independently in the teleosts; living representatives of the holostean fishes, the group from which teleosts evolved, lack a dorsal nucleus (*1*) and are not electroreceptive (*19*), and only 3 of 35 teleost orders are electroreceptive (*20*).

Although only a single type of lateral line receptor has been reported for lampreys (*21*), we have histologically identified at least two populations that differ with respect to their depth from the epidermal surface and the diameter of their canals. We have not yet positively identified the electroreceptors. The homologies suggest, however, that the receptors, like those of chondrichthian and chondrostean fishes (*22*), will be ciliated and excited by cathodal electric stimuli—that is, negative electrical potential at the outer face of the receptor relative to the rest of the fish. In contrast, the electroreceptors of teleosts bear microvilli on their apical surfaces and are excited by anodal stimuli (*23*).

If electrosensory systems in lampreys and primitive jawed fishes are indeed homologous, by definition they have been inherited from the common ancestor of agnathans and gnathostomes. Thus, the earliest vertebrates were probably electroreceptive, and vertebrate electroreceptors may be as ancient as lateral line mechanoreceptors.

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References and Notes

1. C. A. McCormick, thesis, University of Michigan (1978).
2. A. A. Pearson, *J. Comp. Neurol.* **64**, 235 (1936); W. J. A. J. Smeets and R. Nieuwenhuys, *ibid.* **165**, 333 (1976); R. G. Northcutt, in (*3*), p. 117.
3. E. S. Hodgson and R. F. Mathewson, Eds., *Sensory Biology of Sharks, Skates, and Rays* (Office of Naval Research, Department of the Navy, Arlington, Va., 1978).
4. R. L. Boord and C. B. G. Campbell, *Am. Zool.* **17**, 431 (1977).
5. D. M. Koester and R. L. Boord, *ibid.* **18**, 587 (1978).
6. R. G. Northcutt, *Brain Res.* **167**, 163 (1979); in *Comparative Studies of Hearing in Vertebrates*, A. N. Popper and R. R. Fay, Eds. (Springer-Verlag, New York, 1980).
7. P. J. McCready and R. L. Boord, *J. Morphol.* **150**, 527 (1976).
8. D. Bodznick and R. G. Northcutt, *Brain Res.* **195**, 313 (1980).
9. Voltage pulses were supplied by a square-pulse stimulator and isolation unit, and a 10^5 to 10^6 ohm series resistance was used to minimize electrode polarization effects. Electric field intensities were monitored with a pair of electrodes in the water. The fields were only approximately homogeneous in the central area of the tank where the fish were held.
10. J. D. Green, *Nature (London)* **182**, 962 (1958).
11. A. Fessard, Ed., *Handbook of Sensory Physiology* (Springer, New York, 1974), vol. 3, part 3.
12. A. J. Kalmijn, in (*11*), p. 147.
13. ———, *Nature (London)* **212**, 1232 (1966).
14. T. H. Bullock and J. T. Corwin, *J. Comp. Physiol.* **129A**, 223 (1979).
15. C. J. Platt, T. H. Bullock, G. Czéh, N. Kovačević, D. Konjević, M. Gojković, *ibid.* **95**, 323 (1974); T. H. Bullock, *J. Physiol. (Paris)* **75**, 397 (1970).
16. R. Schultz, E. C. Berkowitz, D. C. Pease, *J. Morphol.* **98**, 251 (1956); J. K. Moore and T. H. Bullock, personal communication.
17. H. Kleerekoper and K. Sibakin, *J. Fish, Res. Board Can.* **14**, 145 (1957); E. A. Stensiö, in *Traite de Zoologie*, P. Grassé, Ed. (Masson, Paris, 1958), vol. 13, part 1, p. 173; K. S. Thomson, in *Problems in Vertebrate Evolution*, S. M. Andrews, R. S. Miles, A. D. Walker, Eds. (Academic Press, New York, 1977), p. 247.
18. A. J. Kalmijn, in (*3*), p. 507.
19. R. G. Northcutt, D. Bodznick, T. H. Bullock, paper presented at the 28th International Congress of Physiological Sciences, Budapest, 13 to 19 July 1980.
20. T. H. Bullock, in (*11*), p. 1.
21. J. B. Johnston, *J. Comp. Neurol.* **12**, 1 (1902).
22. R. W. Murray, in (*11*), p. 125; J. H. Teeter, R. B. Szamier, M. V. L. Bennett, *J. Comp. Physiol.* **138**, 213 (1980).
23. T. Szabo and A. Fessard, in (*11*), p. 60.
24. We thank T. H. Bullock for support throughout the project and C. C. Bell for valuable comments on the manuscript. We also thank B. Monk and the National Marine Fisheries Service for animal collection. This study was supported by an NIH fellowship to D.B., and NIH and NSF research grants to R.G.N. and T. H. Bullock. R.G.N.'s participation was made possible by a Guggenheim Foundation fellowship.

