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CONTRIBUTION TO A REVISION OF THE EARTHWORM FAMILY LUMBRICIDAE. II. INDIAN SPECIES

BY G. E. GATES

INTRODUCTION

The domain of the "recently evolved and dominant" lumbricid family, a group which has "almost completely conquered the Palaearctic" (Stephenson, 1930, p. 668), long has been thought to reach well into India. The southern boundary of that domain, on recent distributional maps (for example those of Tetry, 1938, and Julin, 1949), runs from the Mediterranean so as to include the Punjab portion of the Sind Valley and all of the Gangetic Valley to Calcutta from whence it is extrapolated, with question marks or predictions, across northern Burma and through China to the Pacific.

Two routes from European centers of lumbricid evolution to the vicinity of Calcutta could have been available to the advancing lumbricids: through the Himalayas in an easterly direction and then down to the plains, or south along the Indus River and thence easterly through the Gangetic Valley. In either case, lumbricids could be expected throughout an eastern portion of the Gangetic plain as well as in the western part of the Himalayas. A survey of the earthworm fauna of the Allahabad sector (Gates, 1945, 1947) and collecting in such Himalayan sites (Gates, 1951) as could be visited during wartime, provided data that made a review of the taxonomic status of the supposedly endemic species advisable.

The results of that study are presented herewith. The text of the present contribution, except for this paragraph, has been excised from a chapter of an unpublished manuscript written several years ago during tenure of a John Simon Guggenheim fellowship.

SYSTEMATICS

Genus ALLOLOBOPHORA Eisen, 1874

"ALLOLOBOPHORA CALIGINOSA (Savigny, 1826)"

A complex of four or more morphologically distinguishable species long has gone under Savigny's name. The data available in the literature rarely permit a decision as to which species was present in a particular collection. Indian localities from which "*caliginosa*" has been recorded are: Fern Hill and Ootacamund (at elevations of 6-8,000 feet in the Nilgiri Hills, South India), Mt. Abu (Rajputana), Lahore, Ferozepur, Kotla, Murree, Peshawar, Mardan, Chitral (Punjab and Northwestern Frontier Province), Gilgit, Gurez, Gundarbal, Anchar Lake (Kashmir), Almora, Mussoorie, Naini Tal, Simla, Kufri, Junga, Kasauli (western Himalayas). All except the Nilgiri localities are well within the temperate zone. None of the complex ever was found at Darjiling where exotic lumbricids now appear to be dominant (Gates, 1951). There are no records for Ceylon, Burma, the Andaman and Nicobar Islands, the Malay Peninsula, and other parts of southeast Asia, not even for hill stations where introduction might have been expected.

The characterization "cosmopolitan" so frequently applied to "*caliginosa*" obviously implies more than has been warranted by the facts, even if the complex had been but a single species.

ALLOLOBOPHORA JASSYENSIS Michaelsen 1891

This little known species has been reported from a single Indian locality well north of the thirty-second parallel in the Murree subdivision of the Punjab. Individuals of the *caliginosa* complex sometimes have been mistaken for *jassyensis*. Presence of the latter in India, if confirmed, presumably is due to importation by man.

ALLOLOBOPHORA TRAPEZOIDES (Dugès, 1828)

Helodrilus (*Helodrilus*) *mariensis* Stephenson 1917, Rec. Indian Mus., Calcutta, 13, p. 414, fig. 6. (Type locality, Murree. Types, several, presumably in the Indian Museum.)

Allolobophora (*Eophila*) *mariensis*, Stephenson, 1923, Oligochaeta, *in* Fauna of British India, Ceylon and Burma, London, p. 504.

Stephenson's species is known only from the original description. Subsequent collections at the type locality provided only specimens that have been referred to the *caliginosa* complex.

