519; ——— and N. Vinogradova, in *Ornithology in the USSR (Proceedings of the Baltic Ornithological Conference 7th)* (1970), vol. 2, p. 135; L. V. Sokolov, in *ibid.*, p. 129; V. K. Liepa, in *ibid.*, p. 123; F. W. Merkel, *Ann. N.Y. Acad. Sci.* **188**, 283 (1971). For a review of these experiments, together with a discussion of some possible causes of their negative results, see H. G. Wallraff, *Z. Tierpsychol.* **33**, 313 (1973).
8. S. T. Emlen, *Auk* **84**, 309 and 463 (1967); *Science* **165**, 716 (1969); *ibid.* **170**, 1198 (1970).
9. S. T. Emlen and J. T. Emlen, Jr., *Auk* **83**, 361 (1966).
10. For details both of Helmholtz coil construction and radial-perch cage design, see W. Wiltschko, *Z. Tierpsychol.* **25**, 537 (1968).
11. A sequence of cage rotations was prearranged for each bird in each test cage. A cage was considered to have 8 (1,2,3,. . . 8) sectors and the sector facing geographic north was randomly selected from a pool of 1,3,5,7; when these were exhausted, the "north" sector was drawn from the 2,4,6,8 pool. The process was then repeated.
12. The sequence of test conditions for each bird was determined as follows: cards representing the four conditions (two cage types and two magnetic conditions) were made up. These were drawn at random with the constraint that no single condition be repeated more than three times in any set of 12 test runs.
13. E. Batschelet, *Am. Inst. Biol. Sci. Monogr. 1* (1965); *NASA Spec. Publ.* **262**, 61 (1972).
14. The footprint records were quantified by comparison with a computer-generated set of dot densities for which precise numbers of dots are known. Through conversions for the area of a sector and for the average number of dots left by a single bird-jump (determined empirically), an estimate of the actual number of jumps can be made. All footprint records were analyzed "double-blind." Funnels were identified by code only. Analyses were performed by an individual without access to the code and thus without knowledge of either the test condition or the identity of the bird producing the footprint records.
15. G. S. Watson and E. J. Williams, *Biometrika* **43**, 344 (1956).
16. W. Wiltschko, S. T. Emlen, R. Wiltschko, N. J. Demong, S. Bergman, in preparation.
17. S. T. Emlen, *Anim. Behav.* **18**, 215 (1970).
18. ———, in *Avian Biology*, D. S. Farner and J. R. King, Eds. (Academic Press, New York, 1975), vol. 5.
19. We thank H. C. Howland for constructive help in experimental design and R. J. Young and the Department of Poultry Science, Cornell University, for the use of brooder houses. D. R. Griffin, R. P. Larkin, W. E. Southern, and C. Walcott kindly provided helpful and critical comments on the manuscript. This work was supported by NSF grant BMS-72-02198-A02 to S.T.E. and by Deutsche Forschungsgemeinschaft grant WI 404/5 to W.W.

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Biogeography of Free-Living Soil Nematodes from the Perspective of Plate Tectonics

Abstract. *In this first biogeographical synthesis based on the morphology and known distribution of a group of free-living soil nematodes, data indicate a pre-Jurassic origin followed by West Gondwanaland radiation for some genera and Laurasian radiation for others.*

Raven and Axelrod (*1*) presented a convincing case that West Gondwanaland was a primary area of evolution for many orders of angiosperms (possibly the earliest angiosperms) and reviewed the data leading to a similar conclusion for birds, marsupials, snakes, and anurans. Edmunds (*2*) suggested a probable sequence of breakup of Gondwanaland based on the distribution of mayflies and a minimum of geological evidence. It has been variously postulated that the Nematoda constitute an ancient phylum that evolved in upper Proterozoic or early Cambrian time, and, conversely, that the phylum is of fairly recent origin like the Lepidoptera or passerine birds (*3*). We have recently clarified the systematics of the superfamily Leptonchoidea of the Dorylaimida (*4*) so that a reasonable analysis of the biogeography and history of the group can now be made. Our data on this group of free-living soil nematodes point to a pre-Jurassic origin followed by West Gondwanaland radiation for some genera and a Laurasian radiation for others. We now present data for three genera from our larger study of the entire superfamily.

