Cycloalexy: A new concept in the larval defense of insects.

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Introduction

Anyone who has ever seen a Western will be familiar with the defensive tactics employed by the pioneers: The wagon train is formed into a ring, women and children on the inside, with the men firing out at the circling Indians. The larvae of some Coleoptera and Hymenoptera have long employed similar tactics, in defence against their predators (ants, bugs) and parasitoids (wasps, flies).

Historical Background

Over the years, numerous papers have dealt with grouping in tenthredinoid (sawfly) larvae (eg. Wheeler and Mann 1923 and D'Azevedo Marques 1933). Among the chrysomelids (leaf beetles) there are also numerous references, but only Andrade (1981) refers to a circular defense strategy... None of these authors appear to have grasped the full significance of the pattern. The concept of cycloalexy, or circular defense, was crystallised independently by two workers: Joao Vasconcellos-Neto in Campinas, Brazil, and Pierre Jolivet in Paris, France. A joint publication in the Bull. Ent. Soc. Fr. resulted, formalising the concept (1988). Further publications on cycloalexy followed (Vasconcellos and Jolivet 1988, Weinstein 1989), and as a new concept, it is bound to develop further. The behaviour itself is, of course, almost as old as insects themselves, and it is of considerable interest to sociobiologists: All insects demonstrating cycloalexy are subsocial in the larval stage, and often also exhibit maternal care of eggs or larvae (e.g. Stolaini, Pergidae, Gonioctena).

Definitions

Cycloalexy (kuklos = circle, alexo = defend) is defined here as "the attitude adopted at rest by some insect larvae, both diurnal and nocturnal, in a tight circle where either the heads or ends of the abdomen are juxtaposed at the periphery, with the remaining larvae at the center of the circle. Coordinated movements such as the adoption of threatening attitudes, regurgitation, and biting, are used to repel predators or parasitoids."

Cycloalexy is recorded in chrysomelids (Coleoptera) and tenthredinids (Hymenoptera), and has analogues in vertebrates. Penguins and muskoxen, living in familial groups, sometimes adopt a circular formation of males, protecting the young and females from potential predators (Wilson 1978). Other cases are known (*Tauritragus oryx, Cervus canadensis*), and still more undoubtedly await description.

Examples among insects

A: Cycloalexy with heads on outside of circle

Example 1: The chrysomelid *Platyphora conviva* Stal.

Platyphora (*Doryphora*) is closely related to the other doryphorids, which include the notable *Leptinotarsa decemlineata.* This American genus eats hard leaved *Solanum* shrubs rather than the soft leaved varieties preferred by doryphorids, and appears to be obligately viviparous. Vasconcellos-Neto has studied the Brazilian *Platyphora conviva*, and this species demonstrates cycloalexy. The larvae are found at an altitude of 800 to 1200 m, congregating in circles on the underside of leaves, with but a few larvae in the centre of the circle (photo 5-6). Meanwhile, the adult assumes an exposed position on the top surface of the same leaf. These unique larvae also cover themselves with hairs taken from the underside of the leaf. This camouflage/defense is rare among chrysomelids, the only other known occurrence being among the larvae of some neotropical Chlamisinae.

When disturbed, the outer larvae rear up, opening their mouths and raising their front legs in a menacing fashion. A gastric secretion is ejected through the mouth and is presumed to be toxic as a result of its origin from the host shrub *Solanum*. If disturbed further, these larvae attempt to bite the attacker, as is easily demonstrated by presenting a pencil to them. If the circle is broken, larvae fall easy prey to pentatomids and ants.

The larvae feed at dusk and during the night, in a row along the edge of the leaf. The circular pattern is readopted each morning. When moulting, the larvae adopt their defensive posture, but not as a circle. New hairs are stripped from the leaves to replace those lost with the exuvium.

Example 2: Tenthredinoid sawflies.

Sawflies are primitive wasps, and the phytophagous larvae often show a gregarious tendency, including cycloalexy. Their defensive behaviors encompass immobilisation, aggressive posturing, projectile exsanguination and regurgitation. Adult females lay 50 or so eggs which they insert into leaf tissue, and may demonstrate maternal care. In the latter case, the female may guard her eggs/larvae by buzzing her wings to deter intruders, even biting or clinging to the aggressor.

