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Comparative Studies on the Phylogeny and Systematics of the Rhabditidae (Nematoda)

WALTER SUDHAUS* AND DAVID FITCH†

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Updated through footnotes and appendices.

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This work is dedicated to our students.

Editorial Committee: Byron Adams, James G. Baldwin, Ernest C. Bernard, and W. Kelley Thomas.

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PREFACE

About a decade ago, when some of my colleagues (Scott Baird, Gaëtan Borgonie, Lynn Carta, Scott Emmons, Ralf Sommer, Marie Sutherlin, and W. Kelley Thomas) and I were searching for free-living nematode species for phylogenetically based developmental analyses incorporating the model *Caenorhabditis elegans*, we discovered Walter Sudhaus' 1976 monograph on the Rhabditinae. Looking at the figures (I made only moderate attempts to translate the figure legends and cursed my laziness in college German courses), we quickly realized that in the diversity of species represented in just this one subfamily, there was a potentially immense and largely untapped resource for comparative developmental studies. Of course, this was not a new conceptual epiphany for the field, only for us. Outstanding comparative developmental studies using *C. elegans* had already been pioneered by Sulston and Horvitz (1977), Sternberg and Horvitz (1981, 1982), and Ambros and Fixsen (1987), among others. But we were interested not only in making comparisons; rather, we sought an explicit phylogeny for mapping the **evolution** of the developmental components and processes that are rapidly becoming understood in *C. elegans* and other model systems.

What struck me most about Sudhaus' monograph was its deliberately phylogenetic (as opposed to typological) approach to rhabditid systematics, influenced largely by the cladistic theory of Willi Hennig. Significantly, the manuscript was written at a time when the practical aspects of cladistic methodology were just being developed (by Sudhaus and others), and much of the modern terminology was not yet in use. Other monographs on Rhabditidae, while excellent resources

in their own right, did not make such explicit attempts at cladistic reconstruction.

Understanding the evolution of developmental systems requires historical, phylogenetic hypotheses that are explicit and testable. This essential foundation is eminently and dispassionately fulfilled in all the work that Sudhaus has devoted to the study of rhabditids for more than a quarter of a century. Because the 1976 monograph (especially the first part) presents the groundwork for much of his later work on rhabditid ecology, biology, and systematics, as well as a set of concrete phylogenetic hypotheses that can now be tested with much additional data, I wanted to make this reference more available to the admittedly rather Anglocentric world of molecular, cell, and developmental biologists.

Although most of the material presented in this monograph has withstood the test of time, some later nomenclatural revisions and character and taxon descriptions or redescrptions have necessitated extensive footnoting to the translation and an appendix summarizing more recent phylogenetic hypotheses. Additionally, new molecular and developmental data have provided a phylogenetic picture that is in some ways fundamentally different from the view presented in the monograph. For this reason, we have deemed it appropriate to provide two additional appendices—one presenting a phylogeny based solely on molecular data and one presenting developmental criteria for homologies of male tail characters—to clarify these differences and identify future foci for systematic research.

With regard to the translation itself, I must emphasize that it generally does not represent a word-for-word literal translation; rather it is an attempt to preserve the

originally intended meaning (except where revision was necessary, where the original meaning is footnoted), as well as the flavor of the language. This goal could be approached only because Sudhaus himself provided preliminary translations of most of the text, along with numerous footnotes to update the work. In many cases I provided only a moderate editing function. For additional comments about the translation, see the Introduction to the Translation.

I want to express my deep gratitude and obligation to Walter Sudhaus for his generosity in time devoted to this project and with regard to sharing information and nematode strains, for his encouragement and patience ever since we decided to collaborate on a translation nearly three years ago, and for his meticulous attention to scientific and artistic detail that has inspired my admiration of all his work. Although our collaboration has been accomplished mainly by e-mail, I think of him as an educator and adopted mentor as well as my colleague and friend. May all such collaborations be as happy and fulfilling!

I also thank others who have been essential to this project: Scott Emmons and Scott Baird who initiated my interest and education in nematodes; the Fulbright Commission for supporting an all-too-brief semester in Berlin; the Whitehead Fellowship and Research Challenge programs at New York University and Philip Furmanski and the Department of Biology for both financial and moral support of many aspects and extensions of this project; Karin Kiontke for her many discussions, insights, and a thorough and thoughtful reading of the manuscript; James Baldwin, Byron Adams, W. Kelley Thomas, and especially Ernest Bernard for their indispensable assistance and expertise in reviewing and editing the manuscript; and the Society of Nematologists for sponsoring and producing this work. I especially thank my wife and family for their patient support and understanding of an assistant professor's neuroses and needs.

David H. A. Fitch
9 March 1998

INTRODUCTION TO THE TRANSLATION

Because the primary goal of this work was to provide a translation of the primary (mostly morphological) data and conclusions regarding the phylogenetic relationships of taxa within Rhabditinae, only the Introduction and Chapter I ("Phylogenetic System of Rhabditinae, *sensu lato*") of the Main Part of the original monograph have been translated in full. In addition, only those portions of other chapters that are specifically cross-referenced in Chapter I have been translated: Section 3 ("Metastomal structures"), Section 7 ("Bursa formation and its transformations"), and Section 8 ("Number and arrangement of the bursal papillae") of Chapter II ("Character evolution in Rhabditinae"),

and Section 9 ("Copulatory behavior") of Chapter VI ("Comparative ecology and biology of Rhabditinae").

Several points must be noted concerning the translation. For example, because it has been nearly a quarter of a century between this translation and publication of the original text, some revisions and updates have been necessary. Additionally, an explanation of the methods used in the original investigations can now be made using modern terminology not then available.

Footnotes: Comments about revisions and updated information or about the translation itself appear in footnotes. To differentiate these footnotes containing new information from the few footnotes that were in the original text, a note in square brackets with the original footnote number precedes each translated footnote.

Universal revisions and replacements: Some of the terms used in the 1976 text were universally replaced by other terms to reflect either updated thinking or simply conservation of words. For example, "fetalization" has been replaced with "paedomorphism" because in some cases the transformations described refer to juvenile (as opposed to "fetal") features. Where the original text uses the term "homoiologous," it has been replaced here by "parallel evolution." The original used this term to describe independent changes from a character state that was identical by descent (homologous) in two different ancestors to a new character state that is the same in two different descendents.

Where male genital papillae are described in the original as "penetrating the bursa velum outwardly," such papillae are described here as "opening dorsally" on the bursa velum. "Metastom" has been replaced by "metarhabdion" only in those cases where the reference is to one of the three metarhabdions of the metastom. Similarly, "cheilostom" has been replaced with "cheilorhabdion" and "telostom" with "telorhabdion" when these portions of the cheilostom or telostom are meant. Instead of "lip papillae," the more functionally specific "lip sensilla" is used. "Denticles" is used as the translation for "*Zähnchen*," but "teeth" is used for "*Zähne*." For greater precision, "ovary" is replaced with "female genital tract" when the entire tract is meant. In some cases where "larva" was used in the original, "juvenile" has been substituted.

"Synapomorphy" as used in the original text (and as often used in the literature) is synonymous with "apomorphy," which is used in this translation. When a novel character first appears and becomes fixed in a lineage, it is an "apomorphy" (or an "autapomorphy," a derived change unique to a particular species). By speciation, this character comes to be shared by sister species and is therefore an "apomorphy" for a monophyletic clade. Here, "synapomorphy" is restricted in its usage to the **observation** that two taxa uniquely share a common trait not found in the outgroup and are therefore hypothesized to be sister taxa; i.e., the synapomorphy of sister taxa is a result of the apomorphy of

their stem species. In this sense, “synapomorphy” is used methodologically (see Sudhaus and Rehfeld, 1992: 106–109).

When used to characterize taxa, the term “primitive” meant two different things in the original text: either a taxon diverging early in a particular group (i.e., a basally diverged taxon), or a taxon exhibiting many plesiomorphic characters (i.e., primitive characters probably exhibited by the ancestor of a particular group). These two meanings have been differentiated in the translation (and in most instances without footnotes).

Clarification: Additions have sometimes been made within the translated text to clarify the original meaning. These passages or words have been enclosed in square brackets to indicate material that is not present in the original text.

Page numbers: Although all cross-references to page numbers in this translation are to page numbers **in this publication**, the original page numbers are noted in the margins near the text where those pages began in the original. This has been done to assist those scholars interested in checking the original German text.

Taxonomic viewpoint: Readers familiar with *Caenorhabditis elegans* will no doubt find it peculiar to see this organism referred to in the translation as *Rhabditis* (*Caenorhabditis*) *elegans* or *R. elegans*. Because the author found it necessary to consider a broad range of taxa when making taxonomic comparisons or phylogenetic reconstructions, taxa tended to be lumped under generic epithets such as *Rhabditis*; subgeneric categories (such as *Caenorhabditis*) were then used to subdivide the genus *Rhabditis* into smaller groups. Indeed, the subgeneric names are used frequently in the original text almost as if they were genera in some cases. As more knowledge accumulates about the relationships among these species, it will undoubtedly become suitable to raise those subgenera supported as monophyletic groups to the level of genera. *Caenorhabditis* appears to be one such taxon. Therefore, “*C. elegans*” is used in the modern portions of this work, even though it is referred to in the original and in the translation as “*R. elegans*.”

A note about methodology: During the work on Rhabditiidae phylogeny, a practical methodology was developed on the basis of Hennig’s (1966) theoretical foundation. First, all characters of all the species observed and taken from the literature were listed in a matrix. Then the polarity of the characters (i.e., whether a character was a plesiomorphy or an apomorphy) was established by comparison with representatives from different groups (later called “outgroup comparison”). By finding taxa that shared unique characters (synapomorphies), sister taxa could be proposed when convergences could be ruled out following the principle of parsimony. Thus, although much of the modern terminology for cladistic methodology was not yet invented, the approach to re-

construct a cladogram did not differ from that used today (e.g., as presented in textbooks such as Sudhaus and Rehfeld, 1992).

INTRODUCTION

1

1. *On the significance of nematodes and research about them*

The class of nematodes is represented by an enormous number of species in nearly all conceivable habitats (with the exception of the air and plankton). In terms of numbers of species, this class contributes a branch to the animal kingdom that is as successful as that of the insects. (Of the 500,000 nematode species I have estimated, only a small fraction¹ are known.) Like insects, nematodes have maintained a very conserved body plan despite diverse habits of life. Besides the species diversity, an incredible number of individuals exist in different habitats. The upper stratum of one humus-rich meadow can yield as many as 20 million nematodes per square meter, which corresponds to a biomass of 5–10 g, only a small fraction (about 2%) of the total mass of soil organisms therein (Meyl, 1961). As parasites of animals and humans, but particularly as plant parasites, nematodes have achieved a worldwide economic significance with regard to monoculture. Just in the USA, the damage they caused in 1969 was estimated to be as much as 1.2 billion dollars.

Nematode research began with the parasitic forms, which, thanks to their size, were more amenable to study [than small free-living forms] and especially had practical significance. Accordingly, the roundworm *Ascaris* was introduced as a “typical” representative of the nematodes (e.g., in zoological lab practicals) until very recently. In fact, they are considered highly derived forms, as are most parasites. One finds nematodes that are primitive (and thus representative for the entire class) at the marginal zone between land and sea; among the saprophagous nematodes, primitive Secernentea have survived. Research into such free-living, microscopically small forms actually was initiated with the classic work of Bastian (1865) after the vinegar eelworm (*Turbatrix aceti*) had long since attracted attention as a species associated with human culture (first mentioned by the French physician P. Borellus in 1656). The monograph of Bastian (1865), which added 100 species to the approximately 80 known species of free-living nematodes, and the subsequent works of Schneider (1866), Bütschli (1873), De Man (1876), and Cobb (1893), to name only the most important, provided a primary boost for nematology. These works broadened the knowledge of the forms and their organization and development. Scientists (e.g., Schneider and Bütschli) came to realize that there was an extensive spread of

¹ 5–10%.

nematodes into various marine, freshwater, and terrestrial habitats and attention had already turned to the living world of the saprogenic substratum. The discovery of new forms and new types and the phase of description have yet to approach a conclusion. An overview of the wealth of specialized work in this field is additionally hampered by the fact that individual researchers are usually narrowly occupied with ecological instead of systematic groups (e.g., only with marine, terrestrial, zooparasitic, or phytophagous forms).