The Dorylaimida occur mainly as part of a diverse soil and freshwater nematode fauna of relatively natural habitats (Fig. 1). Dorylaimid nematodes reach a high diversity in uncultivated areas, but their diversity and numbers decline rapidly in cultivated fields (except for a few species that are plant parasites), and the dorylaimid fauna can be used as an indicator of degree of disturbance in deciduous forests (*5*).

Generally speaking, man is the most effective dispersal agent for nematodes, and many species that are plant parasites (usually of the order Tylenchida) have been widely spread by movements of plant parts and soil by humans. The Dorylaimida as a whole have poor dispersion characteristics. They do not seem to have a drought-resistant stage, as do some of the successful plant parasites, and they must rely mainly on fresh water or chance adherence in moist soil to the feet or bodies of animals for dispersal. Since in natural areas most dorylaimid species are rare in relative numbers with few or no predominant species, the chances of new colonies becoming established at distant points must be low (*6*).

Insufficient collecting on many continents made a biogeographic study impossible until recently. However, large collections have now been made in many areas of the world (*7*), and distributions of genera and species of Leptonchoidea on a worldwide basis show patterns that can be interpreted in relation to geological events now known to have occurred at various times (*1*). Our approach is closest to the vicariance model (*8*), in which biotic distribution is thought to result mainly from subdivisions (vicariance) of ancestral biotas with secondary emphasis on pathways of dispersal and migration. The vicariance model facilitates generalizations regarding entire biotas.

The Leptonchoidea show various combinations of plesiomorphic (or primitive) and apomorphic (or advanced) character states (*9*). Species of the genus *Dorylaimoides* have the most plesiomorphic characters, including a relatively elongated basal esophageal bulb (Fig. 2, a and b). Modifications of the esophagus and female gonads are represented among the species of *Dorylaimoides*, which can be ordered into two groups, one plesiomorphic and the other relatively apomorphic. Species of the plesiomorphic group, all of which have an unconstricted esophagus (Fig. 2a), have been found in many of the Laurasian countries (with several species on more than one continent) and also in India, Africa, South America, and Puerto Rico. India has several species in common with Laurasian areas and shares one species with South America only. On the basis of these data alone, *Dorylaimoides* might appear to be a northern group with recent dispersal to the south. However, data from the apomorphic forms indicate a different history. India has one species with an apomorphic constricted esophagus (Fig. 2b). All four Australian species also have this character. Elsewhere in the world this character is possessed by one species found only in South America and another species found only in Puerto Rico. The fact that all four Australian species have the constricted esophagus and that this characteristic is found elsewhere only in India, South America, and Puerto Rico tells us that an ancestor of these species was present in West Gondwanaland prior to India's passage to the north, and that a nematode fauna of some antiquity may be present on Puerto Rico.

It follows from these data for apomorphic forms that ancestors of plesiomorphic *Dorylaimoides* present today in India and elsewhere had evolved and become well distributed prior to the breakup of Pangaea, 180 million years ago. After the breakup, those species now shared only by Laurasian continents may have evolved. On the basis of present data it is not possible to decide whether those plesiomorphic species which India shares with the Laurasian countries are Pangaean survivors or

whether they arrived in India from the north after the middle Eocene. *Dorylaimoides leptura*, now found in India and South America, must have evolved no later than the breakup of Gondwanaland. That all six of the known North American species are didelphic (a plesiomorphic character) indicates that extensive evolution may not have occurred in Laurasia. India, Africa, South America, and Puerto Rico, however, have a mixture of didelphic and monodelphic species, with India having the most species of any land area. These data indicate that the Gondwana continents were areas of great radiation and that some species, at least, were present on the Indian plate before it rafted northward in the Upper Cretaceous and early Tertiary.