Although there are many examples of cycloalexy on record from the Tenthridinoidea, their authors do not appear to have grasped the significance of the phenomenon; these include *Bergiana* (Cimbicidae) in Brazil, *Dielocerus* and *Themos* (Argidae) also in Brazil, and *Perga* s.l. in Australia. Prop (1960) suggests that gregarious larval displays in sawflies can intimidate parasitoids, and even, although temporarily, an avian predator. As the gregarious larvae are predominantly nocturnal, cycloalexy is a diurnal resting pattern. In the case of united colonies, younger larvae are sometimes found in the center of the circle (Dias 1975, Lewis 1836, Photo 7).

The circular defense strategy of larvae of the Australian genus *Perga* s.l. has often been cited (Froggatt 1890, Evans 1934, Lewis 1836, Carne 1962) and is the subject of recent studies by Weinstein (1988, 1989). These pergid larvae are nocturnal defoliators of *Eucalyptus*, and appear to all demonstrate cycloalexy. When the circle of 40 or so larvae is threatened, the larvae rear up in unison, regurgitating sequestered eucalyptus oils from their mouths. Such a group, "emitting a penetrating odor of *Eucalytpus,* and waving their tails in unison, presents a formidable and unappetising sight" (Evans 1934). As in *Platyphora* (Chrysomelidae), the larvae will bite if disturbed further, and Weinstein (1989) has photographed the altruistic 'suicide' of a larva biting the ovipositor of a parasitoid wasp.

Upon eclosion, the first larvae assume a ring formation within minutes, and this is augment-

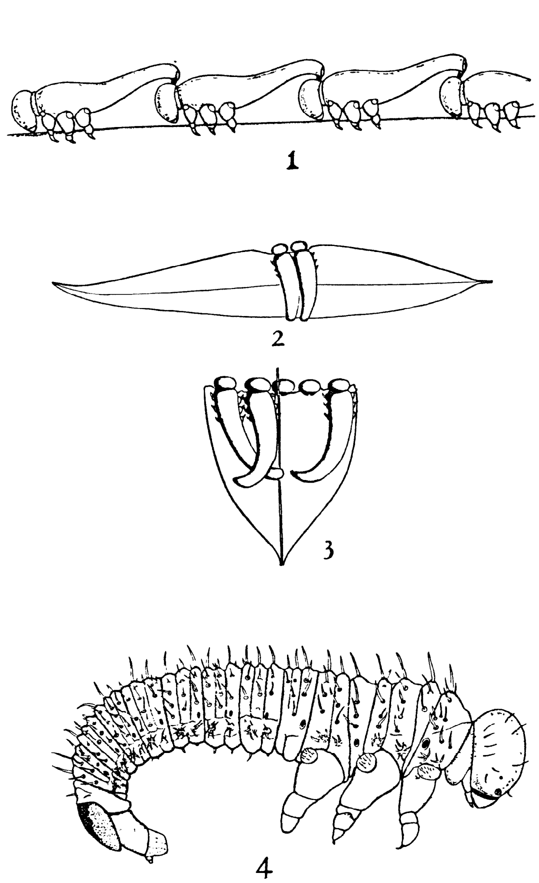


Figure 1-4. *Perga dorsalis* Leach. 1) Diagrammatic sketch to show a method by which larvae may keep in touch with each other when on the move. 2-3) Diagrammatic sketch of larvae feeding. 4) Full-grown larva, Australia (after Evans, 1934).

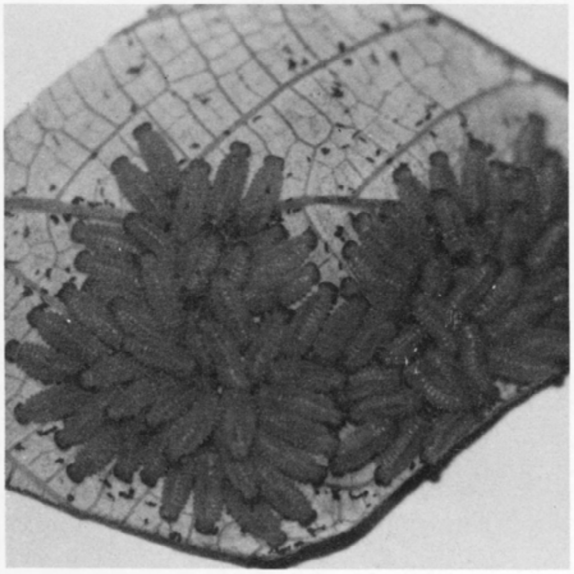
Figure 5. Mass defensive reaction by newly hatched, gregarious larvae of *Ascaloptynx furciger* (Neuroptera: Ascalaphidae), similar to that of Cassidinae pupae or old larvae of Symphyta (after Henry, 1972).

