHO, told us once that one day in Vietnam, as he was busy relieving himself in a rice field, he felt something humid on his rear. It was a pig, which was removing directly the product from the producer. In Borneo, the Dayaks live in houses, raised on poles. People, during night, relieve themselves through gaps between wooden planks in the floor. Below chickens and pigs fight for the manna dropped from the sky. We nicknamed them the crowned pigs of Borneo, as they were generally crowned with excreta, but they all seemed to be happy and to be fighting for the fodder. In Vietnam the piggery is often near toilets, and the pork is excellent, if you don't think of the nourishment source for the pigs. Sweet and sour pork is always good everywhere. Those pigs do not eat their own excreta. They don't live in close confinement, as their food collection requires perpetual movement. Pigs are teachable, and the dwarf ones, used as pets in the US, are as clean as cats and dogs.

Ethiopians, as also Jews or Arabs, do not eat pork meat. Pigs, except wild, are rare in the country. Hyaenas do cleaning during nights in the streets of Addis Ababa. In Brazil and in Guyana, there are the urubus, sort of big crows, which do the job. Nature has an army of nonpolluting cleaners, such as hyaenas, pigs, birds, insects, worms etc. Armadillos also contribute to the cleaning in America. Bacteria and fungi achieve the final destruction. Plastics, however, resist destruction by such natural cleaners.

During the Palaeozoic, recycling of dead bodies was done by the great proto-myriapods, the *Arthropleura*, two metres long monsters, which were feeding on lycopods and decaying matter. Scavengers were numerous at that time. During the Mesozoic, there were necrophagous dinosaurs, like *Tyrannosaurus*, and they were necessary to clean the enormous bodies of their herbivorous 'colleagues'. There were also very probably numerous coprophagous beetles, since the first Coleoptera appeared during the Permian, just before the dinosaurs. The dung beetles were elevated to the rank of sacred animals during Egyptian times, because they symbolically carry the world with their ball of dung.

A folklore runs as follows. During the colonial period, a French administrator flew into a towering rage on seeing pigs wandering on the streets of a village near the Chinese border. He complained to the chief of the village. The chief knew the French people and he agreed formally to send away or to destroy the pigs, but he did not do anything. During his second visit, the administrator saw again the wandering pigs in the streets. He got angry again. The chief again politely agreed to take necessary steps, but again did nothing. During his third visit, the administrator shot at the pigs, and the village chief thought that it was time to do something. With the help of a peasant he carried the pigs to Yunnan on the other side of the border. When the administrator came back for the fourth time, he found the village very dirty. He complained that to the chief, who said that without the pigs it was perfectly normal to see the village dirty. Then the administrator asked to bring back the pigs. The chief brought them back from Yunnan, and again the village was totally clean.

All animals excrete, even the smallest members of plankton in the sea, and almost all the insects. Urinating postures of some Dynastinae in Japan has been described by Ohtani and Kuribayashi (1985). Some, like big saturniid moths, don't have an opened intestine and don't excrete at the adult stage, but they do well as a caterpillar. Some chironomids and many other insects also don't eat or excrete as adults.

There are many books on excretion and we would recommend a classic, the Microscopic Coprology of Langeron and Rondeau du Noyer (1930). Coprology we find in the writings of many authors (Rabelais, Swift, Lord Byron, even Shakespeare). Sigmund Freud, who was victim of a chronic constipation, is one of the celebrities involved. Finally, all living things must excrete at certain moment of their life. I cannot say we must feel proud of it, but we are not ashamed of it. *Ad augusta per angusta*. In view of the universal process of excretion in the animal world the importance of coprophagous cleaners like the dung beetles should be appreciated.

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— 43. Lamarck's Ghost or the Baldwin Effect – a proposed explanation for development of Insect domatia

Anglo-Saxon authors have remained faithful to the Darwinian concept of evolution, though from time to time some black sheep tried timidly to shake the edifice and the dogma of Darwinism. Only some very rare and original "froggies" (meaning here French biologists) still dare to preach in favour of Lamarckism, which emphasised inheritance of acquired characters as an important factor in the working of evolution. Not only because Lamarck was a Frenchman, but also for the pleasure to be different and to annoy their neighbours! It has been also a kind of patriotism that Frenchmen have always been defiant to the dogmatic English.

Darwinian dominance was not the same during the last century in France. Most of the zoologists in the Universities and the Museums were openly or secretly believing in the transmission of the acquired characters. Gould (1980) pejoratively named attempts to solve the problems, which could not be addressed effectively by Darwinism, as "the shades of Lamarck", sometimes with disconcerting shades. Among Lamarck's disciples very few subsist today; they speculate on events in the time parameter, a parameter not directly accessible at present, while the Darwinians have found another explanation, subtle indeed, and always theoretically plausible. Today to be Lamarckian is rare, and is regarded old fashioned, but to be fixist is even rarer. People say that in the Land of Darwinism some rare fixists subsist even in the bowels of the Natural History Museum, the former British Museum. That was around the mid-thirties, that a director of the French Museum of Natural History, Paul Lemoine, wrote: "Evolution is a dogma, in which his priests do not believe, but that they maintain for the people". It was printed at the head of the French Encyclopedia. That was a big scandal then and the biologists of that time, P. P. Grassé and George Teissier called the zoologists to a meeting to discuss openly the matter. Lemoine was a sophist and maintained his point of view, just to be different.