Additionally, nematodes were used early in cytological investigations (by Boveri and others) and played an essential role in the formation of the chromosome theory of heredity and sex determination. Research into the biology and ecology of these species began particularly with the animal and plant parasites, whereas other free-living nematodes were still largely neglected. But it is here that the opportunities exist, in the framework of a “physiological ecology,” to take the study of relationships between organisms and environment down to the molecular level. In this regard, the capability for monoxenic and axenic culture of saprophagous nematodes, already accomplished several times (by Dougherty and others), offers a productive starting point.

2. History of research on the Rhabditidae

As the important “type” for the saprophagous nematodes, the genus *Rhabditis* (the central significance of which has been repeatedly confirmed for the evolution of numerous parasitic lineages ever since the work of Leuckart [1876]) has always been regarded by nematologists as a difficult group because it exhibits a profusion of very similar species. The confusion began with the description of the genus by Dujardin (1845), who supplied no distinct diagnosis, but introduced instead a mixture of different species from several genera under the name *Rhabditis*. A clarification of the type species (*R. terricola*) was first provided by Dougherty (1955), thereby averting nomenclatural difficulty. Knowledge was expanded by Schneider, Bütschli, and De Man, who described a variety of new species. Örley (1880, 1886) provided the first monograph of the group. We are indebted to Maupas (1900) and Reiter (1928) for their classic work, unsurpassed even today, which laid the foundation for further successful investigation with detailed descriptions of the different forms and precise observations (especially by Maupas, 1900) of their reproductive biology. An organization of the group and the construction of a basis for the modern system rests chiefly with Osche (1952b). This [descriptive] work took place at the same time as the understanding of the ecology of free-living nematode species was greatly enlarged by the followers of Stammer² (Völk, 1950; Sachs,

1950; Hirschmann, 1952; Osche, 1952a; Mengert, 1953; Körner, 1954; Weingärtner, 1952/53; Rühm, 1956).

Meanwhile, an additional number of solitary descriptions have appeared, such that a reorganization and overview are now required. I have undertaken this task under the guidance of Prof. Osche. For the many stimulating discussions and for his formative influence, I am deeply indebted to my mentor. I have been receptive to his thoughts on particular questions, some of which have undoubtedly introgressed into this work, but can provide here only a global acknowledgment.

3. Material and methods

“Whoever wishes to become occupied with rhabditids must culture them according to prescribed standards.” (Örley, 1886:9).

Of the approximately 185 valid species of the Rhabditinae, 59 could be kept in culture at least temporarily, such that sufficient material was available not only for a thorough investigation of morphology and the variation thereof, but also for a study of the ecology, biology, and behavior of the various species. The species concerned have been marked in the appended catalog.³ It is important to note that numerous samples were obtained from as many different biotopes and areas as possible (and when possible, also from foreign continents), for which I thank my friends, P. Blum, C. Gack, D. and O. von Helversen, O. Hoffrichter, P. Miotk, P. Nevers, B. Reckert, F. Timm, B. Waldermann, and U. Wirth. An overview of ecological and geographical ranges was thereby obtained.

Species were bred on defined medium only in exceptional circumstances; normally they were kept on “natural” substrate in large and small petri dishes. Cultures were observed regularly under a dissecting microscope. Different species in competition were placed together on agar plates. For cultures of individuals, little chambers were constructed from pieces of glass tubing that were glued onto a holder with Eukitt and placed in a humidity box. Brood size could thereby be determined from individually cultured females, and hybridization tests could be performed between virgin females and males, different “strains,” or different species. Dauer larvae were stored in little test tubes in water and dried in the substrate in constant-temperature incubators, and their survivorship was determined under different conditions. Additionally, a record of data was compiled from the literature and kept as complete as possible to enable a detailed comparison with [my] independent observations of morphology, biology, and ecology.

To investigate the phylogenetic system of the Rhab-

² Prof. Stammer, Erlangen.

³ This catalog of species is not included in this translation, as it has been updated (Sudhaus, 1991) and will be updated again soon (Sudhaus and Fitch, unpub.). A current Rhabditinae list shows 253 species (Sudhaus, unpub.).

ditinae, the different species were compared to each other with respect to all known characters to discover shared derived characters or character combinations. For this purpose, extensive tables⁴ were constructed for the different groups (genera or subgenera) which allowed a comparison of the characters. As a general principle, it should be noted that all well-known characters were used for comparisons. However, clear limits were thereby set such that, for the majority of the species where not enough single characters were well known, the deficiency could be filled only for those species that could be approached through my independent investigations. In the final analysis, the phylogenetic approach has resulted in a wealth of detailed questions, not all of which could be answered, but now demands primarily an expansion of the material and with it the basis for induction. From the main part of this work, several questions become tangibly discernible.

4. Concepts and methods of phylogenetic systematics

An essential part of the work presented here is to construct a phylogenetic system. A little must therefore be said with regard to the phylogenetic method as consistently applied by Hennig (e.g., 1966) and the concepts used. "The proposition of well-formed hypotheses regarding the monophyly of animal groups and their genealogical relationships is what we call phylogenetic systematics . . ." (Hennig, 1969:40). To this end, certain (homologous) characters are compared to examine if their observed states were derived by transformation (and thus apomorphic) or are primitive (plesiomorphic). These concepts are to be understood in relative terms. At a deeper phylogenetic level, plesiomorphies become apomorphies; as such, they are also of interest and will always be specified separately in this work. (The plesiomorphy of "today" is the apomorphy of "yesterday.") They play no role for further reconstruction of a phylogenetic system. Only "synapomorphies" are important for the establishment of monophyly.⁵ The concept of synapomorphy incorporates the hypothesis that the compared characters are truly derived from a shared ancestor and are thus "euhomologous." This must be conceptually distinguished from the establishment of identical apomorphies in different taxa, which can be specializations acquired independently from one another. Their coincidence (homomorphy) could [also] be due to parallel change⁶ (separate origin, but from the same primordium) or—in the

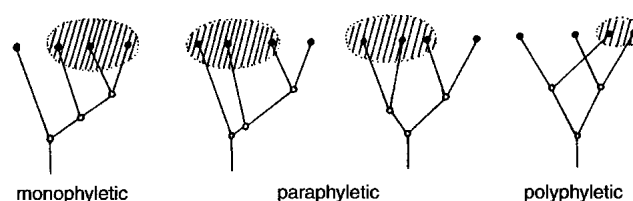


FIG. 1. Grouping by similarity and resulting in monophyly based on synapomorphy, in paraphyly based on symplesiomorphy, and in polyphyly based on convergence (following Hennig [1966]).

most unpropitious circumstance⁷—to convergence. Because they are insignificant for the construction of a [phylogenetic] system, Hennig did not coin different terms for the various types of homomorphous (though not homologous) autapomorphies. However, they appear again and again and interfere with the application [of phylogenetic reconstruction]. The concept of synapomorphy always incorporates a phylogenetic interpretation. Sometimes it is not possible to distinguish between synapomorphies and homomorphies that in reality are convergent apomorphies, such that a faulty [phylogenetic] conclusion will be reached, though occasionally the independent emergence of two homomorphic autapomorphies may be shown. The probability that such homomorphic apomorphies are counted as synapomorphies naturally depends on the number of coincident apomorphic characters in the taxa compared. "The evidence for monophyly becomes more certain the more numerous and unique are the derived characters" (Hennig, 1969:26). Ultimately, all these statements [about phylogeny] are hypotheses that are only more or less certain. I would also like to particularly emphasize that the cladograms depict hypothetical models of the phylogenetic history that are supported only by certain estimates of probabilities.

"Constitutive characters," which are suites of derived characters (the convergent origin of which is thus unlikely), substantiate the monophyly of a group. A "monophyletic group" in the sense of Hennig (= "holophyletic" in Ashlock, 1971, cited by Mayr, 1974) includes all and only those species derived from a single ancestral species. On the other hand, a "polyphyletic group," in which commonality is due to convergence, does not include all known descendants of an ancestral species. Such polyphyletic groups are always dissolved once they have been recognized as such. In contrast, a "paraphyletic group" also does not include all extant descendants of an ancestral species, but excludes a monophyletic species group that is a descendant of a later [ancestral] species in this group (see Fig. 1). Hennig wanted these [paraphyletic taxa] to be treated in the same way as polyphyletic taxa and dissolved. The similarities among these species [in a paraphyletic taxon] are not due to convergences, but rather to

⁴ The modern term would be "matrix." The author independently developed the use of matrices for the cladistic analysis of the morphological characters described in this work, usually with binary states for these characters (e.g., see Sudhaus and Rehfeld, 1992).

⁵ For a clarification of the difference between the usage of "synapomorphy" and "apomorphy," see the Introduction to the Translation.

⁶ The author used the term "homoiology," synonymous with the modern meaning of parallel evolutionary change (see Introduction to the Translation).

⁷ i.e., unpropitious for inferring genealogical relationships.

symplesiomorphies, which are autapomorphies [at a deeper level] for a higher (more encompassing) taxon that includes the paraphyletic group in question and the excluded monophyletic group. The endeavor to highlight and name a smaller monophyletic subgroup of the encompassing monophyletic group, and thus to create a paraphyletic group from the "remaining" [taxa], can be understood in light of the well-established anagenetic evolution that has occurred in this monophyletic subgroup and which is considered so significant. Although it may be logically attractive to conclude that such paraphyletic taxa should be dissolved, it would be a misunderstanding of the goals of a system to ignore a classification that considers anagenesis and allows a clear resolution of a paraphyletic group that is yet traceable to a single ancestral lineage, even if there is no special path of anagenetic evolution that distinguishes an outlying position of the species belonging to this group which still share a high degree of similarity due to homologous correspondences. I consider it correct to maintain a division between the phylogenetic tree (or pedigree) as an accurate genealogical model and the nomenclaturally important taxa. To demand a congruence here⁸ strains the capacity of our language. The largest part of the heated polemic about "phylogenetic systematics" (with both of the exponents, Hennig and Mayr) is centered around this point.

Now to the actual case of the system of Rhabditida. The groups (subfamilies, genera, subgenera) that have been erected up to now have been organized multiple times according to one or a few characters that (explicitly or not) have been viewed as synapomorphies. The difficulty exists, however, in including as many characters as possible in the comparative study. Limitations are approached very quickly. The first limitation involves deficiencies in knowledge that will now be exposed. In this regard, it is hoped that the future will yield many clarifications. The other limitation exists in our use of induction as a way of knowing; it is a question of deciding between different kinds of probabilities. For example, consider a specialized character, from which a classification is to be inferred, that always yields the conclusion of convergence with other derived characters that nevertheless exhibit a high degree of specialization and appear just as "unlikely."⁹ Moreover, it is not always easy to judge the probability of reversal for characters that were acquired once. In *Rhabditis*, for example, the transformation is easily possible from a cupola-shaped female tail (apomorphic) that was acquired once to a conical tail (primarily plesiomorphic) by means of paedomorphism,¹⁰ because the juvenile

stages still have a conical tail. Furthermore, because of the "heterobathmy of the characters," i.e., the mosaic distribution of primitive and derived stages of the characters, it is usually difficult to judge which should be taken as plesiomorphies and which as apomorphies. However, I regard it a legitimate procedure to divide the characters into apomorphies and plesiomorphies by explicit "scoring" based on considerations of probability and thus to work out a classification into a logical system according to phylogenetic considerations. The reason I state the premises explicitly for each case is so they may be reconsidered if new factual material is discovered. Every phylogenetic tree would look different if one assumed different premises.

In the work presented here, I have always attempted to directly consult the sources (i.e., the original species descriptions) and to use these descriptions and data ascertained by myself to achieve a fresh classification and to achieve an especially well-substantiated system that is as impartial and uninfluenced as possible from historically contingent groupings and classifications. It was soon clear that the system, essentially based on the *Rhabditis* systematics carefully elaborated by Osche (1952b) (although there are a few adjustments), withstands examination in principle and is essentially well substantiated. However, a historical influence on my system is presumably not overcome in every case. So I remain conservative wherever two contradictory views are currently difficult to support. Support for the system in such cases might not necessarily be expected.