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Insects as Selective Agents on Plant Vegetative Morphology: Egg Mimicry Reduces Egg Laying by Butterflies

Abstract. *Experiments show that* Heliconius *butterflies are less likely to oviposit on host plants that possess eggs or egglike plant structures. These egg mimics are an unambiguous example of a plant trait evolved in response to a host-restricted group of insect herbivores.*

The idea of coevolution between insects and plants is attractive to biologists attempting to account for patterns of plant chemistry and the use of plants by insects (*1*). However, it is difficult to demonstrate a causal connection between a plant characteristic and a particular selective agent (*2*) because most plants have been exposed through time to a multitude of pathogens and herbivores, any complement of which may have helped to drive the evolution of the presumed defensive chemistry. Thus, instead of a gene-for-gene coevolution, there may be a more diffuse process (*3*) that is intractable to experimental analysis.

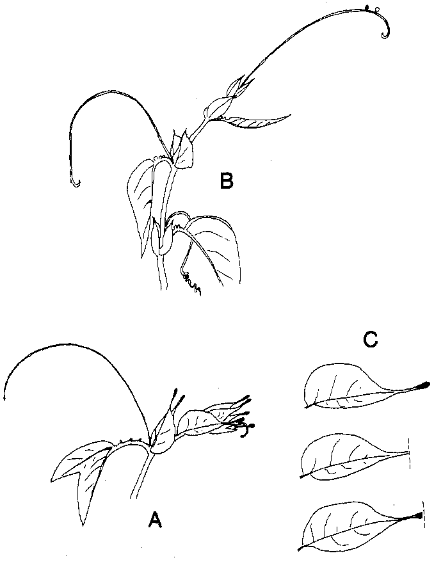

Fig. 1. *Passiflora* cuttings used in experiment: (A) *Passiflora cyanea*, showing display of egg mimics on stipule tips. (B) *Passiflora oerstedii*, showing yellow egg (open circle) placed near green egg (closed circle) on tendril. (C) Enlarged view of *P. cyanea* stipules showing (top) unaltered stipule, (middle) stipule with egg mimic removed, and (bottom) stipule cut but retaining egg mimic for control. *Passiflora cyanea* stipules are 3 to 4 cm in length.

One approach is to study plant groups that support only one or a few important herbivore taxa and that may therefore have traits attributable to coevolution with such taxa. For neotropical vines of the genus *Passiflora*, heliconiine butterflies are likely selective agents on several features of morphology (*4*). Plants such as *Passiflora* may have effectively "filtered out" most potential herbivores at an early stage of the evolution of their defensive chemistry, so that the insects remaining as significant herbivores of these plants are those that circumvent the chemical defenses of these plants. Morphological rather than chemical innovation is the effective evolutionary response to such herbivores (*5*), and herbivore behavior rather than counterdefensive chemistry shapes the course of evolution (*4*).

Structures resembling the yellow eggs of *Heliconius* butterflies have arisen independently on a number of *Passiflora* species in several subgenera and are derived from several distinct structures (*6*). That these structures have evolved specifically to mimic *Heliconius* eggs is indicated by the facts that (i) heliconiines are important defoliating agents of *Passiflora* (*7*); (ii) larvae of many *Heliconius* feed on congeneric eggs and larvae (*6*); and (iii) females exhibit great care in inspecting oviposition sites (*6, 8*). In this report we provide experimental evidence

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which shows that *Heliconius* females discriminate against plants with eggs or egg mimics and are therefore likely to be selective agents in the evolution of these structures.

We studied the oviposition behavior of *Heliconius cydno* in greenhouses, using *Passiflora oerstedii*, a natural host plant without mimetic structures, and *P. cyanea*, which has egg mimics on stipules (*9*). The golden color of the mimics closely resembles that of *Heliconius* eggs just prior to hatching, and mimics tend to be clustered at meristems where many *Heliconius* prefer to oviposit (Fig. 1A). Although the ranges of *P. cyanea* and *H. cydno* do not naturally overlap, *H. cydno* larvae eat and develop successfully on the plant (*10*). Both *P. cyanea* and *P. oerstedii* are members of the series lobatae.