The types probably were brittle and strongly contracted, as female and spermathecal pores were unrecognizable. A number of differences, of a minor sort, apparently were thought to obviate consideration of *caliginosa*. The greenish coloration may have been an artifact. Shape of the posterior portion of the body (shown in fig. 6) may have resulted from unusually strong contraction at preservation and from dehydration in too strong alcohol. A similar condition of the posterior end has been seen in a number of specimens of *trapezoides* recently examined. Location of the first dorsal pore at 4/5 is of little importance taxonomically. A functional pore has been found in *trapezoides* as far forward as 6/7. Just which ones of a series of more or less pore-like markings at mD really are patent apertures through the body wall into the coelomic cavity often is undiscoverable in field-preserved material. Absence of mention of tubercula pubertatis in Stephenson's description presumably means that those structures (as often is the case in browned or other alcoholic museum material) were quite unrecognizable. The crypts or yellowish projections from the oesophagus in x, that were mentioned by Stephenson, are, of course, calciferous sacs. The supposed hearts of xii are only the vertical portions of the extra-oesophageal trunks (cf. *O. cyaneum* below).

Spermatophores have not been found externally nor spermatozoa in the spermathecae of any of a considerable number of specimens of *trapezoides* that have been available from various parts of the world. The male funnels usually have shown no indications of presence of mature sperm. Male sterility requires that reproduction be parthenogenetic and that permits reduction in number as well as in size of the seminal vesicles. Most liable to early elimination after reproduction becomes asexual are the vesicles of x and ix. Absence of those vesicles certainly is no justification for assigning a species to *Helodrilus* or to *Eophila*, whatever those two genera may prove to be. In *Allolobophora*, where the species undoubtedly belongs, there is no good reason for specific distinction from *trapezoides*.

Allolobophora tuberculata Eisen 1874

Among specimens from Simla that were originally (Gates, 1951) referred to *caliginosa* are a number that can now be placed in Eisen's species. Synonyms are: *similis* Friend 1911, *arnoldi* Gates 1952, and *caliginosa* (various authors). Elsewhere, the species now can be recorded from the United States (northeastern portion), Canada, England, Chile, Denmark, Norway, Sweden and probably Germany. The distribution, even as now known, must have resulted in part from transportation. Obviously there can be no imputation of endemicity in India.

Genus Bimastos Moore, 1893

Bimastos parvus (Eisen, 1874)

Jalla, Patna, Bihar, March, 0-0-1, R. C. Lacy.
Rawalpindi, Punjab, May, 0-0-6. F. G. Dickason.

Forty-four specimens of this species were collected at Allahabad during a period of four years. More than half were found in dirt around roots of potted plants. The others were obtained from a single small area (*sansibaricus* habitat) by a drainage canal that was sampled at least once a month through most of the period (Gates, 1945, 1951). The *sansibaricus* habitats, in the region around Jubbulpore to the south of Allahabad were investigated (Gates, 1956) on several occasions during that same period but yielded no specimens of *parvus*.

Indian localities where *parvus* has been found are: Kodaikanal (Palni Hills, South India), Darjiling (eastern Himalayas), Patna (Bihar), Allahabad and Saharanpur (United Provinces), Partabgarh (Rajputana), Lahore, Lyallpur, Ferozepur, Peshawar, Mardan, Chitral (Punjab and Northwestern Frontier Province), Gorai, Srinagar (Kashmir), Kasauli, Barogh, Naini Tal (western Himalayas). All are in the temperate zone except Kodaikanal which is a summer resort where elevations are 6000-7000 feet. The species was found in Burma, during twenty years of intensive collecting, only at elevations of more than 4000 feet, in and around four hill stations where European cultivated plants had been introduced. A hill station also provided the only record for the Malay Peninsula. *B. parvus* obviously is more widely distributed in southeast Asia than the supposedly cosmopolitan

"*caliginosa.*" The species usually is assumed to have originated in America from whence, or indirectly through Europe, it was brought by man to India.

The plants along with which *parvus* was brought to the orient were not taken only to the hill stations of Burma or to the Indian localities just mentioned. Such plants, potted or otherwise, are common throughout the Allahabad sector of the Gangetic Valley and also in the Jubbulpore region. The plants undoubtedly have been taken on innumerable occasions into the tropical lowlands of India, Burma and the Malay Peninsula. Absence in those lowlands after a hundred years and more of such introductions must have resulted from inherent inability of the species to adapt itself to a tropical climate.

Bimastos eiseni (Levinsen, 1883)

This peregrine species, which probably does not belong in *Bimastos,* is known in India only from the region of Naini Tal in the western Himalayas.