5. Explanation of morphological characters

6

The following important features are depicted in a general schematic (Fig. 2):

(A) Anterior end: li = lips (here set apart) with lip sensilla, mu = buccal tube, ph = pharynx (here rhab-

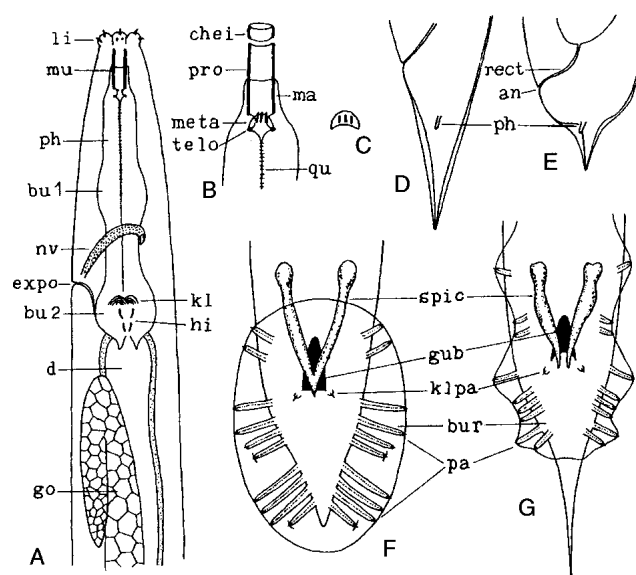


FIG. 2. [Generalized schematic of rhabditid features] explained in the text.

⁸ i.e., between the phylogenetic pedigree and the taxonomic classification.

⁹ Basing a reconstruction on one character may result in the interpretation of convergences, parallelisms, or reversals (i.e., homoplasy) in other characters.

¹⁰ "Fetalization" in the original.

ditoid), bu 1 = median bulb, bu 2 = terminal bulb with valvular apparatus (= kl) and double haustulum¹¹ (= hi), nv = nerve ring, expo = excretory pore, d = midgut, go = gonad with terminal reflex.

(B) Buccal cavity with glottoid apparatus: chei = cheilostom, pro = protostom,¹² meta = metastom with metastomal structures (here denticles), telo = telostom (metastom and telostom together form the glottoid apparatus), ma = pharyngeal sleeve which envelopes the buccal tube, qu = transverse ridging of the cuticle lining of the pharynx lumen.

(C) Metarhabdion¹³ bearing three ridges.

(D) Conical female tail.

(E) Cupola-shaped female tail with spikelet: rect = rectum, an = anus, ph = phasmids (tail glands).

(F) Posterior end of the male (ventral) with peloderan (tail-encompassing) and proximally closed bursa. Bursal papillae in the arrangement (2/1+3+4), of which the sixth and 10th (numbered from anterior to posterior) open dorsally; spic = spicules (here distally fused); gub = gubernaculum; klpa = cloacal sensory papillae; bur = bursa velum; pa = bursal papillae.

(G) Posterior end of the male with leptoderan form of the tail (the tail tip reaches beyond the bursa posteriorly) and proximally open bursa. Bursal papillae in the arrangement (1+2/1+3+2). Bursa is "radially" arranged (not all papillae lie in a line; here the first, fourth, and eighth are sublateral, and the second, third, fifth, sixth, seventh, and ninth are subventral). Abbreviations as in (F). (Here the spicules are separate and the gubernaculum is distally forked).

7

MAIN PART

I. Phylogenetic system of Rhabditinae *sensu lato*

"I also look for the value of such views essentially in [their ability to promote] the formulation of new or more specific questions." (Bütschli, 1876:410).

The family Rhabditidae Oerley, 1880 is subdivided into several subfamilies: Rhabditinae (Örley, 1880) Micoletzky, 1922; Protorhabditinae Dougherty, 1955; Alloionematinae Chitwood & McIntosh, 1934; and Diploscapterinae Chitwood & Chitwood, 1937 (as in Goodey, 1963). More recently, additional subfamilies have been erected (Prodontorhabditinae Timm, 1961; Parasitorhabditinae Lazarevskaya, 1965; Stomachorhabditinae Andrassy, 1970). To what extent all of these subfamilies are justified must be weighed on an individual basis. I personally consider it useful to com-

bine Rhabditinae, Parasitorhabditinae, Protorhabditinae, and Prodontorhabditinae into a single subfamily [i.e., Rhabditinae]. The present work includes only such representatives of the Rhabditinae in this broader sense; Alloionematinae, Diploscapterinae, and Stomachorhabditinae are not considered in this work at all. The first objective is to test the groups (genera, subgenera, species groups) that have been recognized since the fundamental investigations of Osche (1952b) with respect to monophyly or paraphyly (Hennig, 1966) by comparing all known features, and thus to determine the justification for maintaining these groups. The second objective is to depict the course of phylogeny through cladograms (so far as this appears justifiable). Concretion in this area seems important to me, for "to take an unequivocal stand . . . is of greater heuristic value and far more likely to stimulate constructive criticism than to evade the issue" (Mayr, 1963:vi). In contrast, the taxonomic level of the respective species group appears secondary. I have already justified (Sudhaus, 1974b) my view to allow but few distinct genera of the Rhabditinae and hence to facilitate an unobstructed overview and insight. In this respect, only four genera are treated in the following text, namely *Parasitorhabditis*, *Protorhabditis*, *Prodontorhabditis*, and *Rhabditis sensu lato*. However, the species of the different genera are put into more closely defined species groups (so far as possible) and, for *Rhabditis*, are additionally grouped into numerous subgenera.

1. *Parasitorhabditis* Fuchs, 1937

This group, with the taxonomic rank of genus, is "basally diverged"¹⁴ with respect to *Rhabditis* and displays quite a series of primitive features (**symplesiomorphies**): the lips are closed; the typical shapes of the metastom and telostom that are characteristic of a glottoid apparatus are missing¹⁵ (compare Fig. 4a with Fig. 2b), although rather small wart-like denticles are present at the corresponding position; a pharyngeal sleeve is also absent; the transverse ridging of the anterior part of the pharynx (corpus) is very conspicuous for the most part; a typical median bulb is absent; the terminal bulb perhaps has a double haustulum; the vulva is far posterior (at 90–96% of body length); the female genital tract is accordingly unpaired;¹⁶ the bursa is always [8] peloderan, [anteriorly] open, and supported by 10 [pairs of]¹⁷ bursal papillae, 2 of which are located precloacally; a particular grouping of the papillae is not

¹¹ "Haustulum" may not be a good term for this passage between the valvular apparatus in the terminal bulb and the beginning of the intestine, because it also refers to the place where the wall of the intestine (colon) is bulged out.

¹² Protostom = prostom + mesostom.

¹³ "Metarhabdion" replaces "Metastomklappe," or "metastomal valve" in the original.

¹⁴ The original text used the term "urtümliche," which means "primitive." However, this term should be used to describe characters, not species groups. It is meant that the lineage to *Parasitorhabditis* diverged early from a lineage leading to *Rhabditis*. See Introduction to the Translation.

¹⁵ The original states that a glottoid apparatus is missing, with a qualification in parentheses that it is actually the typical forms of the metastom and telostom that are proposed to be missing.

¹⁶ i.e., with a single arm.

¹⁷ Note that the bilaterally symmetrical bursal papillae are usually described for only one side, so that "pairs of" is generally omitted but implied.

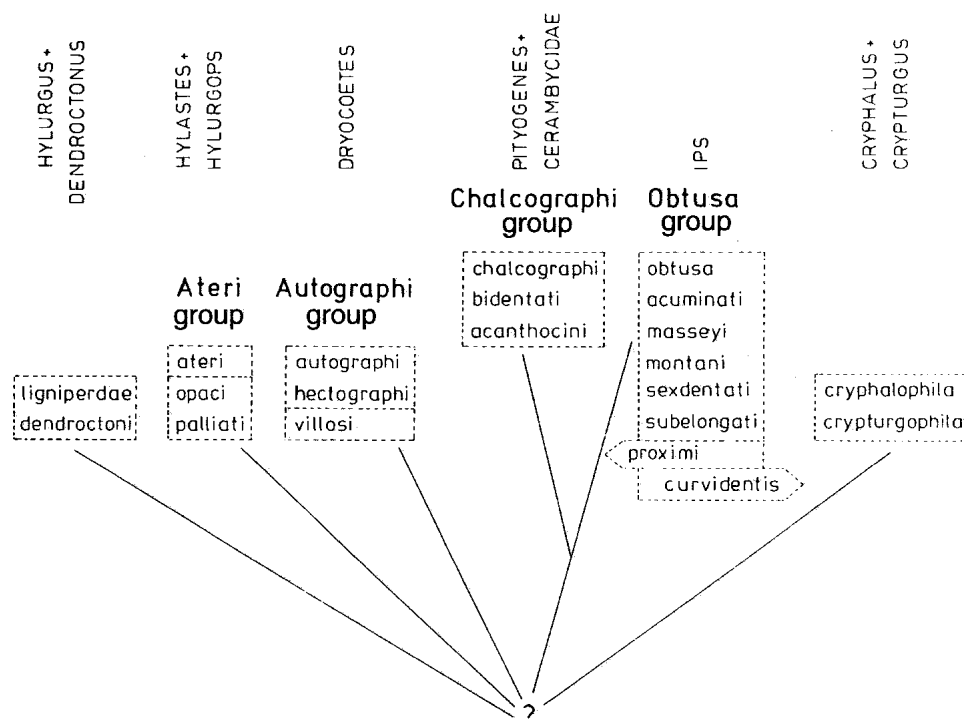


FIG. 3. Relationships among the *Parasitorhabditis* species (except the following insufficiently known forms: *P. ali*, *P. cembraei*, *P. crenati*, *P. pini*, *P. piniperdae*, and *P. thornei*). [*Cryphalus*, *Crypturgus*, *Dendroctonus*, *Dryocetes*, *Hylastes*, *Hylurgops*, *Hylurgus*, *Ips*, and *Pityogenes* are genera of Scolytidae, the family of bark and ambrosia beetles (Coleoptera) with which these nematodes are associated. Cerambycidae are longhorn beetles.]

always recognizable and varies from one species to the other; the gubernaculum is always slipper-shaped; the tail of the dauer larva is generally long and pointed and in one species group [*Chalcographi-Obtusa*] is jagged at the end (*Dreihöckerschwanz*, a triply pointed tail; cf. Osche, 1955a). Besides these diagnostic—although plesiomorphic—features, there are additional characters in common that are **constitutive**¹⁸ in the sense of Hennig (1969:25) and which support the monophyly of this group: the buccal tube is not perfectly cylindrical, but is most narrow near the middle (its walls are thus convex¹⁹); the female tail is never threadlike, but very short, plump, and pointed like a wedge or even dome or cupola shaped (i.e., [rounded and] without or with a pointed tip, respectively); the sixth bursal papilla²⁰ is always short and a little thicker than the others; the proximally knobbed and usually long and slender spicules (30–51 μ m) are fused distally; and the usually distinct texture of the cuticle extends partially onto the bursa velum. The species are of medium length and rarely longer than 1 mm (502–1,440 μ m).

This genus is also uniform biologically and ecologically (because of its rather close association with Scolytidae) and shows only slight differences between the species. Therefore, a further subdivision of the group—

with the objective of presenting cladograms for distinct subgroups—is not possible given the present knowledge (see Fig. 3). Rühm (1956, 1960, and in Rühm and Chararas, 1957) tried to differentiate²¹ at least four species groups—the *Ateri* group, the *Chalcographi* group, the *Obtusa* group, and the *Autographi* group—without being able to identify unequivocal characters supporting the relatedness of the species in each case. Nonetheless, these groups can be maintained with minor modifications.

Within *Parasitorhabditis*, a cupola-shaped tail in the female is apomorphic. Species with this feature often have further characters in common (Fig. 4): specifically, they have a similar arrangement of the bursal papillae such as (2 / 3 + 2 + 3)²² or (2 / 3 + 5), in which the fourth and fifth are fused a little at their bases and the 10th is shortened; the pseudolips are rounded; and the “metarhabdions” each bear a wart-like denticle (if at all). Moreover, the dauer larvae possess a triply pointed tail only in this group (though not in all the

²¹ The term “*herauszuschälen*” (“to peel off,” as to remove layers of an onion) was used in the original text, but it is difficult to translate this imaginative metaphor.