The genus *Basirotyleptus* is more apomorphic than *Dorylaimoides*, as evidenced by the short valvulated esophageal bulb (Fig. 2c). The ancestral form probably had two equal female gonads (didelphic, symmetrical). The only known modern species with such female gonads is *B. bunocephalus* in Africa (Uganda). Two additional didelphic species have been discovered in Australia, both of which have asymmetrical gonads tending toward prodelphism (a fully developed anterior gonad only). A third species in Australia is monoprodelphic, and this species is shared with India. These data indicate early distribution in Gondwanaland prior to India's separation from Antarctica. To date, *Basirotyleptus* has not been reported in New Zealand, and if it is not discovered there eventually, we will have to assume that the New Zealand population became extinct (*10*). As yet, only one *Basirotyleptus* species has been reported in South America (Brazil), but, given the present distribution of the genus and its apparent history, we anticipate that more South American species will be found and that the genus will also be found in Central America, which was undoubtedly its route to North America. *Basirotyleptus* is apparently absent from Eurasia.

A third genus, *Tyleptus*, has an esophagus similar to that of *Basirotyleptus* (Fig. 2c). Three species are found in India, and one of these is also found in South Africa. There is another species in Africa (Zaire), three more in South America (one of these is shared with North America), and one more in Puerto Rico. As far as we know, no *Tyleptus* species has been reported in Australia, New Zealand, Europe, or Asia, although the genus has been known since 1939. The distribution indicates West Gondwanaland radiation after direct migration to the

Fig. 1. Representative nematodes from a forest soil showing variation in size and conformation among species of several different orders. Scale bar, 0.5 mm.

Australian plate ceased about 110 million years ago. Entry into North America was undoubtedly recent (not before 5.7 million years ago) and occurred by way of Central America, and we predict that *Tyleptus* species will be found in Central America. All species of *Tyleptus* and *Basirotyleptus* in North America have been found in natural wooded areas of the eastern United States, where they were isolated as the southwestern United States became warm and dry.

Our hypothesis requires acceptance of the view that some species (for example, *Dorylaimoides leptura*) evolved in Gondwanaland and persisted in some areas until the present. The fact that a comparable claim for species longevity has not yet been made for species in other biota does not seem sufficient reason to assume it could not be so for nematodes. Annelid worms are known to have been well established by the early Paleozoic. Although essentially no fossil record of the free-living nematodes exists, it is reasonable to assume that they also invaded land during the Paleozoic and diversified throughout that period. The organizational plan of nematodes is effective but it is simple, and invertebrate zoologists tend to agree that the very simplicity may have been evolutionarily limiting (*11*). The success of nematodes in the many habitats invaded has depended on only minor modifications of the basic plan. Stanley (*12*) has suggested that the closely related rotifers and certain gastrotrichs may have low rates of extinction because of their small size, abundance, physiological traits, and characteristically broad niches, and that, because of these low extinction rates, the groups do not need high diversification rates to ensure their survival.

We are confident that further collecting will confirm a pre-Jurassic origin for the Leptonchoidea and much evolutionary radiation in the Cretaceous, coinciding with the rapid evolutionary events in other animal groups and in the angiosperms (*1*). An important difference between our findings and those of biogeographic analyses of other groups is the absence of great numbers of extinctions in India as it rafted northward. Unlike the angiosperms (*1*), many Leptonchoidea seem to have survived the trip. We suggest that some of these species have persisted until the present, a claim for species longevity not made for other biota. Further collecting is needed to determine the extent of radiation of nematode groups on early landmasses and to aid in answering questions regarding extinctions in large areas and rates of dispersal to new areas including islands.

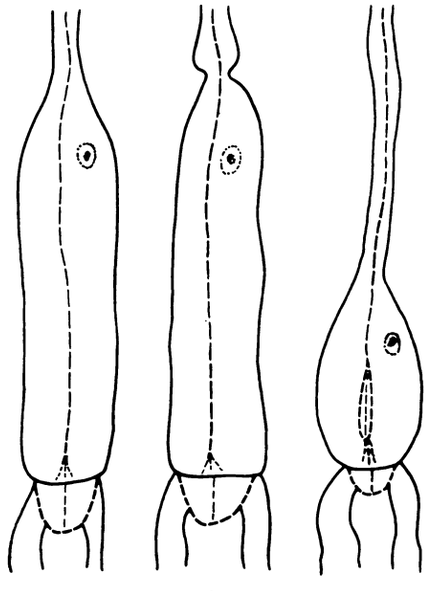

Fig. 2. Basal esophageal bulbs. (a) Long, unconstricted bulb in *Dorylaimoides*. (b) Long, constricted bulb in *Dorylaimoides*. (c) Short bulb with thickened valvular chamber in *Basirotyleptus* and *Tyleptus*.