ed as further larvae eclose and join the group. The formation is the normal resting position until the second or third instar, when the larvae can no longer fit under a single leaf. A cylindrical mass is then formed about a twig or branch (Carne 1962, Weinstein 1989); this is similar behavior to that demonstrated by cassidine larvae of the tribe Stolaini (photo 12). When moving out to feed, the larvae maintain contact by the ones in front holding the ends of their abdomens over the heads or thoraces of the larvae behind (fig. 1). To reunite the dispersed colony, the substrate is tapped with the hardened terminal abdominal sclerite (uropod), and the larvae converge by means of the resulting vibrations. The latter behavior may result in the fusion of unrelated colonies, forming polyspecific and even polygeneric circles.

B: Cycloalexy with abdomens on outside of circle.

Example 1: The galerucine (Chrysomelidae) *Coelomera*.

Living on *Cecropia* in Central America, the larvae of all 35 species of this genus demonstrate cycloalexy. When disturbed the larvae raise their abdomens, which are protected by a supra-anal shield, and eject a nauseating fluid from the anus. The defense is directed mainly at *Azteca* ants, which are symbiotic with the host plant *Cecropia*. The eggs are deposited in oothecae inside the tree or under folioles, and



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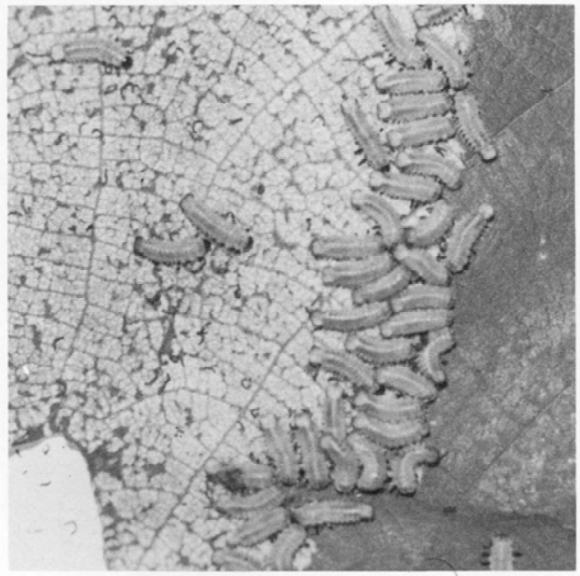

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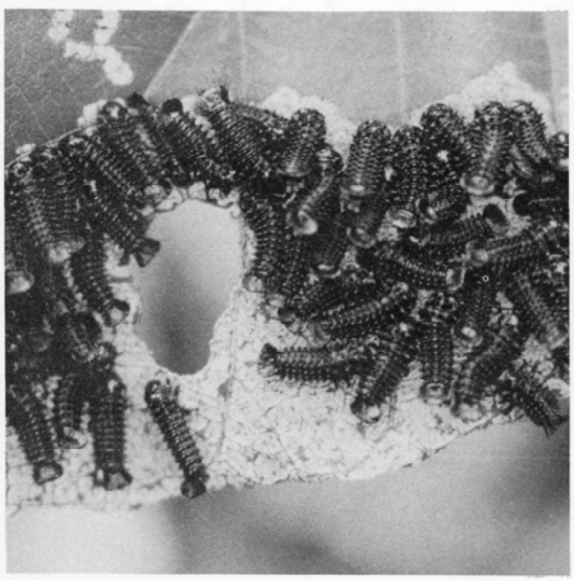