²² [Footnote 1 of the original text.] This formula means that there are 10 pairs of papillae, 2 of which are anterior and 8 of which are posterior to the cloaca, forming clusters of 2, 3, 2, and 3 (see Fig. 2). [In this notation, the pattern of papilla clustering is depicted as the numbers of papillae in each group, with each group set off with either ‘+’ or ‘/’, the latter symbol designating the relative position of the cloaca. An “r” designates the relative position of a short or “reduced” papilla, generally the most posterior, and usually corresponding to the phasmid.]

¹⁸ i.e., apomorphic.

¹⁹ “Convex” replaces “concave” of the original, although the concavity simply depends on the point of view.

²⁰ This papilla is the phasmid (Kiontke and Sudhaus, 2000).

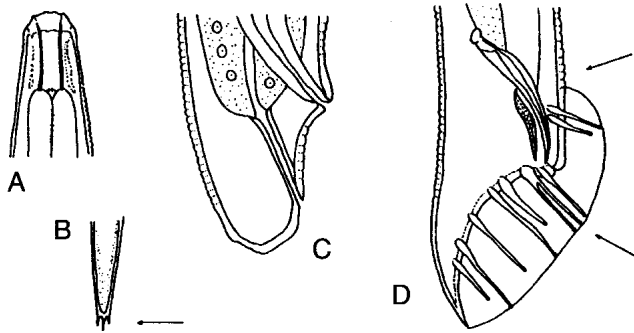


FIG. 4. *Parasitorhabditis subelongati* Slobodianiuc, 1973. A) Anterior end. B) Triply pointed tail of the dauer larva. C) Posterior end of the female, lateral view. D) Posterior end of the male, lateral. (After Slobodianiuc, 1973).

species). I attach considerable systematic importance to the fact that the fourth and fifth papillae have a common base, which was not sufficiently noted before. Biologically, these species are associated with members of the genus *Ips*. This species group corresponds to an expanded version of the “*Obtusa* group” of Rühm (1956).

Parasitorhabditis curvidentis is somewhat divergent in its characters (the tail is not cupola-shaped and the bursal papillae are arranged differently), and is unique within the genus in that its dauer larvae always travel up to the midgut of the beetle. *Parasitorhabditis crypturgophila* and *P. cryphalophila* show a certain similarity to *P. curvidentis*. In all three species, metarhabdion denticles are missing; the pseudolips are rounded; the tail of the dauer larva is short, wedge-shaped, and rounded like a fingertip; and the spicules bear a thin velum distally. *Parasitorhabditis crypturgophila* and *P. cryphalophila* are undoubtedly close systematically. Their ninth papilla is slightly shortened, and the dauer larvae crawl up to the Malpighian vessels of the “host.” It remains uncertain, however, if these two species can be connected to the *Obtusa* group.

Some of the features named for the *Obtusa* group can also be found in the species of the *Chalcographi* group; e.g., both groups are characterized by a wart-like denticle on each metarhabdion and are associated with *Pityogenes* species. *Parasitorhabditis proximi*, which associates with *Ips*, shares characters with both of these groups.

A cupola-shaped tail also occurs in the females of *P. piniperidae*, a species which cannot be easily classified and diverges biologically in forming semiparasitic larvae that live in the body cavity of the beetle. The other species that have a plesiomorphically pointed tail often have a bursal papilla arrangement of (2 / 4 + 4), two denticles on the dorsal “metarhabdion” and only one on each subventral metarhabdion, pseudolips that are usually pointed, and dauer larvae that nearly always pos-

sess a conically pointed tail. The unity²³ of this expanded *Ateri* group is quite uncertain (see Fig. 3), although *P. opaci* and *P. palliati*²⁴ surely are closely related in this group. For instance, these two species possess a gubernaculum that is characteristically thorned proximally, a state that appeared convergently, however, in *P. obtusa*. *Parasitorhabditis ligniperdae* and *P. dendroctoni* are also similar to one another, e.g., in the formation of the spicules and the granular, wart-like structure of the cuticle. *Parasitorhabditis autographi* and *P. hectographi* are quite similar to each other, particularly in the organization of the bursa. With respect to the combination of features like the female tail, bursal arrangement, metarhabdion denticles, etc., these latter two species bridge the *Chalcographi* and *Ateri* groups. However, *P. villosi*, likewise placed in the “*Autographi* group” by Rühm and Chararas (1957), does not fit very well with the character mosaic of this group. The last three species mentioned are associated with *Dryocoetes* species.

It seems noteworthy that the tail of the dauer larva, which undoubtedly was primitively long and conically pointed, became very shortened and often rounded like a fingertip in those species that invade the Malpighian tubules, the midgut, or the body cavity of the “host” beetles. Certainly, the ecological²⁵ value that obviously exists for such a tail shape diminishes its taxonomic value. On the other hand, a “triply pointed” tail (Fig. 4B) is restricted to the dauer larvae of only the *Chalcographi* and *Obtusa* groups (as previously mentioned), where it is thought to serve in locomotion and in attachment to the rectum of the host (Fuchs, 1937). According to Osche (1955a), however, the triply pointed tail is a primitive feature of nematodes that was cryptotypically²⁶ harbored²⁷ for a long time.

2. *Protorhabditis* Osche in Dougherty, 1955

This genus name refers to a certain number of primitive characters in this group. The following **symplesiomorphies** are exhibited by this group: the lips are closed, the typical forms of the metastom and telostom are lacking,²⁸ the female tail is conical, the bursa is peloderan with two pairs of precloacal papillae, the terminal bulb (presumably always) has a double haustulum, and the body length is relatively short (270–965 µm). The following characters may be interpreted as **apomorphies**: the midbody vulva and the accompanying paired ovaries, the fact that the fifth and seventh bursal papillae open on the dorsal surface of the bursa

²³ i.e., monophyly.

²⁴ The original text lists instead *P. poligraphi*, which is a synonym of *P. palliati*.

²⁵ By which the author additionally implies “adaptive.”

²⁶ That is, the genetic potential for this feature was maintained, but was not phenotypically expressed.

²⁷ The original text applies the adjective “mitgeschlepptes” (dragged along), but this metaphor is difficult to work into the translation.

²⁸ The original states that the glottoid apparatus itself is lacking, adding the qualification in parentheses that by this was meant the metastom and telostom.

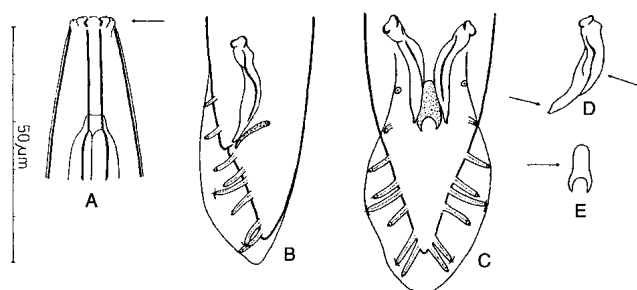


FIG. 5. *Protorhabditis postneri* (Körner, 1954). A) Anterior end. B) Posterior end of the male, lateral view. C) Posterior end of the male, ventral view. D) Lateral view of spicule. E) Ventral view of gubernaculum. From a *Dorcus parallelopipedus* [Coleoptera:Lucanidae] from the Neusiedler See [Austria].

velum, and the reduction of the number of bursal papillae to nine or fewer (generally eight). (Since I found two males of *P. oxyuroides* with a distinct, stub-like remnant of a 10th papilla, I would like to assume that the last²⁹ of the 10 papillae of the ground pattern of the Rhabditinae has been lost.)³⁰ These features support the monophyly of this group. Additional primitive characters, which surely have to be ascribed to the ancestor of *Protorhabditis*, are cuticularized cheilorhabdions distal³¹ of the buccal tube; the lack of a pharyngeal sleeve and median bulb; a conspicuously developed transverse ridging in the cuticular lining of the pharynx lumen; a narrow lateral field of the cuticle; a presumably long, thread-like female tail; an [anteriorly] open bursa; and separate, more or less dagger-shaped spicules.

Within this group, *P. elaphri* (Fig. 6) is an outlier because it has many primitive traits: cheilorhabdions are differentiated, the pharynx is still anguilluloid³² with distinct transverse ridging of the cuticular lining of the pharynx lumen (the valve plates are “not yet” fully developed³³), the female tail is long and whip-like, and the bursal papillae are not arranged in fixed clusters. Moreover, the number of the papillae varies markedly in this species up to a maximum of nine pairs. The gubernaculum is spatula-shaped. Of course, special derived characters also exist; e.g., a very long pharyngeal sleeve and particularly large amphids.

All other *Protorhabditis* species diverge from *P. elaphri* in their development of a median bulb, lack of transverse ridging in the cuticular lining of the lumen of the

corpus insofar as is detectable with the light microscope (the formation of a “normal” valvular apparatus), and a more or less clear arrangement of bursal papillae into groups, in which the last three papillae (or the last two in the case where one pair is lost) lie close together. The gubernaculum (probably) became forked distally and diverges proximally from the spicules (in lateral view).

Five species that look remarkably similar to one another are considered to form a monophyletic group (i.e., the “*Xylocola*” group, see Fig. 6) with the following **apomorphies**: the ninth bursal papilla is completely reduced,³⁴ such that only eight papillae are formed; the spicules are markedly curved (sickle-shaped); the gubernaculum is always shaped like a bootjack and is accordingly more or less strongly forked distally; the female tail is short and conical; and all species possess a very small but clear pharyngeal sleeve, enveloping up to 25% of the length of the buccal tube (Fig. 5A). With respect to the shape of the female tail and the formation of a short sleeve, *P. virgo* (for which males are unknown) should be placed in this group. This species and *P. ruehmi* lack cuticularized cheilorhabdions, which contrasts with the other species of this group. Concerning the arrangement of the papillae and the structure of the spicules and gubernaculum, *P. xylocola* appears to be the most primitive species of this group.³⁵ *Protorhabditis parvovelata*, with its markedly reduced and somewhat radially organized bursa, is the most derived. A specific subdivision of this group is not possible with the present data. (It can be shown that the ninth papilla has actually been reduced in the *Xylocola* group.³⁶ Since the seventh papilla of these species opens dorsally on the bursa velum, only the eighth or ninth papilla of the most posterior group of three could have been lost. An aberration of *P. macrovelata* that I found has a supernumerary, ninth papilla on one side, thus supporting this papilla reduction hypothesis.)

As described by Körner (1954), the tail of small *P. parvovelata* females is cupola shaped to obtusely conical, but conical and pointed in large, well-fed females. The fourth-stage juveniles also have a cupola-shaped tail. It is currently unknown if this phenomenon [i.e., the correlation between tail morphology and nutrition] applies to the entire *Xylocola* group or if it applies to *P. parvovelata* alone. In the dauer larvae of an unidentified *Protorhabditis* species associated with *Trichius fasciatus* (Coleoptera: Scarabaeidae), I observed something similar (the association with *Trichius* supports the position of this species in the *Xylocola* group). Therefore, an

²⁹ i.e., most posterior.

³⁰ More likely, this “remnant” is actually the posteriorly positioned phasmid which has failed to retract fully with the tail tip during morphogenesis before the last larval molt. No bursal papillae would thus be lost in species with nine pairs of papillae if the ground pattern is actually nine pairs of genital papillae and one pair of phasmids.

³¹ i.e., anterior.