Genus Dendrobaena Eisen 1874

Dendrobaena octaedra (Savigny, 1826)

This species, hitherto unknown from India, is now recorded from Kodaikanal (Palni Hills, South India) where it appeared to be quite common. This is another form to which the characterization of cosmopolitan has been erroneously applied. South of Siberia, the species has been found only at the Kodaikanal summer resort. The species is also absent from almost all of South America.

D. octaedra is not usually geophagous and, accordingly, would not have been expected to be carried around the world as much as the earth-eating species. Nevertheless, specimens of this species have been intercepted at American ports during the last few years, in shipments of plants from Spain, Belgium, Holland, Germany, Denmark, Norway, Sweden, Italy, Czechoslovakia and Portugal. Importations into North America in days when quarantine restrictions were unenforced or lacking must have been much more numerous. The species obviously is exotic in India as well as in South and North America.

Dendrobaena rubida (Savigny, 1826)

Athecal Indian specimens that have been identified as *Bimastos constrictus* or *Bimastos tenuis* belong here. *D. subrubicunda* also is a synonym.

Indian localities from which the species is now known are: Kodaikanal, Fern Hill and Ootacamund (Palni and Nilgiri Hills of South India, at elevations of 6000-8000 feet), Darjiling (eastern Himalayas), Almora, Naini Tal, Simla and vicinity (western Himalayas).

Genus Eisenia Malm 1877

Eisenia foetida (Savigny, 1826)

Indian localities from which the species has been recorded are: Ponmudi, Travancore; Kodaikanal and vicinity (Palni Hills) where it is very common; Fern Hill, Coonoor (Nilgiri Hills); Calcutta; Darjiling and vicinity (eastern Himalayas) where it is also very common; Simla, Kasauli, Dharmsala (western Himalayas). Absence of records for the Punjab, where Stephenson and his students worked, is noteworthy.

The Travancore and Calcutta records never have been confirmed. *E. foetida* was deliberately introduced, by the hundreds or thousands, on various occasions within the last twenty years, to lowland tropical areas of the Malayan and Indian peninsulas. All such introductions have been failures. Many more times the species must have been brought into the plains near the hill stations. Some such importation, most probably from Darjiling, may well have been responsible for the Calcutta record.

Eisenia hortensis (Michaelsen, 1890)

Eisenia veneta f. *hortensis,* Gates, 1951, Proc. Nat. Acad. Sci. India, B, vol. 21, pp. 19, 21.

This peregrine species has been found, in India, only at two Himalayan localities, Darjiling and Simla.

Eisenia rosea (Savigny, 1826)

Helodrilus (*Bimastus*) *indicus* Michaelsen 1907, Mitt. Nat. Mus. Hamburg, vol. 24, p. 188. (Type locality, Calcutta. Types, five, presumably in

the Indian Museum but probably valueless as they already were "weakened" from maceration in 1907.)

Helodrilus (*Allolobophora*) *prashadi* Stephenson 1922, Rec. Indian Mus., Calcutta, vol. 24, p. 440. (Type locality, Gundarbal, Kashmir. Types, several, in the British Museum.)

Allolobophora (*Allolobophora*) *prashadi* + *Allolobophora* (*Bimastus*) *indica*, Stephenson, 1923, Oligochaeta, *in* Fauna of British India, Ceylon and Burma, London, pp. 501 and 506.

Stephenson's species is known only from the original description. Insofar as can be determined from that description the types differed from Savigny's *rosea* only by the absence of spermathecae. As various strains of *rosea* are now known to be athecal there is no longer any reason for recognition of *prashadi*.

Michaelsen's species is known only from the types the descriptions of which contain no indications that external characteristics or internal anatomy warrant distinction from athecal, quadrivesiculate strains of *E. rosea*. Tubercula pubertatis, not mentioned, may have been unrecognizable because of poor condition or they may have been lacking — they are disappearing in some of the athecal strains. The diameter, 6 mm., is 2 mm. greater than the maximum usually mentioned for *rosea* but the types may have been bloated (as are some recently examined specimens where thickness in the clitellar region is about 7 mm.).