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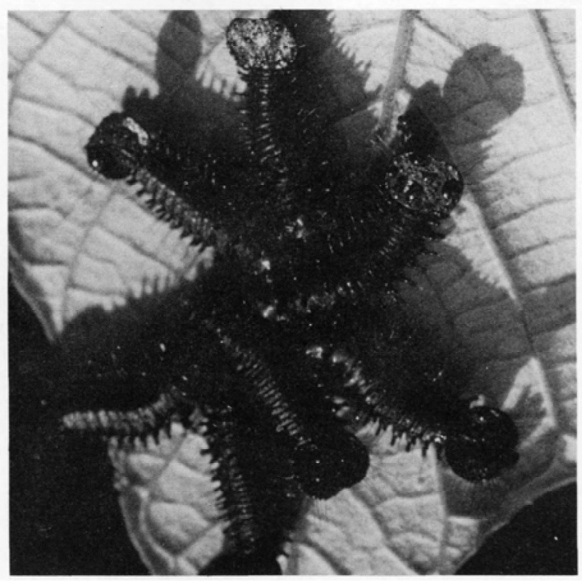

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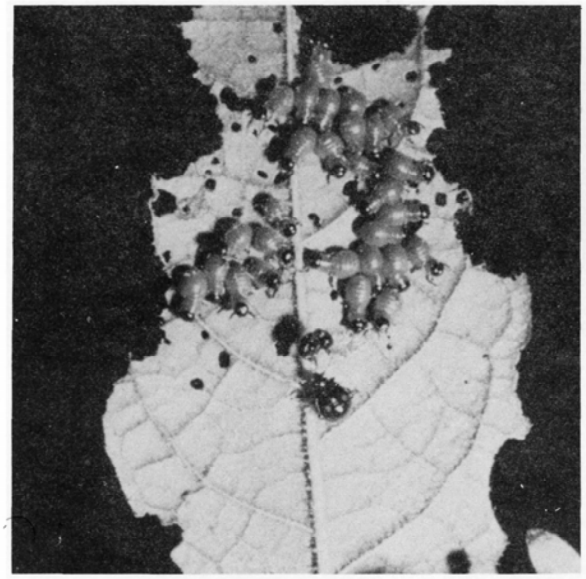
Photographs 1-4. 1) *Coelomera helenae* Jolivet (Chrysomelidae). First instar larvae showing subdivision of the circle as a result of their large number. (Brazil -photo H. de Morais). 2) *Coelomera helenae* Jolivet (Chrysomelidae). Line of first instar larvae feeding.(Brazil - photo H. de Morais). 3) *Coelomera lanio* Dalman (Chrysomelidae). Feeding third instar larvae about to form defensive rings. (Brazil - photo P. Jolivet). 4) *Coelomera lanio* Dalman (Chrysomelidae). Cycloalexy in fourth instar larvae exposing the supra-anal shield. (Brazil - photo P. Jolivet).

the 70 or so emergent larvae form two or three defensive rings (Andrade 1981). The latter are nocturnal resting formations under leaves, the larvae feeding by day. The formation persists during moulting, and is reflected in the disposition of old exuviae adherent to the substrate (Andrade 1981, Jolivet 1988) (photo 1-4).

Example 2: The cassidine *Chelymorpha informis* Boheman (Chrysomelidae)



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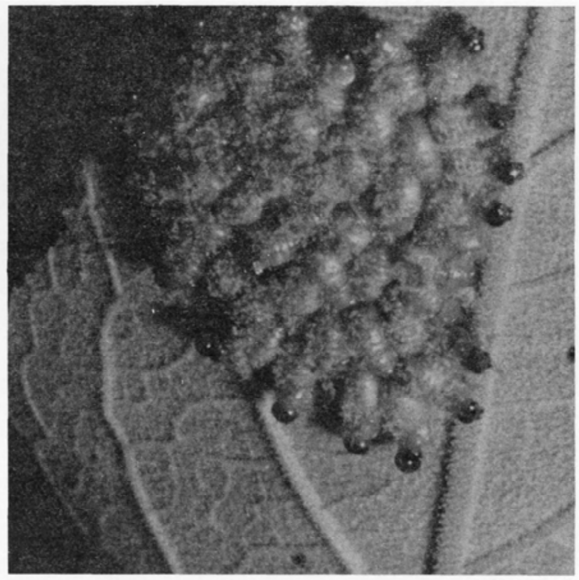