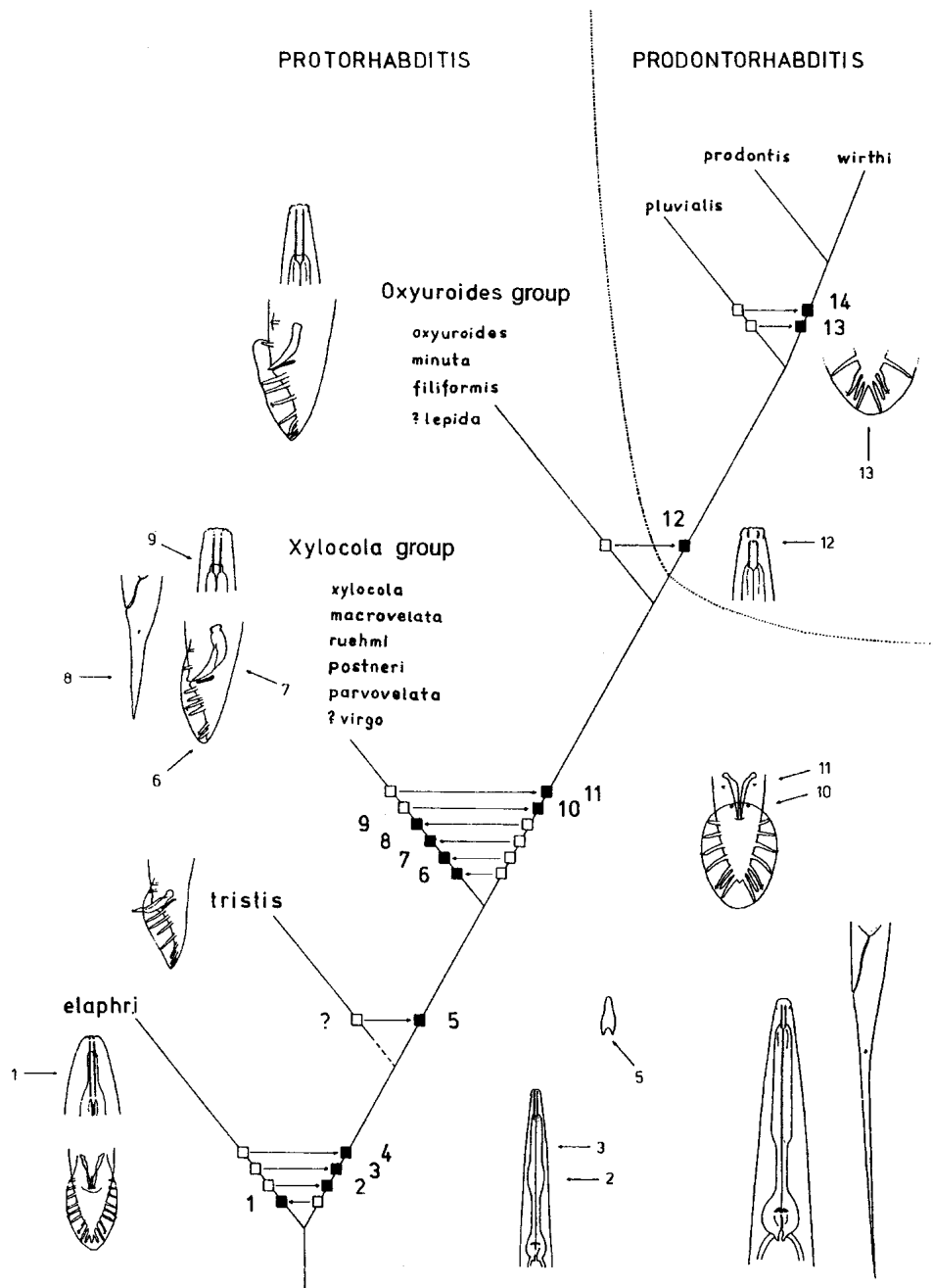
³² i.e., without a median swelling.

³³ [Footnote 2 in the original text.] A difficulty arises here [with the evolutionary reconstruction]. If we regard the incomplete valvular apparatus in *P. elaphri* as a primitive feature (Osche, 1952b), then complete valve plates must have evolved convergently (at least twice in Rhabditinae, in Cephalobidae, and in other groups as well). This is possible, especially if completion of this structure simply involved the “perfection” of pre-existing transverse ridges in the terminal bulb into valves. Nonetheless, it appears more likely that the simple state of this feature in *P. elaphri* represents a derived situation.

³⁴ i.e., lost.

³⁵ By “primitive” is meant that this species has many plesiomorphic features and is the first species that diverged in this group.

³⁶ Most likely, the homologue of ray 8 has been lost, convergent with the loss of this ray homologue in *Rhabditis blumi* (see Fitch and Emmons, 1995).



13 FIG. 6. Cladogram from *Protorhabditis* and *Prodontorhabditis*. (Here and in following figures a filled square denotes apomorphy and an open square denotes plesiomorphy.) The numbers denote the following apomorphies: (1) with pharyngeal sleeve; (2) median bulb formed; (3) transverse ridging lost; (4) papillae in groups; (5) gubernaculum forked; (6) only 8 bursal papillae present (loss of papilla nine [actually r8; see footnote 36]); (7) spicule sickle-shaped; (8) female tail short and conical; (9) short pharyngeal sleeve; (10) bursa closed; (11) first papilla prebursal; (12) prodonty; (13) reduction of the tail spike in males; (14) shortening of the buccal tube. — Depictions based on figures from Hirschmann (1952), Körner (1954), Andrassy (1958), and Sudhaus (1974b).

ancestor of this group may be hypothesized to have had a cupola-shaped tail, in contrast to the generally very long-tailed *Protorhabditis* species outside of this group; if so, then a cupola-shaped tail appearing in this group could thus be interpreted as an ontogenetic recapitulation. A similar circumstance exists in *Mesorhabditis* (discussed in Section 4).

Another evolutionary lineage within *Protorhabditis* (i.e., the "*Oxyuroides*" group; see Fig. 6) is characterized

by a bursa that has become proximally [anteriorly] closed, with the first papilla located prebursally and the second papilla moved just to the anterior margin of the bursa velum. The species of this group have remained primitive in having nine bursal papillae, simple dagger-shaped spicules, and lack of a pharyngeal sleeve.

Protorhabditis tristis appears to have branched after *P. elaphri* and before the *Xylocola* and *Oxyuroides* groups (Fig. 6). The derived features named previously [i.e.,

for the sister group of *P. elaphri*] all hold for *P. tristis* as well (although it is unknown if the gubernaculum is forked). However, special characters [of *P. tristis*] shared with either the *Xylocola* or *Oxyuroides* groups cannot be discerned. On the other hand, the amphids of *P. tristis* are conspicuous, similar to those of *P. elaphri* (both live along the edge of fresh water). Plesiomorphies are the open bursa with nine papillae and the long whip-like female tail. One possible but uncertain apomorphy shared by the *Xylocola* and *Oxyuroides* groups is the forking of the gubernaculum, which cannot be properly assessed until this character is known in *P. tristis*.

From these studies, the following conclusions can be made. In *Protorhabditis*, a pharyngeal sleeve has evolved twice, namely in *P. elaphri* and in the *Xylocola* group where it is quite short.³⁷ The reduction of the bursa in *P. parvovellata* is not correlated with the bursa becoming leptoderan, in contrast to some groups in *Rhabditis*. Supporting this lack of correlation [between a leptoderan tail tip and reduction of the bursa] is the very short cupola-like female tail in this species. Additional special structures of interest (autapomorphies) are the strongly developed [cuticularized] cheilostom consisting of several plates³⁸ in *P. postneri* (Fig. 5A), a pointed crenellation of the lips³⁹ in *P. ruehmi*, and the occurrence of waving larvae in *P. xylocola*.

No apomorphies can be demonstrated to support a [monophyletic] relationship between *Protorhabditis* and *Parasitorhabditis*.

3. *Prodontorhabditis* Timm, 1961

Because members of this group possess a specific construction of the buccal tube to be described below as “prodonty,” this group has been assigned the rank of genus. As I have already shown (Sudhaus, 1974b), *Prodontorhabditis* evolved from within the genus *Protorhabditis* (which is therefore paraphyletic). By comparing these taxa, the following characters turn out to be **symplesiomorphic** [in *Prodontorhabditis*]: the lips are closed; the buccal tube has distinct⁴⁰ cheilorhabdions, but [the typical shape of] the glottoid apparatus and a pharyngeal sleeve are missing; inconspicuous cuticular “denticles” are located at the connection between the buccal tube and the pharynx; the pharynx is rhabditoid with a median bulb; the double haustrulum of the terminal bulb is weakly developed; the vulva is at midbody; the amphidelphic gonads are flexed dorsally; the female tail is long and thread-like; the peloderan bursa is proximally closed; two of the nine papillae are precloacal, with the first located anterior to the bursa and the

second at the anterior rim of the bursa; the fifth and seventh papillae open dorsally on the bursa, and the seventh is bent dorsally; the spicules are separate; the body size is small (340–930 µm); and the cuticle has fine transverse stripes and a narrow lateral band. The following characters are hypothesized to be **apomorphies**: the flattening of the lips resulting in an obtuse anterior end (Fig. 6), the formation of three denticles inside the anterior end of the buccal tube (prodonty) and possibly the gutter-shaped gubernaculum, which is curved upward proximally like the prow of a boat. Perhaps the particularly long female tail (129–202 µm) is apomorphic as well.

So far, a large portion of the features common to *Prodontorhabditis* species appears to be plesiomorphic, as these features also occur in the very closely related *Oxyuroides* group of *Protorhabditis* (see Fig. 6) or are secondarily derived in the *Oxyuroides* group (e.g., the cheilostom and female tail). Within *Prodontorhabditis*, *P. prodontis* and *P. wirthi* are more closely related. In the lineage to their common ancestor, the buccal tube became shortened and widened, the cheilostom became more developed, and the tail tip in the male became so reduced that the most posterior bursal papillae join at their bases. Possibly in the same lineage, the distal forking of the gubernaculum was nearly reversed.

4. *Rhabditis* Dujardin, 1845

As already implied in the introduction of this chapter, I lump the genus *Rhabditis* broadly and therefore do not follow the splitting into numerous genera performed by Dougherty (1953, 1955). The important evolutionary step that distinguishes *Rhabditis* from the other species treated up to now lies in the area of the buccal cavity, similar to the case of *Prodontorhabditis*. A characteristic glottoid apparatus⁴¹ arose in the posterior region of the buccal tube, formed by three glottis-like arches of thinned cuticle projecting into the lumen, one from the dorsal side and two from the subventral sides of the buccal cuticle, and stabilized primarily by ridge-like denticles (presumably occurring ancestrally in triplets, see Chapter II). These glottises

⁴¹ “Übergangsstelle” of the original text is translated here as “glottoid apparatus.” The pentapartite scheme first presented by Steiner (1933) and subsequently modified by several workers (see De Ley et al., 1995, Baldwin et al., 1997) has been widely applied as a homology hypothesis for the parts of the buccal cavity. This scheme and its subsequent versions were based primarily on cuticular differentiations observed (or inferred) by light microscopy. Recently, De Ley et al. (1995) proposed a tripartite scheme (with further subdivisions of one of the main parts) based on the cells underlying the buccal cuticle as visualized by transmission electron microscopic reconstruction. Accordingly, the “glottoid apparatus” of rhabditids appears to be a differentiation of the “metastegostom,” roughly equivalent to the anterior part of the “telostom” of Steiner (1933) or the “metastom” of Sachs (1950) and Andrassy (1962). Specifically, the cuticular differentiations of the metastegostom overlie the anteriormost adradial muscle cells near the base of the buccal tube. De Ley et al. (1995) have also provided explicit definitions for the “buccal cavity” (the lumen of the digestive tract from the mouth opening to the anterior end of the triradial lumen of the pharynx), the “buccal capsule” (the cuticular lining of the buccal cavity), and the “stoma” (the buccal cavity in combination with the buccal capsule).

³⁷ The original has “in Ansätzen,” implying an initial stage in a potential evolutionary trend toward a longer sleeve.

³⁸ i.e., cheilorhabdions.

³⁹ With each lip extending into an outer tip. The original text has “Lippenkronen,” here translated as “crenellation of the lips.”

⁴⁰ i.e., “cuticularized.”

are part of the metastom, to which a ring of thickened cuticle joins posteriorly, representing a differentiation of the telostom (cf. Sachs, 1950, Osche, 1952b). This ring forms the termination of the buccal tube and provides attachment sites for the "pharyngeal tubes."⁴² The specific and decidedly complex formation of the glottoid apparatus is hypothesized to be an **apomorphy** of *Rhabditis*. This species-rich genus can be arranged into several distinct subgenera, which are to be subdivided again into individual species groups as appropriate for those groups with large numbers of species. The individual subgenera are treated first in the following sections.

a. Subgenus Mesorhabditis Osche, 1952

The species of *Mesorhabditis* obviously form a very close group, characterized by the following **symplesiomorphies**: presence of a small glottoid apparatus, clear transverse ridging in the anterior area of the pharynx (i.e., the corpus), a double haustulum posterior to the valves, a conical dagger-shaped female tail, a posteriorly positioned vulva (at 66–92% of body length) and hence an unpaired and prodelphic gonad, an [anteriorly] open bursa, and a relatively small body size (304–1,017 μm). On the other hand, the following common features are to be regarded as **apomorphic**: the lips are offset and partly pointed extending into setiform sensilla; the buccal tube is fairly long and slender; typically for each sector of the glottoid apparatus, two oblique denticles project into the lumen (in *R. spiculigera* they are either difficult to detect or absent); and a median bulb is always more or less heavily developed. On the basis of these features, a monophyletic origin of this group appears to be sufficiently substantiated. In addition to the symplesiomorphies given above, the ancestor of *Mesorhabditis* is assumed to have the following primitive characters, which are widely shared (sometimes disjunctly) by members of this subgenus: lack of a pharyngeal sleeve, an extension of the transverse ridging of the cuticular lining of the pharynx lumen into the median bulb, a peloderan bursa with a normal velum and 10 papillae⁴³ (2 precloacal), separate spicules, and possibly a lateral "crease" on the tail of the female. Additionally, the ancestor was presumably gonochoristic.