The types of *indicus* could have been collected at the Botanical Gardens in Sibpur where there were secured types of at least one other earthworm species erroneously thought to be endemic in Bengal. Indeed, in absence of subsequent records to confirm domicile in the area, it now seems possible that the specimens in question may have been secured directly from earth around roots of imported plants. Certainly, there is now not the slightest reason for believing that any lumbricid is endemic in Bengal.

All individuals of athecal strains of *rosea* that have been studied by the writer were male sterile. Two spermatophores, each containing "two oval sperm masses" were, however, present on one of the types of *indicus*. Acquisition of ability to reproduce asexually often precedes male sterilization. As soon as reproduction becomes parthenogenetic, important organs such as the spermathecae and male terminalia can be eliminated. In the genus *Pheretima*, for example, several instances are known in which extrusion to the exterior of sperm has become impossible though

maturation still is profuse. Too little is known as yet about the consequences of becoming parthenogenetic, in the Lumbricidae, to permit attribution of much taxonomic value to the presence of spermatophores even if containing sperm.

Savigny's species obviously does not belong in the genus *Eisenia* but may as well remain there until lumbricid genera can be defined by reference to structures that are less liable to rapid evolutionary change than are the organs of the reproductive system.

E. rosea has been reported from Kashmir, Murree Subdivision of the Punjab, Chitral in the Northwestern Frontier Province, Simla (western Himalayas), Darjiling (eastern Himalayas), and to the south only from Kodaikanal (Palni Hills). The new synonymies require no additions to the distribution as domicile in the region of Calcutta is improbable.

Genus LUMBRICUS L.

L. rubellus Hoffmeister 1845 has been recorded from the Nicobar Islands. No confirmation has been provided in the last sixty years. Subsequent collections from those islands have contained no lumbricids and domicile is improbable. The specimens may have been found in imported earth.

L. terrestris L. This species has been found only once in India and then at Simla in the western Himalayas.

Genus OCTOLASIUM Orley 1885

OCTOLASIUM CYANEUM (Savigny, 1826)

Helodrilus (*Dendrobaena*) *kempi* Stephenson 1922, Rec. Indian Mus., Calcutta, vol. 24, p. 441. (Type locality, Kufri, Simla Hill states. Types, two, presumably in the Indian Museum.)

Allolobophora (*Dendrobaena*) *kempi*, Stephenson, 1923, Oligochaeta, *in* Fauna of British India, Ceylon and Burma, London, p. 502.

Octolasium cyaneum, Cernosvitov, 1937, Rec. Indian Mus., Calcutta, vol. 39, p. 111. (Murree, Punjab.)

Dendrobaena kempi, Gates, 1939, Vest. Cesk. Spol. Nauk, Praze, 1938-1939, p. 151. (Ootacamund, Nilgiri Hills, South India, at elevations of 6700-8000 feet.)

Octolasium cyaneum, Gates, 1951, Proc. Nat. Acad. Sci. India, B, vol. 21, p. 19. (Simla.)

Stephenson's species was distinguished from other Indian lumbricids, except *mariensis,* by presence of hearts in xii. The Ootacamund specimens also appeared to have an extra pair. Junctions with the ventral blood vessel, which lateral hearts must have, were not found in specimens secured at Simla not far from the type locality of *kempi.* However, the supposed hearts are only dorsally directed continuations of the extra-oesophageal trunks. These continuations, unfortunately, do look very much like hearts in a dissection from the dorsal side. There remain then no taxonomically important differences from *cyaneum.*

Reproduction probably is not biparental as no sperm have been found in the spermathecae (nor any spermatophores externally) of any of the specimens that have been available from various parts of the world. Uniparental reproduction, whether sexual or asexual, presumably would predispose to successful colonization after introduction.

The species would appear to have been much more common at Ootacamund than elsewhere in India or indeed at any of the localities from which the writer has collected it.

Octolasium lacteum (Orley, 1881)

Eophila himalayana Cernosvitov 1937, Rec. Indian Mus., Calcutta, vol. 39, p. 109. (Type locality, Simla. Types, two, presumably in the Indian Museum.)