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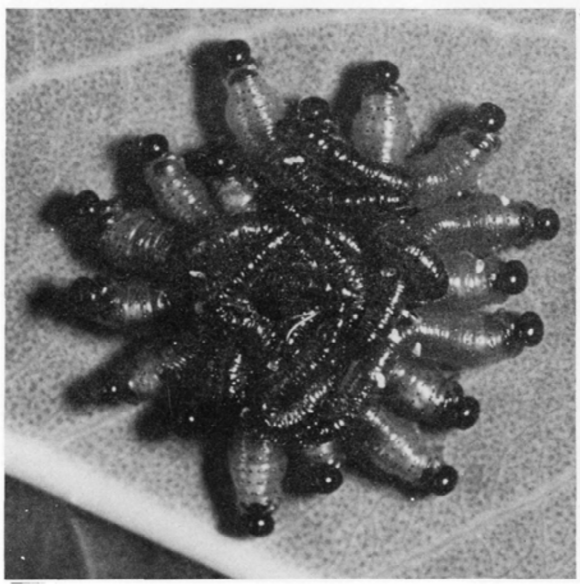

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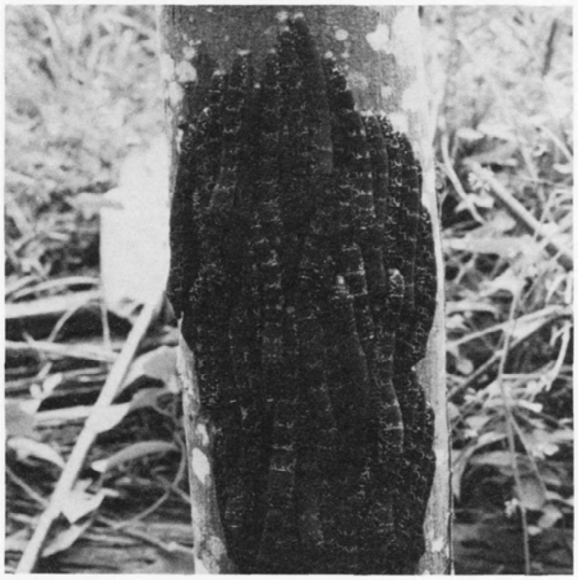
Photographs 5-8. 5) *Platyphora conviva* Stal (Chrysomelidae). Pentatomid attacking a broken circle of larvae. (Brazil - photo J. Vasconcellos-Neto). 6) *Platyphora conviva* Stal (Chrysomelidae). Older larvae in defensive ring showing use of *Solanum* hairs for added protection/camouflage. (Brazil -photo J. Vasconcellos-Neto). 7) *Perga dorsalis* Leach (Pergidae). Defensive ring of larvae, with tails interlocking over smaller larvae at the centre.(South Australia - photo P. Weinstein). 8) *Trigona* sp. (Apidae). Ring of bees defending their hive. (Brazil - photo P Jolivet.)

These larvae demonstrate cycloalexy on the upper surface of *Ipomoea* leaves, also during the night, and mainly in defense against *Pseudomyrmex* ants. The species is interesting because the disturbed larvae rear up in successive waves, waving the abdominal furca. Many other cassidines also demonstrate cycloalexy, as well as a maternal care (Vasconcellos and Jolivet 1988) (photo 10-11).

Two other species of Cassidinae show larval cycloalexy and female parental care. According to Windsor (1987), *Acromis sparsa* Boheman



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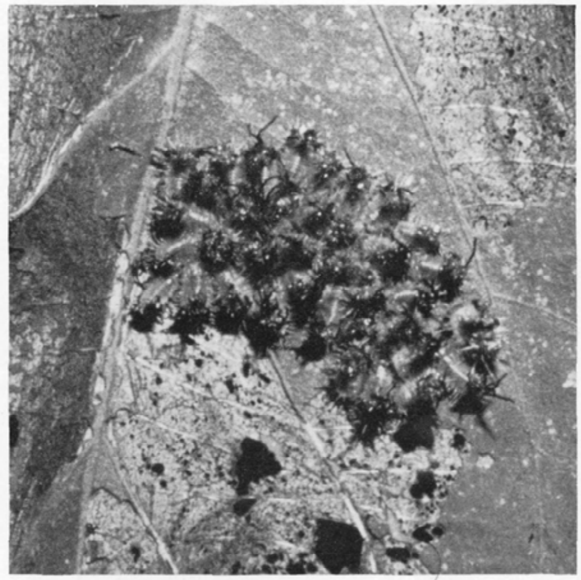