In the first set of experiments, we examined the response of the butterflies to the presence of real eggs on *P. oerstedii*, the host without mimics. Host plants were available to the butterflies only during experiments, when females were presented with combinations of plant cuttings with and without eggs. The cuttings were of similar morphology, and *H. cydno* eggs were placed on tendrils near meristems where eggs are naturally laid. Eggs laid in the course of each trial were immediately removed from the test plants.

Three types of *H. cydno* eggs were placed on the cuttings: bright yellow eggs, just as they appeared in the field; green eggs, which were eggs that had been tinted with food coloring and rinsed with distilled water to blend with the plants' coloring; and washed yellow eggs, which were yellow eggs washed with distilled water and which served as controls.

In each test of oviposition preference, the butterflies were offered four *P. oerstedii* cuttings; two had single eggs of one type and two had no eggs or had a single egg of a different type. The cuttings were arranged at random with respect to one another and the butterflies were allowed to oviposit until they lost interest in the plants. Most trials lasted 1 to 2 hours and the butterflies laid eight to ten eggs per trial.

The oviposition behavior of *H. cydno* was consistent. The butterflies, probably responding to a combination of olfactory and visual cues (*11*), usually noticed the host plants as soon as the plants were brought into the greenhouse. While fluttering around a plant, they repeatedly tapped it with their antennae, then landed on the leaves to drum the cuticle with their forelegs, presumably using chemoreceptors to "taste" and further identify the plant (*12*). They would then fly around the plant, tapping and searching for a satisfactory oviposition site, or reject the plant by flying away. Often, when a butterfly noticed an egg or egg mimics, it would stop searching the plant and fly to some other part of the greenhouse.

Percent oviposition (ratio of number of eggs deposited to number of inspections) on plants with no eggs was significantly higher than on plants that had either a natural or washed yellow egg present (Fig. 2, A and B) (*13*), indicating that the presence of a yellow *Heliconius* egg does indeed reduce oviposition on plants. When eggs were laid on plants already bearing a yellow egg, they were usually placed several centimeters away on another part of the cutting.

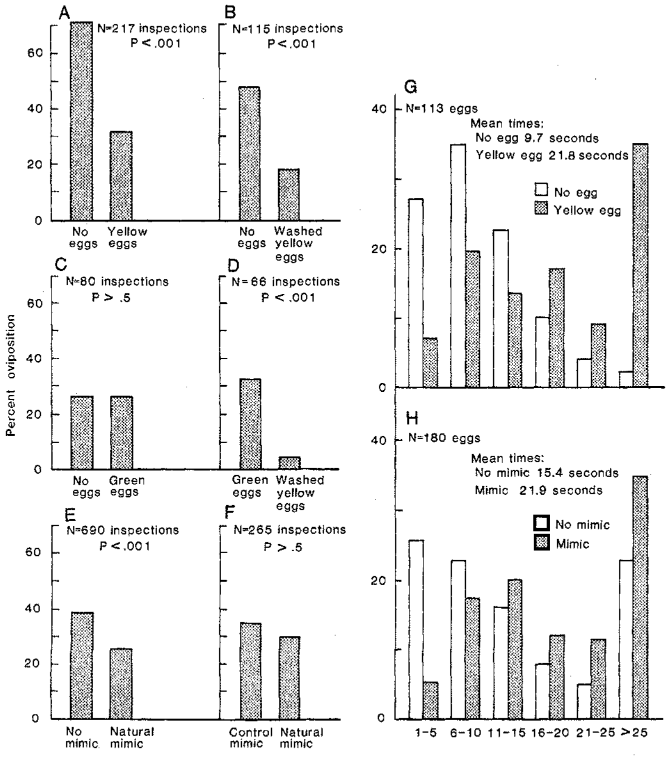

Fig. 2. Graphs which show oviposition response to various treatments. (A to D and G) Experiments were done with *P. oerstedii*. (E to G) Experiments were done with *P. cyanea*. In (G) and (H) the *x*-axis indicates seconds elapsed between recognition and oviposition. See text for details.

Egg-free cuttings and those with green eggs had equal oviposition frequencies (Fig. 2, C and D), showing that green eggs were not recognized as something to be avoided. In fact, several eggs were laid within 2 cm of green eggs (Fig. 1B). Washed yellow eggs reduced oviposition as effectively as untreated yellow eggs (Fig. 2, A and B), demonstrating that no repellant chemical was washed off the eggs in the coloring treatment.