Cernosvitov's species is known only from his description. Several days' search at the type locality in 1944 by a good collector yielded a number of specimens of *lacteum* as well as representatives of two other peregrine forms that were previously unknown in India.

Absence of seminal vesicles in segments ix and x is the only character available to distinguish *himalayana* from *lacteum.* Undoubtedly the quadrivesiculate condition was the reason, and indeed the only one, for referring types of *himalayana* to the genus *Eophila.* Unfortunately the condition of the material submitted to Cernosvitov for study was poor, as the writer saw before it was mailed. Most of the specimens were more or less softened or brittle and alcohol-browned. In macerated individuals the smaller vesicles of the ix-x, especially when vestigial, may be indistinguishable from adjacent tissues. In brittle material the

vesicles are apt to be broken off during dissection so as to leave no macroscopically recognizable traces of their former presence.

Reproduction in *lacteum* probably is not biparental (though copulating couples have been seen, Gates, 1953), spermatophores never having been found externally nor sperm seen in the spermathecae of any of the specimens that have been available from various parts of the world. Some strains probably are male sterile but in others maturation of sperm appears to be so sparse as to warrant anticipation of parthenogenesis. With reproduction now asexual, seminal vesicles no longer are necessary and can be eliminated without harmful results to the individual or the strain. Seminal vesicles of ix-x have been quite small to vestigial in some strains recently examined and apparently have been lacking in others. The pair in ix alone or that in x alone has been quite small, vestigial, or unrecognized in other strains. Occasionally even the vesicles of xi have been vestigial when those of ix or ix and x were better developed. As these reductions or eliminations take place within the limits of what must otherwise be considered a species, there is now no good reason for recognition of *himalayana*.

Indian localities at which *lacteum* has been found are Darjiling, Mussoorie, Simla (all Himalayan), Murree subdivision (Punjab). All are well within the temperate zone.

DISCUSSION

Fourteen lumbricid species, if the unallotted residue of the *caliginosa* complex is counted as one, are now known to be present in the Indian subcontinent. All of them obviously are exotic there. No evidence is available to indicate any endemicity in adjacent regions of Baluchistan, Afghanistan and Tibet, below the Hindu Kush and Karakorum ranges. Lumbricids never were found in northern Burma and no endemics were discovered by Chen (1933, 1946) in the Yangtze Valley and the interior province of Szechuan in China. There is now no reason to anticipate lumbricid endemicity south of the Tian Shan and Altai mountains, Mongolia and Manchuria. Korea and Japan appear to have one or more native forms but none is known from Manchuria.

Twelve of the Indian lumbricids are present in the British Isles where no members of the family now seem to be endemic.

Twelve are widely distributed in North America. Many of them are present in South America, Africa, Australia, New Zealand as well as in various oceanic islands. One species, *Bimastos parvus*, usually is assumed to have had an American origin. The others certainly are all from Europe, from whence the worms were ferried to other continents and to the oceanic islands. The only way earthworms are known to be transported for such distances is in ballast or in earth with those plants that are cultivated by man. Transportation of the plants is unquestionable. The data now available (in MS) show that even a handful of the fertile, unsterilized earth surrounding the plant roots is liable to have contained cocoons or small juveniles and that larger samples often must have contained one or more adults. From the earliest transoceanic centers of successful colonization the exotic worms may have been transported by flood waters as well as by anglers, and, certainly, were distributed, on a geometrically increasing scale, by florists and horticulturalists as well as by innumerable householders. The alien species accordingly are properly called peregrine, the original meaning of which is foreign or imported.

In India, lumbricids are common in the Punjab and in the Northwestern Frontier Province. In the Himalayas, lumbricids never have been reported from Sikkim, Bhutan and Assam where there are no summer resorts, nor from Nepal where until very recently Europeans were excluded. Only in the region around Darjiling and in the sector west of Nepal are these worms known to be present. In the regions around the hill stations of both sectors lumbricids not only are common but also, in some part of the year at least, dominant. In the Gangetic Valley, which is well within the temperate zone, lumbricids are rare. Only 44 individuals, all of one species (*B. parvus*), were included among the 30,000 earthworms identified during the course of a four-year survey of the fauna of the Allahabad sector. No lumbricids were present among some 15,000 thousand earthworms collected in a Jubbulpore sector of the Deccan below Allahabad. Farther down the peninsula lumbricids have not been found until well into the far south and then at elevations of 5000-8000 feet but only in and around summer resorts.