From time to time, rare biologists pretend that they could prove Lamarckism by experiments on bacteria, protozoa or viruses (Anonymous, 1981), but more recently on gerbils. An old experiment: a French amateur entomologist, around the forties, used to cut the mediodorsal horn of a *Sphinx* caterpillar and pretended to obtain a significant proportion of hornless caterpillars in the next generation. Correctness of his findings is doubtful, but only for fun the experiments could be repeated. Cutting the mouse tail for generations to prove Lamarckism is wrong is absurd; it is a mutilation, not a gradual change by evolution.

Jeannel, the French coleopterist, was Lamarckian, as he believed openly in the inheritance of acquired characters, because he dealt a lot with cave insects, and he found a Lamarckian explanation satisfying (Jeannel, 1950). He could not see any other explanation adequate to account for degeneration of some organs and of hypertrophy of others resulting from their non-use or over-use in the cave environment, for example, the blindness of the cave insects, the physogastry of certain beetles, the lengthening of their antennae, the discoloration of their bodies, and the elongation of their legs. In Cuénot's classical books (1932, 1925; Cuénot and Tétry, 1951), though all Darwinist, sometimes appear the shades of Lamarck. One book, written by Wintrebert (1962), entitled "The Living Being Creator of its Evolution", is purely Lamarckian, as well as the one written by Hovasse (1950). As the Phoenix, Lamarckism is rising always from its ashes, and Wintrebert defended what he called the chemical Larmarckism or as Jean Rostand (1958, 1962) used to say "the intelligence of the inanimate matter".

During PJ's youth, he was a student of L. Cuénot, of P. P. Grassé and others, and at that time they were all officially Darwinian, as well as Georges Teissier. That was the same Teissier who proved in Roscoff that wingless *Drosophila* survived better on a roof exposed to wind than winged ones. From that experiment, the loss of wings on mountains and islands was theoretically explained. Rabaud, another crypto-Lamarckian, succeeded to stop the creation of a chair of genetics in Paris until 1947. He was materialist, but against any finalism in evolution. It was also in fashion at that time to negate the mimetism. That was the situation with home naturalists, and also of some outside France. The reason was not specially to be Lamarckian (Lamarckism does not explain the mimetism), but to be anti-Darwin. In the modern world, the minds have evolved, and there are even sociobiologists among the young French workers.

The chief merit of Lamarck was to express for the first time clearly the idea of evolution as a reality in nature. That is what even the fiercest disciples of Darwin recognize, even if the Lamarck's basis of the evolutionary mechanism theory remains unprovable. Darwin, who did not like Lamarck and criticised him openly, accepted some of his theories.

There is, however, a small problem, which still remains difficult to explain, and that J. Mark Baldwin (1896) named a "new factor of the evolution", and which was baptized later as the "Baldwin effect". Cuénot discussed that in details in his books (namely 1925 and 1951) and later on S. J. Gould (1980) recalled the matter in "Panda's Thumb". Really the Baldwin effect has been often used to explain the inexplicable or not easily explicable. If the Lamarckian explanation is appealing, we can also use the adaptive effect of the natural selection on a great number of generations. Another problem, which is not raised here and remains also difficult to explain is the Hopkins' principle, which states that chemical experience (food selection habit) acquired by the larva of an endopterygote insect can be transferred through the pupal stage to the adult and to the next generation (Van Emden *et al.*, 1996). There are also Darwinian interpretations of the principle, and no unambiguous evidence for it has ever been obtained.

Baldwin effect is a sequential process in which characters, acquired under the effect of the environment, are assimilated by genetic factors, i.e. they become heritable. It is Hovasse (1950) who baptized the concept as "Baldwin principle", which was preferred to "Baldwin effect". In brief, the selection would be based on the aptitude to acquire new characters in agreement with the phenocopies, i.e. the somations provoked by the environment. Baldwin effect or genetic assimilation was the reason to question the Darwinian theory several times in Cuenot's writings.

A good interpretation of the Baldwin effect is the one given by Mayr (1974): "The situation where, due to an appropiate modification of the phenotype, an organism can stay in favourable environment, until the selection has achieved the genetic fixation of its phenotype". This interpretation was in some ways a tempting reconciliation between Larmarckism and neo-Darwinism. Huxley (1942), himself a passionate Darwinian, believed in the Baldwin effect, to which he attributed the formation of races.