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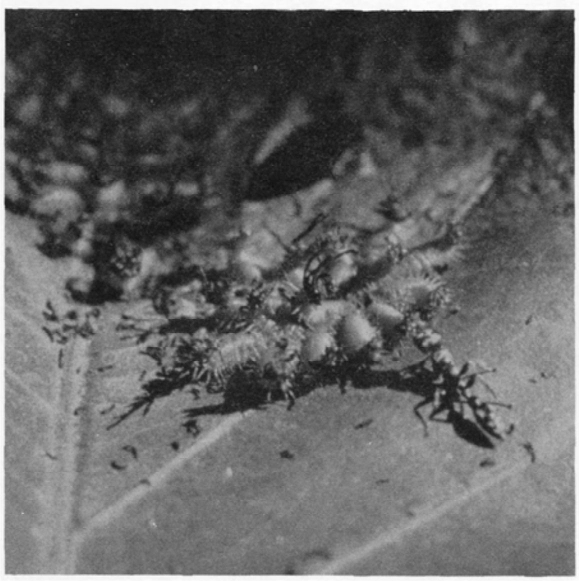

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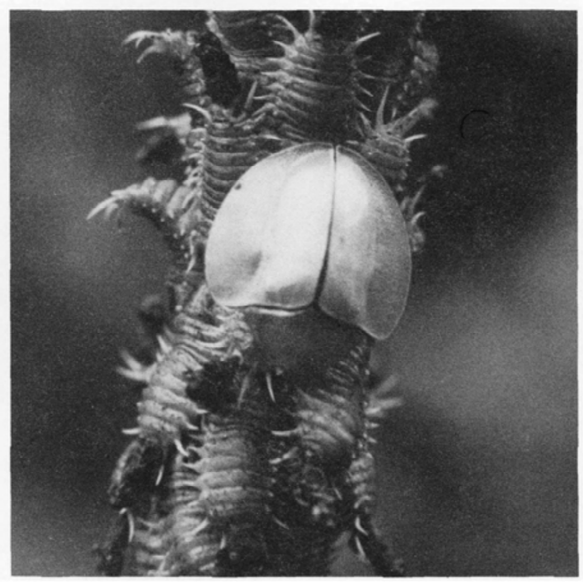

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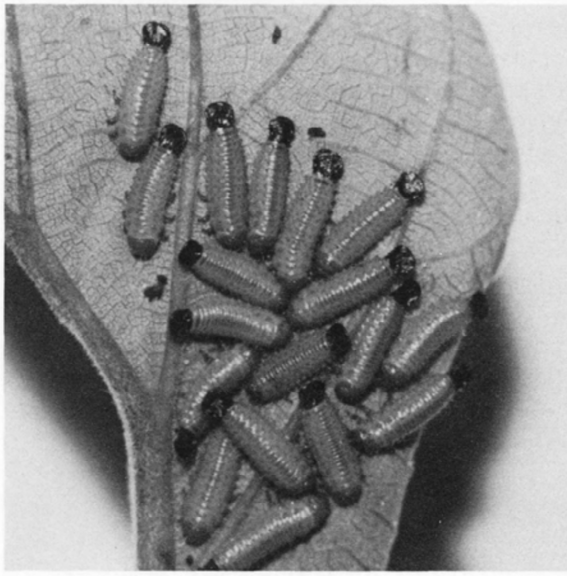
Photographs 9-12. 9) Resting position during the day of caterpillars of *Arsenura* (Lepidoptera Saturnidae) (Brazil - photo P. Jolivet). 10) *Chelymorpha informis* Boheman (Chrysomelidae Cassidinae) in defensive ring (Brazil - photo J. Vasconcellos-Neto). 11) *Chelymorpha informis* Boheman (Chrysomelidae Cassidinae). Broken ring attacked by a *Pseudomyrmex* (Brazil - photo J. Vasconcellos-Neto). 12) *Omaspides sobrina* Boheman (Chrysomelidae). Adult female demonstrating maternal protection of her unhatched young. (Brazil - photo P. Jolivet).

larvae assemble as a tight knot of bodies, either encircling the stem or forming a flat rosette under the leaf; however, he did not recognise this behaviour as a defensive strategy. *Omaspides tricolorata* Boheman has an elaborate defensive behaviour, combining female parental care and larval cycloalexy (Frieiro-Costa and Vasconcellos-Neto, in prep.).