In experiments in which *P. cyanea* was used to test responses to egg mimics, the *H. cydno* were kept in a greenhouse with *Passiflora* hosts and with other species of *Heliconius*. On days of experiments all *Passiflora* were removed from the greenhouse so that butterflies would oviposit only on the test plants. For each experiment two *P. cyanea* of similar morphology were brought into the greenhouse, and all butterflies were allowed to oviposit.

Three types of plants were paired in these tests: one with natural egg mimics, one with all egg mimics removed, and one with the tip of each mimic clipped off so that the mimic's general appearance was not affected (control plants). The mimic tips were clipped off to control for chemical effects of removing stipule tips when mimics were removed from experimental plants (Fig. 1C).

Plants without egg mimics seemed to be more satisfactory for oviposition than plants with egg mimics (Fig. 2E). The percentage of oviposition on control plants was not different from that on natural plants (Fig. 2F), so again, the negative oviposition response appears to be due to visual rather than to chemical cues.

The mean oviposition times for eggs laid on *P. oerstedii* with real yellow eggs was longer than for *P. oerstedii* with no eggs present (Fig. 2, G and H) (*14*). A female spends more time selecting a satisfactory place to oviposit on plants with yellow eggs or egg mimics than on plants devoid of eggs or structures mimicking eggs. Indeed, in crowded greenhouse cultures, when all tendrils have eggs, females switch to secondary sites such as older leaves, dead tendrils, or nearby structures not normally used. The increase in oviposition time appears to arise from the search for safe sites that are close to new growth without exposing eggs to cannibalism. Although egglike structures do not completely prevent oviposition, they do reduce oviposition frequency.

Heliconius can have a severe impact on its host plants. Females of several species frequently oviposit on seedlings and small vines in their forest understory habitats (*10*); single larva can totally defoliate individual plants. We routinely observe suppression of flowering and increased incidence of root disease in greenhouse plants exposed to heliconiine defoliation (*15*).

Although we have stressed coevolution, the plant mimicry of this example has also received attention (*16*). The existence of nonmimetic populations of *Passiflora* within some widespread species suggests that the evolution of egg mimicry is an ongoing process (*17*). However, every population in which we observed mimicry was monomorphic for the trait and was used by at least one *Heliconius* species. Under conditions in which a nonmimetic population containing a few mutant individuals is used by one or more cannibalistic *Heliconius* species, the egg-mimic genotypes might eventually replace all nonmimetic individuals on the basis of relative (rather than absolute) protection.

In a complex community containing ten or more species each of *Passiflora* and *Heliconius*, the microevolution of egg mimics by one *Passiflora* could all but eliminate that species from the host range of several coexisting *Heliconius* (*18*). At the same time, a new niche is then available to specialists able to utilize the mimetic species (*19*). *Passiflora* with egg mimics should also excel at expanding into new habitats already infested with *Heliconius* since fake eggs would provide some protection during the vulnerable establishment phase. Thus it appears that egg mimicry represents one way that a coevolutionary step might promote local diversity within a food web (*20*).

We have demonstrated that (i) *Heliconius* females respond to the presence of eggs; (ii) this response has a strong visual basis (*8*), although chemical cues are not altogether excluded; and (iii) the response to egglike structures of *Passiflora* and to real eggs both reduces the probability that eggs will be laid after host discovery and increases the time required to oviposit. Whereas other visual aspects of *Passiflora* that may be related to the defense of *Heliconius* are directed toward making the potential host plants less apparent or less recognizable to the butterflies (*21*), egg mimicry deters oviposition after the host has been discovered (*22*). Our study supports the egg mimicry hypothesis and is an instance of a plant structural trait resulting from coevolution with an insect herbivore.