As the existing descriptions of the species are partly inaccurate or incomplete, it is difficult to arrange the species in this group. Repeatedly and independently, 1 of the 10 bursal papillae originally present in the common ancestor was lost (though probably not the same papilla was lost in each case; see the following [descrip-

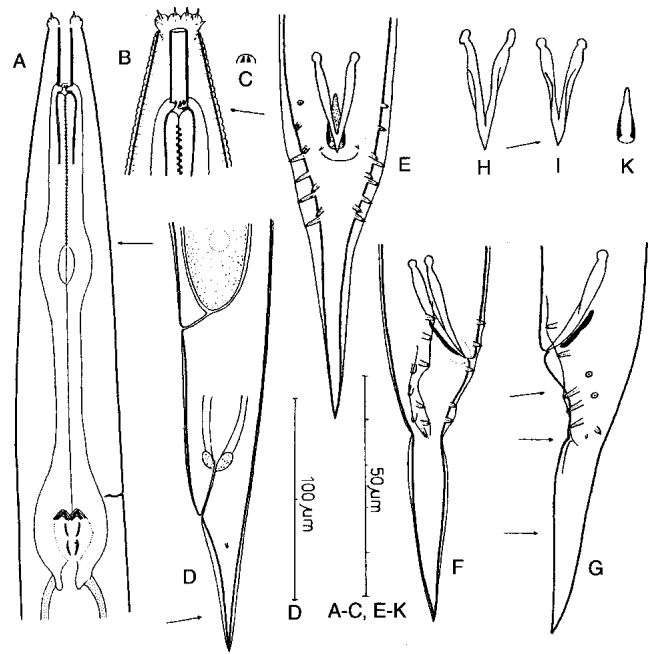


FIG. 7. *Rhabditis (Mesorhabditis) monhystera* Bütschli, 1873. A) Anterior end and pharynx of the male, lateral view. B) Anterior end of female, ventral. C) Metarhabdion. D) Posterior end of female, lateral. E) Posterior end of male, ventral. F) Posterior end of male, subventral. G) Posterior end of male, lateral. H, I) Spicules, ventral. K) Gubernaculum, ventral view.

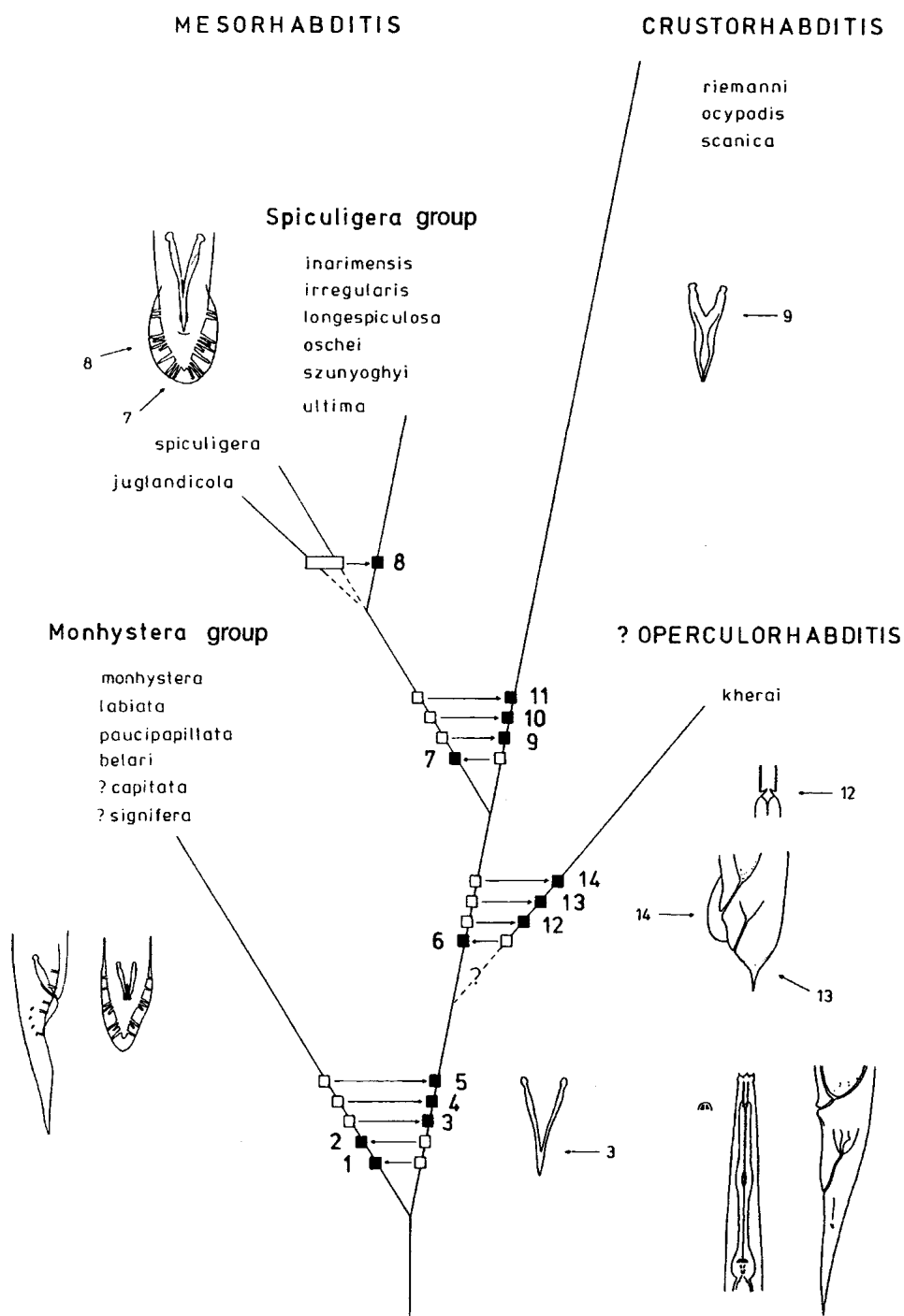
tion of the *Spiculigera* group]). However, the descriptions of species with fewer than nine papillae (e.g., 5–7) must be examined critically. For example, *R. monhystera* has nine partly inconspicuous papillae, although rarely more than five of these papillae are visible (cf. Fig. 7G). The full number of papillae is difficult to demonstrate in such cases.

It appears that there are two natural groups. In the first group (the "*Monhystera*" group, see Fig. 8), which I regard as the basally diverged,⁴⁴ only a narrow bursa velum is present on the conical male tail, sometimes regarded "leptoderan" to a small degree (in *R. paucipapillata* and *R. monhystera*), and the not particularly long spicules (20–27 μm) are separate (except in *R. paucipapillata* and *R. monhystera*). Without giving specific reasons at present, this form of the bursa is regarded as a reduction; this hypothesis is supported by the fact that some species have a rather small number of papillae (6–7 in *R. labiata* and *R. paucipapillata*). However, the special arrangement of the papillae in *R. monhystera*, where not all of them are included within the bursa velum (Fig. 7), suggests that the narrow bursa may be primitive. Separate spicules must be regarded as plesiomorphic. Moreover, it is only in this [*Monhystera*] group that nongonochoristic species exist (*R. monhystera* and *R. labiata*). It is possible that this mode of re-

⁴² "Pharyngeal tubes" replaces "esophageal tubes of the pharynx" of the original text.

⁴³ In this group, one pair of papillae (the sixth or seventh, depending on the species) is the phasmids (Kiontke and Sudhaus, 2000; Fitch, unpubl.). Plesiomorphically, therefore, there are only nine genital papillae.

⁴⁴ "Primitive" in the original text. Andr  ssy (1976) called the *Monhystera* group *Bursilla*.



17 FIG. 8. Cladogram of *Mesorhabditis* and *Crustorhabditis* and the possible relationship of *Operculorhabditis* (not considering *R. (M.) crangonensis* and *R. (M.) graciliformis*). Numbers denote the following apomorphies: (1) bursa and papillae strongly reduced; (2) transverse ridging ends anterior of the median bulb (?); (3) spicules distally fused; (4) spicules long and thin; (5) arrangement of papillae (2/5+3); (6) third papilla opens dorsally; (7) last [most posterior] papilla opens dorsally; (8) fourth papilla opens dorsally; (9) spicules fused two-thirds their length; (10) increased body size; (11) reduction of transverse ridging; (12) only one tooth per metarhabdion; (13) females with cupola-shaped tail; (14) with cuticular vulval flap. With figures from De Man (1927), Nigon (1949), Körner (1954), Khera (1969), and Sudhaus (1974b, 1974c).

production helped to preserve the more primitive bursa form. As long as the monophyletic origin of the glottoid apparatus in *Rhabditis* is maintained, *Mesorhabditis* has to be derived from an ancestor that in all probability possessed a well-developed peloderan bursa with

10 papillae. Because of these reasons, the narrow bursa of the species considered must actually be regarded as a reduction. This feature thus serves as an **apomorphy** of the *Monhystera* group. Additional apomorphies, besides a considerably reduced bursa, could be that the

transverse ridging of the cuticular lining of the corpus lumen does not include the median bulb and that the phasmids open at the level of the anus on the female tail. In this case, *R. capitata* and *R. signifera*—from which males are completely unknown and which presumably are non-gonochoristic as well—would also have to be classified here. Only *Mesorhabditis* species that are in this [*Monhystera*] group have a pharyngeal sleeve (i.e., *R. labiata* and *R. capitata*).

The second group (the “*Spiculigera*” group, see Fig. 8) displays the following **symplesiomorphies**: reproduction is gonochoristic;⁴⁵ the bursa is well-developed and peloderan; 10 or 9 bursal papillae are present, two of which are positioned precloacally; a pharyngeal sleeve is missing; and the transverse ridging of the cuticle lining of the corpus lumen extends into the median bulb. In contrast, the following shared features are considered **apomorphies**: the arrangement of the papillae is (2 / 5 + 3) or (2 / 4 + 3), depending on the number of papillae; the spicules are very long (30–76 µm), slender, and distally fused. Additionally, the last papilla always appears to open on the dorsal side of the bursa velum.

There are difficulties with a further subdivision of the monophyletic “*Spiculigera*” group.⁴⁶ In part this is because there are very small differences between the species. In *R. spiculigera*, the seventh papilla can occasionally be lost, on the basis of which a separate species (*R. tenuispicula*) was erroneously established. Likewise, the seventh papilla is in the process of reduction in *R. inarimensis*.⁴⁷ It appears that this papilla is “labile,” such that it has also been lost during the evolution of other species in the *Spiculigera* group that have only nine papillae (*R. juglandicola*⁴⁸). In other cases, there are indications that the sixth papilla may be involved in this reduction, as it is (already) much smaller in *R. oschei*, *R. longespiculosa*, and *R. szunyoghii*. So there is some reason to believe that, in the *Spiculigera* group, the reduction of one pair of papillae occurred repeatedly. Therefore, the number of papillae (9 as opposed to 10) cannot be used for the systematics of this group without reservation. Most of these species appear to belong to a natural group in which the fourth and the last papilla (i.e., the papilla corresponding to the 10th papilla in the ancestor) open dorsally on the velum (as opposed to the third and the last, as described for *R. spiculigera* and apparently for *R. juglandicola*). *Rhabditis irregularis* has diverged from the rest of this group with respect to the

reduction and radial arrangement of its bursa [see Appendix 1].