Many other cases of this most common "abdomens out" cycloalexy are known from the



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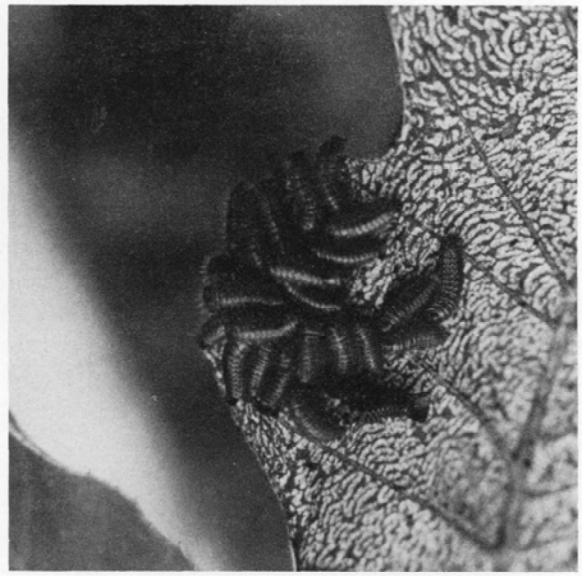

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Photographs 13-14. 13) *Coelomera helenae* Jolivet (Chrysomelidae). First instar larvae beginning to form a circle. (Brazil - photo H. de Morais). 14) *Coelomera raquia* Bechyne (Chrysomelidae). Second instar larvae in defensive ring formation. (Brazil - photo P. Jolivet).

Chrysomelidae, but have not been studied in detail. *Gonioctena rufipes* Degeer (Chrysomelidae) demonstrates this behaviour, as well as maternal care, on poplar leaves in Europe. The Australian Paropsini contain several cycloalexic species feeding on *Eucalyptus* (Selman, Weinstein, pers. com.). As was the case with sawflies, polyspecific aggregations are possible (Gregoire 1988).

Discussion

Circular defense strategy, of cycloalexy, is found irregularly in the animal kingdom, and attains perfection in some leaf-beetles and sawflies. It is intimately linked to aggressive displays (biting, regurgitation, exsanguination), and sometimes also to maternal care.

Wilson discusses the major effect of grouped defenses in his classic book on sociobiology (1975): isolated caterpillars form easier prey than do groups of caterpillars. He also cites aggregations of ascalaphid Neuroptera (Henry 1972), which, in a similar fashion to cassidine or pergid larvae, form masses around the branch of a tree. If disturbed, they raise their heads in unison, smacking their mandibles; although not strictly cycloalexy, such behavior is clearly related. A further elaboration is seen in certain noctuid caterpillars in Southeast Asia: they ' mimic' the head of a snake by rocking back and forth in unison - certainly convincingly enough to frighten the uninitiated. The *Arsenura,* Amazonian Saturnidae, show a kind of cycloalexy when resting on tree trunks during the day (Photo 9). Pupae and larvae of certain ceratopogonids (*Forcipomyia*) show perfect cycloalexy in cacao plantations in Costa Rica (Saunders 1924; Hinton 1955; Young 1984).

Cycloalexy, like maternal care, can only be the result of a long evolutionary history. The behavior protects the larvae during their most vulnerable periods (at rest, during moulting), and is effective against predators and parasitoids. However, no sooner has an effective defense developed than a new attack follows; trigonalyid parasitoids, for example, have succeeded in having their eggs swallowed by sawfly larvae, thus obviating the need to confront the defensive ring (Weinstein 1989).

Protection is enhanced by a variety of means; caudal shield, projectile emission of glandular or digestive secretions, exsanguination, biting, threatening posturing, and so on. Siblings and sometimes younger larvae are protected inside the circle, and to the sociobiologist, this could be interpreted as altruism on the part of the larvae at the periphery. Reciprocal altruism takes place when the inner and outer larvae exchange positions, as is often the case.

Finally, let it be said that many cases of cycloalexy await description - several palaearctic Tenthredinoidea and *Gonioctena* demonstrate behavior closer to cycloalexy than one might at first think. It is our hope that more such cases be reported in the future.

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