Exotic plants are grown in pots as well as in the ground at all Indian, Burmese and Malayan localities where lumbricids are

present. These plants were taken to the hills since 1800, as summer resorts were developed by Europeans, but could have been introduced into many lowland areas of southeast Asia during the previous three centuries. Much earlier than 1500, during the period between Alexander's invasion and the downfall of the Graeco-Bactrian kingdoms, some cultivated plants may have been taken from Europe to the Punjab and Kashmir.

The exotic plants with which European earthworms were taken to the hill resorts of southeast Asia are common in the western portion of the Gangetic plains, in the Jubbulpore region of the Deccan as well as in Ceylon where there are no lumbricids. The same plants also have been taken many times from the hills to the lowlands, probably most frequently to larger municipalities quickly reached from hill resorts, e.g., from Darjiling to Calcutta. Absence of all lumbricids in most of such plant transportations and presence of only *B. parvus* in the remainder is improbable. Deliberate mass introductions of lumbricids to certain sections of India and the Malay Peninsula in the last twenty years have been no more successful.

Failure of the very lumbricids that have successfully colonized in the Americas, Africa, Australia and New Zealand to establish themselves in so many parts of southeast Asia to which they were introduced does not now appear to be attributable to the rigor of any competition provided by native species. An American glossoscolecid earthworm, *Pontoscolex corethrurus* (Müller, 1856), possibly introduced more recently and much less frequently, is widely domiciled throughout southeast Asia as well as Malaysia and in some localities appears to have become the dominant species. An exotic ocnerodrilid and a peregrine megascolecid, as well as a south Indian species of *Lampito*, now are common throughout the Gangetic Valley. A score or more of other exotic earthworms are established in Ceylon.

Moreover, the very numerous unsuccessful introductions that there must have been do not now seem to be attributable, as a rule, to absence of appropriate habitats. Most of the peregrine lumbricids seem to be tolerant of considerable variation in pH, moisture content and basic chemical constitution of the soil as well as in the amount of digestible organic matter. Nor has the reversal of seasons that exists below the equator prevented acquisition of domicile.

A first approximation to an explanation of the unsuccessful introductions probably could have been given long ago if distributional data had been particularized instead of being camouflaged by geographical generalizations and erroneous adjectives such as cosmopolitan. The Lumbricidae, prior to human intervention in the situation, were confined to the temperate zone of the Northern Hemisphere and, possibly, to some adjacent Arctic portions of Eurasia. Transported to every part of the world where Europeans have lived, lumbricids have acquired permanent domicile in the temperate zones and the tropics but in the latter only on the highlands. The elevations at which worms were collected usually are not stated in the literature but the tropical sites appear to be above the 5000 foot level. An inherent inability to survive in the less rigorous and more equable climate of the tropical lowlands seems to have been demonstrated.

All lumbricids are able to withstand the rigors of a temperate zone winter. Forms such as *D. octaedra, L. rubellus* and *A. chlorotica* (Savigny, 1826), that now live respectively in Nova Zemlya, northern Siberia and Greenland, must be able to withstand freezing temperatures (and being frozen?) for long periods. *D. octaedra* also has been able to colonize around Mexico City and Bogotá (Colombia) as well as on the Palni Hills of south India. The other two species appear to be somewhat less adaptable as they are not known to be present anywhere in the tropics though more liable to transportation. *A. trapezoides* appears to be even less adaptable as it is certainly known only from areas with a climate more like that of the Mediterranean lands from which it presumably was taken. The "endemic" lumbricids occasionally must have been transported but without being able to take advantage of the opportunities for extending their range. Furthermore, the distributional records published in the last fifty years seem to hint that even in their own areas the natives are being replaced by peregrine forms that may have been introduced there too by man. Accordingly, the family, as a whole, seems now to be definitely limited in ability to "advance," by climatic factors (presumably thermal), and seems to lack the youthful characteristics implied by such words as "powerful" or "conquering." Even in the area that the lumbricids have "conquered" without human assistance, dominion is shared with two other families, the Hormogastridae and Criodrilidae.