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References and Notes

1. P. H. Raven and D. I. Axelrod, *Ann. Mo. Bot. Gard.* **61**, 1 (1974).
2. G. F. Edmunds, *Ann. Rev. Ent.* **17**, 21 (1972).
3. A. R. Maggenti, in *Plant Parasitic Nematodes*, B. Zuckerman, W. F. Mai, R. A. Rohde, Eds. (Academic Press, New York, 1971), pp. 65–81; C. W. Schaefer, *Syst. Zool.* **20**, 77 (1971).
4. C. G. Goseco, V. R. Ferris, J. M. Ferris, *Purdue*

Univ. Agric. Exp. Stn. Res. Bull. **911**, 1 (1974); *ibid.* **913**, 1 (1974); *ibid.* **928**, 1 (1975).
5. S. R. Johnson, J. M. Ferris, V. R. Ferris, *J. Nematol.* **6**, 118 (1974); V. R. Ferris and J. M. Ferris, *Agro-Ecosystems* **1**, 275 (1974).
6. The question of ease of dispersal is crucial. Clearly, any movement of a soil mass from one continent to another or from a continent to an island could serve to disperse nematodes to a new area, and probably this has happened at times. However, certain genera are well distributed on some continents and are found rarely or not at all on others. The nematodes of Europe have been studied for years, whereas those of South America are hardly known. Nevertheless, the few collections from South America reveal a greater diversity in Leptonchoidea than is known from Europe after decades of intensive collecting.
7. These include North America, Europe, India, Australia, New Zealand, and some of Africa and the U.S.S.R. In South America, limited collecting has been done in Argentina, Brazil, Venezuela, Paraguay, and Chile. Islands studied include Puerto Rico, New Guinea, New Hebrides, Mauritius, and Japan.
8. J. Craycraft, *Ann. Mo. Bot. Gard.* **62**, 227 (1975); L. Croizat, G. Nelson, D. E. Rosen, *Syst. Zool.* **23**, 265 (19 → G. Nelson, *ibid.* **22**, 312 (1973).
9. Few precise data exist regarding feeding habits of Leptonchoidea, but none are thought to be predators, and all abound in plant rhizospheres. We have observed some that feed on fungi in culture.
10. P. H. Raven and D. I. Axelrod, *Science* **176**, 1379 (1972).
11. P. A. Meglitsch, *Invertebrate Zoology* (Oxford Univ. Press, London, 1967), p. 961; L. H. Hyman, *The Invertebrates: Acanthocephala, Aschelminthes, and Entoprocta* (McGraw-Hill, New York, 1951), p. 572.
12. S. M. Stanley, *Science* **190**, 382 (1975).
13. Supported in part by grant BMS72-02296 A01 from the National Science Foundation. We thank P. H. Raven and G. F. Edmunds for helpful suggestions.

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Sustained Tolerance to a Specific Effect of Ethanol on Posttetanic Potentiation in *Aplysia*

Abstract. *Perfusion with 0.8 molar ethanol in seawater specifically accelerates the rate of decay of posttetanic potentiation observed after repetitive electrical stimulation of an identified synapse in the abdominal ganglion of* Aplysia californica. *Repeated perfusion with seawater alternately with and without ethanol leads to a progressive diminution of this specific effect of ethanol, such that after the third application ethanol no longer has any effect on the rate constant of decay of posttetanic potentiation. This tolerance to the specific effects of ethanol persists for at least 11 hours after the last application of ethanol.*

Tolerance to alcohol refers to the diminution of its pharmacological efficacy with repeated exposures. In mammals, including humans, tolerance to ethanol is due in large part to adaptive changes in the nervous system rather than to an acceleration of ethanol metabolism (*1*, *2*). The nature of the adaptive change that produces tolerance is not known. In a previous study we used an identified synapse in *Aplysia californica* to demonstrate a specific neurophysiological effect of ethanol and other alcohols, namely an acceleration of the decay of posttetanic potentiation (PTP) (*3*) (Fig. 1). We now report that repetitive administration of ethanol over the course of a number of hours leads to the development of tolerance to this specific, neurophysiological effect.