A similar situation to that previously described for *Protorhabditis parvovulata* (p. 11) exists in some *Mesorhabditis* species. In the juveniles⁴⁹ of three species (*R. irregularis*, *R. inarimensis*,⁵⁰ and *R. spiculigera*), a cupola-shaped tail appears. In contrast, a cupola-shaped tail is never found in adult females. Only in *R. irregularis* is there sometimes an obtuse conical tail [in females], which is fairly similar to a cupola-shaped tail,⁵¹ although this is found only in small and poorly fed specimens (compare with *P. parvovulata*). Also, the dagger-like shape of the tail that is typical for the group is expressed under favorable feeding conditions (Körner, 1954). One could postulate that a cupola-shaped tail is being recapitulated in the juveniles.⁵² Such a tail shape would then be suggested for the common ancestor of the *Spiculigera* group. (To suggest this shape for the more ancient stem species of *Parasitorhabditis*, *Protorhabditis*, and *Mesorhabditis* is too speculative and there are many counter-arguments. Incidentally, it must be pointed out that the groups just mentioned are inhabitants of rotten wood, suggesting that convergences [in adapting to these similar habitats] are likely.)

Protorhabditis parvovulata and *R. irregularis* are similar in another way, namely that the bursa is reduced and more or less radially arranged in both species. Both tendencies (reduction of the bursal velum and radial arrangement of the bursal papillae) appear to be coupled (i.e., these characters may be correlated). *Rhabditis graciliformis* cannot be classified as a result of the insufficient description of the species. The presence of only seven bursal papillae suggests that this species could be a member of the *Monhystera* group.⁵³ Despite strong correspondences, Khera (1968) failed to discuss the possible placement of *R. cranganorensis* (described without males) in the subgenus *Mesorhabditis*. Presumably because of the small body size of the nematodes, Khera may not have been able to be certain about the presence of three metarhabdion warts [that he described] as the only significant difference [from *Mesorhabditis*]. Even considering this feature [three metarhabdion warts], a different taxonomic assessment [from that of Khera] is still allowed.⁵⁴ From the preceding discussion, it appears likely that the following

⁴⁹ The original text has “larvae.”

⁵⁰ The original text had the name *R. ultima*, which is synonymous with *R. inarimensis*.

⁵¹ The female tail in the more recently discovered *R. megachilis* is more cupola shaped (Sudhaus, 1978).

⁵² The original text has “larvae.”

⁵³ Sudhaus (1978:449) transferred *R. graciliformis* to the subgenus *Cruzinema* of genus *Rhabditis*.

⁵⁴ Khera (1968) suggested that *R. cranganorensis* was the only species known with one ovary and a posterior vulva, thus revealing that Khera did not consider possible affinities with the other *Mesorhabditis* species that bear such features. (Indeed, such situations are aggravated by taxon “splitting” as performed by some systematists.) Because the body size of this species is so small, the author also questioned the accuracy of Khera’s observation of three denticles on each metarhabdion.

⁴⁵ “Gonochoristic” has been substituted for the “bisexual” of the original text.

⁴⁶ For a revision of this taxon, see Sudhaus (1978); a cladogram from this reference is provided in Appendix 1.

⁴⁷ In the revision of this taxon by Sudhaus (1978), the species name *R. ultima* in the original text was synonymized with *R. inarimensis*.

⁴⁸ *Rhabditis inarimensis* was also listed with *R. juglandicola* in the original. However, this species bears the papilla in question. This papilla is actually the phasmid, which is the seventh in *R. spiculigera* and the sixth in species related to *R. oschei* (Kiontke and Sudhaus, 2000).

derived characters arose independently several times within *Mesorhabditis*: formation of a small [cuticularized] cheilostom, fusion of the spicules, and the reduction of bursal papillae.

b. Subgenus Crustorhabditis Sudhaus, 1974

Just as the genus *Prodontorhabditis* evolved from within the genus *Protorhabditis* (p. 13), the subgenus *Crustorhabditis* evolved from within *Mesorhabditis*. With this close phylogenetic relationship, a majority of the diagnostic characters of *Crustorhabditis* appear to be **plesiomorphies**, in an analogous manner to those of *Prodontorhabditis*: the cuticle is annulated and longitudinally striated, the buccal cavity (23–34 µm long) lacks a [cuticularized] cheilostom and a pharyngeal sleeve, each metarhabdion bears two inconspicuous and obliquely oriented denticles, the pharynx possesses a median bulb, the valved bulb has a double haustulum, the excretory system is H-shaped, the vulva lies far posterior (at 82–94% of the body length), the female genital tract is correspondingly unpaired, the female tail is conical and daggerlike and has a lateral cuticular velum, the bursa is open and peloderan and is supported by 10 papillae (2 of which are precloacal), and a pair of blind sacs are found at the vas deferens. **Apomorphies** of *Crustorhabditis* are as follows: transverse ridging [of the cuticular lining of the pharynx lumen] is reduced to inconspicuous remnants, the edge of the bursa velum is proximally⁵⁵ ruffled and distally⁵⁶ notched, the stout spicules (38–71 µm long) are fused for about two-thirds of their length and (by means of their ventrally folded lateral edges) form an almost completely closed channel (Fig. 8), the spatula-shaped gubernaculum covers 41–54% of the length of the spicules, and the body size is enormously increased (785–3,980 µm).

Of the characters mentioned, the formation of an H-shaped [excretory] system and paired blind tubes at the end of the testis are somewhat critical in their value as plesiomorphies. As such, an H-shaped [excretory] system is known so far in only two *Mesorhabditis* species (*R. longespiculosa* and *R. irregularis*) and, for example, is certainly not existent⁵⁷ (reduced?) in *R. spiculigera*.
 [19] There is little indication for the pre-existence of paired blind sacs at the vas deferens (in *R. spiculigera*, *R. longespiculosa*, and *R. inarimensis*).⁵⁸ However, since both characters have been described for *Parasitorhabditis obtusa* (Fuchs, 1915) and, moreover, an H-shaped [excretory] system is found in *Protorhabditis*, *Cephalobidae* and *Panagrolaimidae*, these features were likely to have been primitively inherited by all Rhabditinae.

Within *Crustorhabditis*, *R. scanica* is primitive in mul-

iple respects and occupies an intermediate position with regard to *Mesorhabditis*: the lips are offset from the body and each bears a bristle-like sensillum, the denticles on the glottoid apparatus are clearly visible, as are remnants of transverse ridging [in the cuticular lining of the pharynx lumen], and the body size is still small (785–1,516 µm). This does not absolutely imply that the other two species (*R. ocypodis* and *R. riemanni*) are more closely related to each other. Such a conclusion [for a close relationship between *R. ocypodis* and *R. riemanni*], though possible, would not necessarily follow because it is based on trivial, derived commonalities (increase in body size, lips not offset, pharynx lumen without ridging on the cuticular lining). Neither would such a conclusion be supported by a shared biological association with *Ocyropode* [ghost crabs, *Brachyura*], since *R. scanica* also appears to be associated with these crabs (cf. Sudhaus, 1974b).

The question concerning the point of divergence of *Crustorhabditis* in the *Mesorhabditis* stem lineage (cf. Fig. 8) is difficult to reconcile. This subgenus has certainly shared at least a part of the phylogeny of the *Spiculigera* group, as indicated by the long and fused spicules. Similarly, the bursa arrangement (2 / 5 + 3) is recognizable in *R. scanica*, which embodies the primitive bursa type for *Crustorhabditis*. Moreover, the third papilla opens dorsally on the bursa velum, a primitive state with regard to the *Spiculigera* group. However, the 10th papilla differs [in this regard from that of the *Spiculigera* group]. Because of this, I suggest that the currently available information supports the branching of the *Crustorhabditis* group before the *Spiculigera* group. In this view, *R. riemanni* has evolved a bursa convergently with the species around *R. oschei* (*Spiculigera* group), in which the fourth and 10th papillae open dorsally on the bursa.

c. Subgenus Operculorhabditis Khera, 1969

This monotypic subgenus has the following **primitive characters**: the six lips are closed, cheilorhabdions are inconspicuous, the glottoid apparatus bears denticles, a pharyngeal sleeve is missing, the vulva is situated near the anus (V = 94.5–96%), the female genital tract is single and prodelphic, the bursa is peloderan and open, 10 bursal papillae are present (two of which are precloacal), and the body size is relatively small (800–1,060 µm). **Derived** characters are the slightly offset lips each with an apical bristle-like sensillum; metarhabdions each with but a single hollow tooth; a well-developed median pharyngeal bulb (the presumable absence of transverse ridging in the pharynx); the cupola-shaped female tail with a spike (Fig. 8); a cuticular flap (heart-shaped in ventral view) covering the vulva; the (2 / 5 + 3) bursal arrangement; the long (62–66 µm), slender, and distally fused spicules; and a long gubernaculum reaching 64% of the length of the spicules.

⁵⁵ i.e., anteriorly.

⁵⁶ i.e., posteriorly.

⁵⁷ This is an error corrected later by Sudhaus (1978:402); lateral channels do exist in *R. spiculigera*, but are barely visible.

⁵⁸ Blind sacs are indeed present in these three species (Sudhaus, 1978).

This subgenus is unique within the Rhabditinae because of its cuticular vulval flap⁵⁹ (Khera, 1969). A similar structure is known in the Panagrolaimidae from *Cuticonema vivipara* Sanwal (1959), which also has a vulva situated far posterior. Such a flap is more frequent in the parasitic Trichostrongylidae.

This subgenus shows correspondences indicating possible relationships with *Mesorhabditis* and *Teratorhabditis* only. Derived correspondences (homomorphic apomorphies, see p. 6) with *Teratorhabditis* are the median bulb, the fusion of the spicules, a relatively long gubernaculum, and the cupola-shaped female tail. On the other hand, *Operculorhabditis* and part of *Mesorhabditis*, namely the *Spiculigera* group, have in common the offset lips each with a bristle-like sensillum, the median bulb, the (2 / 5 + 3) arrangement of bursal papillae, and the long, thin, distally fused spicules. Because of the insufficient description of *R. kherai*, only a small number of shared derived characters are known which are possible synapomorphies and could be handed down from a common stem species with one of the groups. Here the correspondences with *Mesorhabditis* are stronger than those with *Teratorhabditis*. The structures of the bursa and spicules particularly seem to correspond to such a degree with those of the species of the *Spiculigera* group that a natural relationship between them might be suspected. Presumably, *Operculorhabditis* would then have diverged from the branch leading to the *Spiculigera* group and *Crustorhabditis* (see Fig. 8). The consequence of this would be that *Mesorhabditis* is polyphyletic and therefore should be dissolved into two subgenera (one comprising the *Monhystera* group and the other the *Spiculigera* group) or that *Operculorhabditis* should be incorporated into *Mesorhabditis*, which is especially contradicted by the characteristic metarhabdion "dentition."⁶⁰ A decision does not appear possible until *R. kherai*⁶¹ is reinvestigated accurately or further species of *Operculorhabditis* become known.

d. Subgenus *Cruznama* Artigas, 1927

This similarly monotypic subgenus is represented by an obviously "ancient" species (*R. tripartita*, see Fig. 9C, D) showing numerous **plesiomorphies**: the glottoid apparatus bears 3 (conspicuous) teeth on each metarhabdion, the excretory system is H-shaped,⁶² the vulva is situated far posterior ($V = 82\text{--}87\%$), the female genital tract is single and prodelphic, the female tail is obtusely conical, the bursa is peloderan and open and has two precloacal papillae, and the simple dagger-shaped spicules are separate. To be regarded as **apomorphic** are

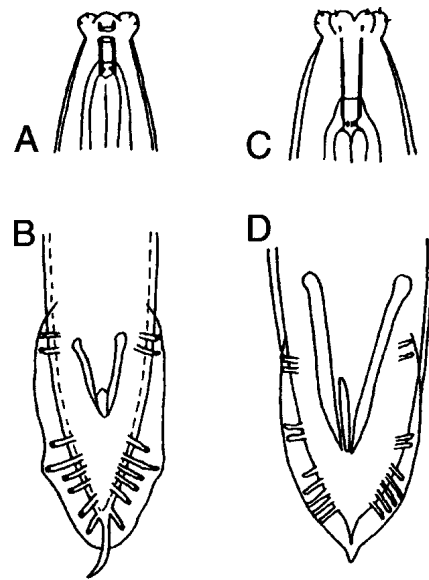


FIG. 9. The subgenera *Rhabpanus* and *Cruznama* in comparison. A, B) *Rhabditis* (*Rhabpanus*) *ossicula* (Massey, 1971) male. A) Anterior end. B) Posterior end, ventral view (after Massey, 1971). C, D) *Rhabditis* (*Cruznama*) *tripartita* von Linstow, 1906 male. C) Anterior end (from Sudhaus, 1974b). D) Posterior end, ventral view (after Marinari, 1957).

the open and strongly offset lips, the triangular prismatic buccal tube with [conspicuous] cheilorhabdions, the formation of a short pharyngeal sleeve enveloping about one-third of the buccal tube, a median bulb, the ovary flexure nearly reaching the level of the vulva, the position of the phasmids at the level of the anus in the female, the complete reduction of one bursal papilla (which one?), the specific arrangement of the bursal papillae as (2 / 2 + 5) (with the third, fifth, seventh, and ninth papillae pointing toward the dorsal side), the cuticle with very conspicuous annules, and the increase in body size (660–2,210 μm).