According to Simpson (1953), who did not believe much in the Baldwin effect, the effect itself would comprise three steps:

(1) The organisms react with the environment so as to produce behavioural, physiological or structural changes, which are not hereditary (somatic), and which show some advantages for survival, i.e. adaptative for the individuals.
(2) There happen mutations in genetic factors; such mutations, which produce hereditary characters similar to those mentioned above, having the same adaptive advantages
(3) Mutant genetic factors, as mentioned under (2) are selected by the natural selection process, and show the tendency to spread among the population through the generations. The result is that those non-hereditary adaptations become hereditary.

The classic cases of the callosities of the ostriches, rheas, emus, or phacocheres, which appear already in the embryos (Cuénot, 1925; Cuénot and Tetry, 1951), are typical cases, which need deep consideration. "I don't know any clearer and at the same time more favourable example to the Lamarckian thesis than the thickening of the plantar sole and the mammal callosities", wrote Cuénot. Really, the adaptation is flagrant, but no more surprising than other adaptations. A long natural selection can perhaps explain the callosities for the fixation of acquired characters. Evidently some questions remain unanswered. Nothing is perfectly clear in this area. It is evident also that the mite pockets are present in the reptile embryos (see the chapter "Pocket mites") as well as the domatia (dwellings) of ants or mites among plants existed before the arrival of ants and persist in greenhouses where ants or mites don't exist.

An example among the *Acacia*: the horned *Acacia* of East Africa harbour ants and also symbiotic beetles. The horns are stipular spines, sometimes very big and variable from tree to tree. The explanations about their origin vary: Lamarckian (Beccari), galls (Jeannel), preadaptation (Schnell) and coevolution (Janzen). Hocking (1970, 1975) gives a Baldwinian interpretation!

Only the Central-American or East-African *Acacia* have those enormous inflated spines and are regularly inhabited by ants. Among the Central American *Acacia*, the differentiations are so big that the tree provides the protein rich food called trophosomes or the beltian bodies, and sugars from extra-floral nectaries. Among the East-African *Acacia*, only lodging is offered to ants with a bit of nectar. The ants compensate by rearing coccids. Australian *Acacia*, the most numerous and the most diversified, have never offered something similar to ants, perhaps because the big browsing mammals were absent from the continent. Ants, not specialized there, use to collect nectar from the trees. How then should we explain the occurrence of stipular spines in two different parts of the world, the adaptation to certain ants and even the providing food to the insect guests?

The first explanation, which comes to the mind, it is the preadaptation of those structures, occupied later on by the ants. It is Schnell's thesis (1970). The second is the coevolution of plants and ants, dear to Janzen, which could explain that way the close adaptation between the American *Acacia* and their hosts. All those theories have been explained in detail in Jolivet (1986; 1996 a and b).

Hocking (1975) invokes the Baldwin effect. Here goes how he explains this evolution. The *Acacia* spines, in Africa, according to him, originally were Homoptera galls, probably from aphids. Certain galls would have had sometimes a rough resemblance with poplar galls, even with a histological similarity. The sensitivity of the plant to this initial stimulus would have been selected in view of the big advantages that it confers to both ants and to plants. While ants got lodging and readily available food, plants got protection by lodging ants against herbivorous animals. If the threshold of the response by the plant is such that development of a gall takes place only in presence of an insect, then galls would be of different types due to diversity of the gall producing Homoptera. The diversity of shape of the ant lodging *Acacia* galls then becomes understandable. According to Hocking, this explanation amounts to the Baldwin effect, and is similar to the one used to explain the early development of callosities in ostriches.

This explanation, for us, is not a good one. It is a far-fetched argument. Either it has been a coevolution between *Acacia* and ants, or there has been a preadaptation of stipular horns, since these spines can develop easily without ants and without any kind of stimulus. We must also reject a modification of the stipules under the effect of the ants, as believed by Beccari and Delpino, modification becoming later on hereditary. It is not so simple as that.

Hopkin's explanation to the problem, as mentioned earlier (see van Emden *et al.*, 1996, cited above), is debatable. According to this explanation, adults of polyphagous and oligophagous herbivorous insects show a tendency to deposit their eggs on the host plant, on which they were previously reared as larvae. Certain experiments with the vinegar fly *Drosophila* support this assumption. But how is the plant's preference in the larvae transferred to the adult insect? Suitable experiments should provide an answer.

In choosing among all these interpretations, time remains the main hurdle, the "deus ex machina". However, we must say that Baldwin effect seems to offer an explanation as to the origin of certain fixed adaptations, even if the explanation offered remains to some extent vague and tortuous. Lamarckism has never been proved. Animals, living in dark, do not lose their eyes; they lose some of their function, at least on a short time. Experiments of Kammerer on *Proteus* were pure lies, also the theories of the sinister Lysenko. We have seen that natural selection and Darwinism explains very well the microevolution. For the macroevolution, it is another matter. Not ignoring the factor time, over millions of years, we must accept the classical explanation of Neodarwinism. Gould had added the concept of punctuated equilibrium, but since we have seen probably a very small part of the fossils which exist, particularly among insects, we have not been able to present an acceptable tree of evolution, and to visualise if some events in the past were due to the Baldwinian effect or to any other reason.

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— 44. **Acknowledgements**

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