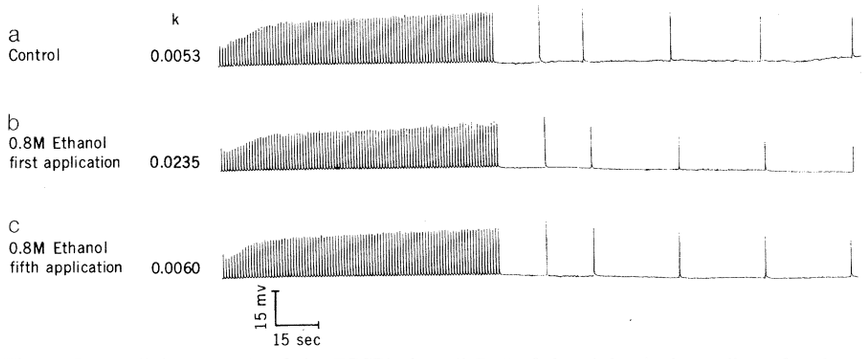

Fig. 1. Intracellular records of the EPSP's in cell R15 of the abdominal ganglion of *Aplysia californica* during stimulation of the right visceropleural connective by a train of 100 pulses at one pulse per second, followed by two test pulses at 15-second intervals and then test pulses every 30 seconds. Cell R15 was hyperpolarized to about −100 mv by injecting current through the second barrel of a double-barrel recording electrode. (a) Control preparation in fortified artificial seawater (*5*). (b) The stimulus pattern was given 30 minutes after starting the first application of artificial seawater containing 0.8*M* ethanol. The response during the train of stimuli is similar to that of the control preparation; however, the PTP observed after the train decays with a much faster time course. Beginning 10 minutes after this train the preparation was washed for 120 minutes before the second application of ethanol. (c) The stimulus pattern was given 30 minutes after starting the fifth application of 0.8*M* ethanol. The rate of decay of PTP here is similar to that in the control preparation. The calculated rate constant of PTP decay (*k*) is shown for each case.

Posttetanic potentiation is a presynaptic phenomenon which is produced after repetitive stimulation of an identified synapse in the abdominal ganglion of *A. californica* (*4*). Electrical stimulation of the right visceropleural connective gives rise to an excitatory postsynaptic potential (EPSP) that may be recorded with an intracellular electrode in cell R15 of the isolated abdominal ganglion by using standard electrophysiological methods (*4*, *5*). During and after repetitive stimulation of this synapse at a frequency of one pulse per second, a series of changes in the amplitude of the recorded EPSP is observed, as has been described in detail (*4*, *5*). After termination of a train of 100 stimuli, the test EPSP's elicited at 30-second intervals are of larger amplitude than the characteristic isolated EPSP of this synapse. This PTP decays with a single exponential time course toward the size of an isolated EPSP, so that after the train of 100 stimuli at one pulse per second, the EPSP amplitude returns to the control level within 20 minutes. When an identical experiment is conducted in the presence of 0.8*M* ethanol all responses during the train are, on the average, identical with those observed in the absence of ethanol. However, the rate constant of decay of PTP is strikingly accelerated (*3*) (Fig. 1). The effect of repeated administration of ethanol on this specific action (acceleration of the rate of decay of PTP) is the subject of this report.

In this investigation we alternated trains of stimuli in the presence and absence of 0.8*M* ethanol and studied the amplitude of all EPSP's elicited by each train as well as the rate constant of decay of PTP. In a typical experiment a train of 100 stimuli at one pulse per second was given and the rate of decay of PTP was determined by eliciting test EPSP's 15 and 30 seconds after the end of the train and then at 30-second intervals for 10 minutes. This stimulus pattern was repeated at 40-minute intervals, allowing about 30 minutes of rest between experiments. Solutions were changed at the beginning of the 30-minute rest period. Three consecutive control experiments with fortified artificial seawater (*5*) without ethanol were alternated with a single experiment with a solution of 0.8*M* ethanol in fortified artificial seawater. Continuous application of ethanol was not feasible since axonal conduction block often developed after prolonged perfusion with 0.8*M* ethanol.

In the absence of ethanol, PTP was observed to decay with an average rate constant of 0.0053 ± 0.0006 sec^{-1} (± the