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References and Notes

1. P. R. Ehrlich and P. H. Raven, *Evolution* **18**, 586 (1965).
2. D. A. Jones, in *Taxonomy and Ecology*, V. H. Heywood, Ed. (Academic Press, New York, 1973), p. 213.
3. L. E. Gilbert, in *Coevolution of Animals and Plants*, L. E. Gilbert and P. H. Raven, Eds. (Univ. of Texas Press, Austin, 1980), p. 247.
4. ———, in *ibid.*, p. 210.
5. ———, *Science* **172**, 585 (1971).
6. W. W. Benson, K. Brown, L. E. Gilbert, *Evolution* **29**, 659 (1975).
7. L. E. Gilbert, *Colloq. Int. C.N.R.S.* **265**, 399 (1977). Flea beetles apparently are the only other serious herbivore of *Passiflora*.
8. The visual acuity of *Heliconius* is documented by C. A. Swihart and S. L. Swihart [*Zoologica* **48**, 155 (1963); *Anim. Behav.* **18**, 60 (1970); see also (*6*)].
9. Original *H. cydno* stocks were collected by L. E. Gilbert at the Organization for Tropical Studies, La Selva station, Costa Rica. *Passiflora oerstedii* and *P. cyanea* stocks originated from populations at La Selva and Arima Pass, Trinidad, respectively. *Heliconius* and *Passiflora* species are maintained in temperature-controlled Lord and Burnham glass houses (5 by 8 m) at the University of Texas.
10. J. Smiley, thesis, University of Texas, Austin (1978).
11. M. D. Rausher has recently described search image formation for leaf shape by the pipe vine swallowtail, *Battus philenor* [*Science* **200**, 1071 (1978)].
12. Tarsal chemoreceptors are present in many other insects [W. H. Calvert, *Ann. Entomol. Soc. Am.* **67**, 853 (1974); C. J. C. Rees, *Entomol. Exp. Appl.* **12**, 565 (1969)].
13. Data were analyzed with an arc sine transformation for testing the equality of two percentages [R. R. Sokol and J. Rohlf, *Biometry* (Freeman, San Francisco, 1969), pp. 607–610].
14. Time was measured from the butterfly's initial inspection until her abdomen curled and oviposition began. A *t*-test of the difference between two means was used (*ibid.*, pp. 220–223).
15. This statement is based on 10 years' experience by L.E.G. in growing *Heliconius* with *Passiflora*.
16. D. Wiens, in *Evolutionary Biology*, M. K. Hecht, W. C. Steere, B. Wallace, Eds. (Plenum, New York, 1978), vol. 11, p. 365.
17. *Passiflora ariculata* has well-developed egg mimics in Trinidad (modified petiolar nectar glands) but *P. ariculata* in Costa Rica is not mimetic.
18. Selection of oviposition hosts by *Heliconius* may reduce the number of potentially suitable *Passiflora* species used as larval hosts [J. T. Smiley, *Science* **201**, 745 (1978)].
19. *Heliconius ethilla* in Trinidad, for example.
20. L. E. Gilbert and J. T. Smiley, in *Diversity of Insect Faunas*, L. A. Mound and N. Waloff, Eds. (Blackwell, Oxford, 1978), pp. 89–104.
21. L. E. Gilbert, in *Analysis of Ecological Systems*, D. Horn *et al.*, Eds. (Ohio State Univ. Press, Columbus, 1979), p. 117.
22. In our trials, butterflies were forced to choose between two potential oviposition hosts, since *Heliconius* butterflies rarely encounter patches of *Passiflora* in nature. M. Rothschild and L. M. Schoonvoven [*Nature (London)* **266**, 352 (1977)] reported that *Pieris brassicae* chose between two hosts with discriminatory behavior similar to that of *Heliconius*. With more potential hosts available, *Pieris* butterflies might spread their eggs less discriminantly throughout the plant population, spreading the risks of overcrowding, cannibalism, predation, and parasitism as P. M. Ives [*Aust. J. Ecol.* **3**, 261 (1978)] proposes.

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Internal Fertilization in an Oviparous Frog

Abstract. Eleutherodactylus coqui, *an oviparous frog, undergoes internal fertilization. If this mode of fertilization occurs in other species of anurans, interpretations of anuran reproductive strategies based on the assumption of external fertilization must be reviewed.*

Mode of fertilization is a fundamental factor in the evolution of reproductive strategies, in part because it constrains the nature of the parental investment by each sex (*1*). In species with internal fertilization, the lower certainty of genetic relatedness of the male to the offspring (compared to that of the female) has often resulted in the evolution of maternal care systems, along with various mechanisms to ensure paternity. Parental care by males alone has been reported primarily in species with external fertilization (*2*).

Biologists have long assumed that most frogs employ external fertilization, and anuran reproductive strategies have been interpreted in light of this assumption (*3*). The only frog demonstrated to have internal fertilization is *Ascaphus truei*, a unique species in which adult males have a tail used as an intromittent organ. Internal fertilization has been inferred for the few known live-bearing frog species (*4*, *5*) but has never been demonstrated for an oviparous frog. We present evidence that the oviparous frog *Eleutherodactylus coqui* Thomas has internal fertilization.

Eleutherodactylus coqui is a nocturnal, terrestrial-breeding frog of Puerto Rico (*6*). Males call from elevated perches and exhibit parental care by attending eggs from oviposition to hatching. Eggs undergo direct development and hatch as tiny froglets. Males may remain with the froglets for up to 5 days after hatching. Courtship may occur at any time of night. A gravid female approaches a calling male and makes contact. The male

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