Characteristics of youthful vigor and great evolutionary adaptability, it now appears, were too hastily imputed to the Lumbricidae as a whole because of the distributions of less than a score of peregrine forms. Reproduction in some of these forms is parthenogenetic which has been thought to predispose to successful colonization. Peregrine forms with obligatory biparental reproduction, however, are much more common in considerable areas of North America. More important then than parthenogenesis now seems to be an ability to tolerate human interference in the earthworm environment. Those species, the haemerophiles, which are able to endure the disturbances of the soil involved in agricultural and horticultural practices are predisposed, as it were, to transoceanic and subsequent intraregional carriage as well as to survival in new areas that are also cultivated or otherwise influenced by man. One of the peregrine species, *Eisenia foetida,* has been thought to be haemerobiontic, i.e., dependent on culture, though that characterization, at least in the vicinity of Darjiling, seems exaggerated. Even *D. octaedra,* sometimes said to be haemerophobic, certainly lives so close to sites of human activity as to be frequently transported.

Introduction of lumbricids, according to Stephenson (1930, p. 905), "frequently causes the disappearance of the endemic earthworm fauna." The evidence usually cited for that conclusion is absence of native species in and around municipal areas of Chile and Australia that were investigated by Michaelsen during the present century. Whether endemics previously had been common at those sites is of course unknown, and the earthworm habitats therein had been long subject to modification by man. Such little information as is now available hints that indigenes are haemerophobic. Culture, then, could have left areas formerly inhabited by earthworms open to rapid colonization by any of the preadapted species. These, of course, were most likely to be from Europe, as were the settlers.

As the supposed competitive virility of the Lumbricidae also seems to be evidenced by little more than the predisposition of a few species to colonization in vacant but climatically restricted areas, there remains no reason for believing the family to be the "youngest" of the earthworms. Although India and China now must be excluded from the lumbricid domain, there still seems to be little reason to question a former range from the Mississippi

River in North America across Europe and through Siberia to Japan. Most of the earthworm families of Michaelsen's last classification (1928), such as Sparganophilidae, Criodrilidae, Hormogastridae, Syngenodrilidae, Eudrilidae, Moniligastridae, are much more restricted geographically. If area is an indicator of family age (and there is at present little else from which to judge), the Lumbricidae are much older than has been thought, possibly as ancient as any of the four remaining families in Michaelsen's system.

Prior to the Pleistocene ice ages there may well have been, in the vast area between the Mississippi and Japan, many more lumbricid species than are extant. Advance of ice sheets resulted in disappearance of earthworms from Greenland, Iceland, Canada, the northeastern part of the United States, northern Europe and perhaps also the British Isles. In North America a few species of two lumbricid genera survived but to this day they are largely confined to infrequently investigated habitats in the Appalachians. In Europe, the endemics, with a few exceptions that need further consideration, also have not advanced into the glaciated area. In that region the common species are those which seem most likely to have been living, during the glacial periods, just south of the ice cap. How closely they were able to follow the northward retreating ice remains to be learned. As none is known to be haemerophobic and many are haemerophilic the influence of man on their distribution in northern Europe must be determined first. That influence, hitherto underestimated for much of the world, enabled peregrine lumbricids, mainly from northern Europe, to acquire domicile throughout most of the settled regions of non-tropical North America in less than 500 years.

SUMMARY

Soil around roots of plants has carried lumbricids to every part of the world where Europeans have lived. A high degree of tolerance for human disturbance of their habitats predisposes a score of species to transoceanic as well as subsequent intraregional carriage and also colonization in vacant habitats where haemerophobic endemics have been eliminated by agriculture.

Acquisition of domicile in the tropics only at elevations above 5000 feet by otherwise successful colonizers shows an inherent inability to adjust to the milder and more equable climate of the lowlands. The size of the lumbricid domain, though India and China are excluded, indicates that the family is old. The Lumbricidae are conservative except as parthenogenesis permits more rapid accumulation of mutations.

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