Osche (1952b) still counted this species in the "*Lambiensis*" group in subgenus *Pelodera*, the species of which were mostly characterized (in this broad view) by the existence of three more or less conspicuous denticles per metarhabdion, a peloderan bursa, gonochorism (always), and the "trend" to form offset lips and a median bulb. As nearly all of these characters are plesiomorphic at the origin of *Rhabditis*, the question is legitimate whether the marked formation of three denticles per metarhabdion really is a shared derived character (of *Pelodera sensu lato*) or whether perhaps a parallel evolution of such structures should be assumed as originating from triply ridged metarhabdions,⁶³ as represented, for instance, by *R. plicata* (see *Caenorhabditis*) and interpreted as primitive (following Osche, 1952b) (compare Chapter II). I think the latter is more likely, and have therefore judged the existence of three

⁵⁹ i.e., "operculum."

⁶⁰ "... characteristic metarhabdion 'dentition'" is translated from the original "... Metastombezahnung."

⁶¹ "the species" in the original is substituted with "*R. kherai*."

⁶² This remark about the excretory system should be disregarded.

⁶³ Translated from "*Dreileistenapparat*."

metarhabdion denticles as plesiomorphic (see Osche, 1952b). Their conspicuous protrusion, however, should be regarded as apomorphic. Since there are no special correspondences known between *R. tripartita* and the subgenus *Pelodera* in a narrow sense (i.e., the *Teres* group plus the *Coarctata* group) besides the [prominent] metarhabdion denticles, there are no reliable arguments at present for the monophyly of a broader group [consisting of *Pelodera sensu stricto* and *R. tripartita*]. Therefore, *R. tripartita* has to be removed from the *Pelodera* group and placed in a separate subgenus (*Cruznema*), as there is no direct relationship to any other group except the subgenus *Rhabpanus* discussed in the following paragraph. The greatest regular similarity exists with *Mesorhabditis* (posterior vulva, conical female tail) such that confusion has occasionally occurred, particularly between *Cruznema tripartita*⁶⁴ and *Mesorhabditis belari* (see Fig. 8) and also *Mesorhabditis monhystera*. At most, the offset lips and the development of a median bulb could be cited as possible synapomorphies of both of these groups, in contrast to the significant differences, for example, in the metarhabdion dentition. Therefore, a close relationship between *Cruznema* and *Mesorhabditis* cannot be asserted. Possible correspondences⁶⁵ in particular cases, which so far are not [regarded as] symplesiomorphies, must be explained by convergent evolution. For instance, the organization of the bursa of *R. tripartita* is superficially similar even to that of *R. (Crustorhabditis) riemanni*.

e. Subgenus *Rhabpanus* Massey, 1971

With regard to this monotypic subgenus,⁶⁶ Massey (1971) already suggested that it is closely related to *Cruznema*. The correspondences between both species concerned are actually so obvious and multifaceted (see Fig. 9) that they can hardly be explained by convergent evolution (see below [the paragraph following the next one]). On the other hand, there are enough important differences in the formation of the gonad and the bursa to justify the erection of separate subgenera.⁶⁷

Plesiomorphies include the following: the vulva is posterior of the middle of the body, the single female genital tract is prodelfic, the female tail is obtuse-conical, the bursa is open and has two precloacal papillae, the spicules are straight and separate, and the body size is small (580–840 µm). **Apomorphies** include the strongly offset lips that are supported interiorly by cheilorhabdions, the two small metarhabdion teeth, the median bulb, the considerable anterior shift in vulval position ($V = 65\text{--}67\%$), the flexure of the ovary far

posterior beyond the level of the vulva, the formation of a short posterior uterine sac, the loss of one bursal papilla (which one?), the beginning of a radial arrangement of the bursa (?), and the reduction of the last bursal papilla to a stump (described as the phasmid by Massey, 1971).

It is difficult to judge the significance of the leptoderan bursa, which is the main difference from the peloderan subgenus *Cruznema*. On the other hand, *R. ossicula* does not fit into the character composition of all the other leptoderan *Rhabditis* species, for which the following are characteristic (discussed later): a median vulva, paired amphidelphic ovaries, a pharyngeal sleeve surrounding half the buccal tube, and three precloacal papillae. In all probability, therefore, the leptoderan bursa in this case represents a derived character. There are good reasons to suppose that the formation of a peloderan bursa is an apomorphy of the Rhabditinae *sensu lato*. This does not automatically imply that the leptoderan bursa of *Rhabpanus* is an autapomorphy; it could also be a novelty that appeared in the common ancestor of *Cruznema* and *Rhabpanus*. The relationship of both of these taxa is supported by the following **synapomorphies**: strongly offset lips; a buccal tube with prominent cheilorhabdions; the development of a median pharyngeal bulb; a flexure of the ovary reaching far posteriorly; the existence of only nine bursal papillae in a similar arrangement, with presumably the third and ninth opening dorsally on the velum; and correspondences in the complex of spicules and gubernaculum. 22

The question regarding the shape of the bursa of the stem species of *Cruznema* (peloderan) and *Rhabpanus* (leptoderan) appears not to be answerable. To resolve this issue, an additional feature of the bursa is required. The beginning of a radial arrangement of the bursal papillae in *R. ossicula* could be such a character. This cannot be observed in *R. tripartita*. In this species, however, the rounded tail of the male bears a conspicuous spike, and the terminus of the bursa velum is⁶⁸ often pointed as well (Fig. 9D). I know of a similar situation only in the peloderan *R. nidrosiensis*, which can be shown to descend from leptoderan ancestors (see below [*Cephaloboides*, Section 4m]). One may very cautiously assume, by analogy, that the shape of the tail and bursa in *R. tripartita*, combined with the existence of a closely related leptoderan species, indicates that it had a leptoderan stem species. This would mean that a leptoderan bursa constitutes a synapomorphy for *Cruznema* and *Rhabpanus*, and that *Rhabpanus* remained primitive in this character with respect to *Cruznema*. On the other hand, *Rhabpanus* acquired special characters; e.g., only two metarhabdion denticles, the anterior shift in the

⁶⁴ If *Cruznema* were the genus name, the species epithet would have to be *tripartitum*; here *Rhabditis (Cruznema) tripartita* is meant.

⁶⁵ In the original text, "Gemeinschaften" was a misprint of "Gemeinsamkeiten."

⁶⁶ The only species in this genus is *Rhabditis (Rhabpanus) ossicula*.

⁶⁷ The original text actually erects but one subgenus, by which is meant *Rhabpanus*.

⁶⁸ The original uses the word "scheint," or "appears to be"; this qualification should be disregarded.

position of the vulva, and the formation of a posterior uterine sac. With regard to the characters of the female genital tract, the species is curious within *Rhabditis*.

The particular characters of *R. ossicula* are too little known to ascertain further phylogenetic relationships. Therefore, according to present knowledge, the two metarhabdion teeth that are similar to those in *Mesorhabditis* and the organization of the bursa in a manner somewhat reminiscent of *Xylorhabditis bakeri* must be regarded as convergences with these subgenera.

f. Subgenus Xylorhabditis Sudhaus, 1976a

Because it has three teeth on each metarhabdion, Rühm (1964) placed the species described by him as *Pelodera bakeri* in the *Pelodera* group, which he stated was a heterogeneous group. This group will be treated here in a more restricted manner as a natural unit. Therefore, *R. bakeri* must also be removed [from *Pelodera*]. But because *R. bakeri* has no connection to one of the described groups, a new (currently monotypic) subgenus of the genus *Rhabditis* has been erected for it.

The **plesiomorphies** [for this subgenus] are the following: the lips are not offset, the buccal tube lacks pronounced cheilorhabdions and has but a weakly developed glottoid apparatus with three strong teeth on each metarhabdion, a pharyngeal sleeve is absent, a median bulb is but weakly developed and is missing in the dauer larvae, the female tail is conical, the bursa is open and peloderan and possesses two precloacal papillae, the spicules are separate, and the body size is relatively small (713–1,000 µm). **Apomorphic** characters are the following: the buccal tube wall is transversely striated, the vulva is positioned nearly midbody, the ovaries are accordingly paired (amphidelphic), the bursa velum is narrow, nine stocky bursal papillae are present in the arrangement (2 / 1 + 3 + 3) or (2 / 4 + 3), the ninth papilla is very short and lies subventral, the spicules are distally notched and exhibit a cuticular dorsal velum, and the narrow groove-shaped gubernaculum turns up with a pointed tip proximally.

It is uncertain whether this species is a true *Rhabditis* with the corresponding formation of a glottoid apparatus (cf. pp. 13–14). Concerning this point, Rühm (1964:217) writes: “the metastom bears small, flat, projecting curves or swellings.”⁶⁹ This could also be the “origin” of a typical differentiation, about which the figures unfortunately do not provide a satisfying answer. At least the metarhabdion teeth are certain: “to each flat projection are fastened three stout denticles, of which the central tooth sticks out somewhat lower than the others” (Rühm, 1964:217).⁷⁰ This has to be regarded as a primitive character.⁷¹

Rhabditis bakeri has a certain similarity to the genus *Protorhabditis*, particularly to the species of the *Xylocola* group. Possible shared derived characters are a median vulva and amphidelphic ovaries; a median pharyngeal bulb; the existence of only nine bursal papillae, of which the last one is in the process of reduction; a similar arrangement of these papillae, the shape of the spicules, and the proximal part of the gubernaculum not being in contact with the projection of the spicules in lateral view. Unfortunately, it is not known which papillae open on the dorsal surface of the bursa velum,⁷² a feature that would be important for comparison. Particular differences [from *Protorhabditis*] are as follows: *R. bakeri* is larger than the species of *Protorhabditis* as a rule, cheilorhabdions are inconspicuous, and a glottoid apparatus is well-developed with 3 teeth on each metarhabdion. If the similarities with *Protorhabditis* are to be interpreted as an indication of phylogenetic relationship, then either the absence of a glottoid apparatus in *Protorhabditis* must be explained by reduction, or it must be assumed that metarhabdion structures with three teeth as in *Rhabditis* evolved convergently in *R. bakeri*. Both are unlikely in the face of the assumption that the features generally shared between *Protorhabditis* and *R. bakeri* result from convergence.

A correspondence with other groups of *Rhabditis* cannot be demonstrated. For the present, therefore, *Xylorhabditis* must be regarded as an independent evolutionary lineage that diverged early within *Rhabditis*.

g. Subgenus Pelodera A. Schneider, 1866

Formerly, this group was a heterogeneous one, despite the fact that all members shared three denticles on each metarhabdion. It becomes homogeneous with the exclusion of two subgenera (*Cruznema* and *Xylorhabditis*), as suggested above [Sections 4d and 4f], and the removal of *R. plicata*, which is now placed within *Caenorhabditis*. There are several arguments favoring the monophyly of *Pelodera* in the restricted sense. As such, all species have a vulva in midbody position, the ovaries are correspondingly amphidelphic, the spicules are relatively long (32–97 µm) with proximal heads and are particularly fused distally. Furthermore, the stem species undoubtedly possessed a cupola-shaped tail with a spike in the female sex; the conical female tail in *R. punctata* and *R. parateres*⁷³ is secondarily derived and resulted by “paedomorphism” (cf. Osche, 1954). The spine of the cupola has been lost independently in *R. stammeri* and *R. cylindrica*. The body length is usually between 1 and 2 mm (623–3,610 µm). Besides these characters that are considered **apomorphic**, all species retain the primitive 10 bursal papillae, the bursa re-

⁶⁹ The original quotation is “Das Metastom besitzt kleine, flache Vorwölbungen.”

⁷⁰ The original quotation is “Auf jeder dieser flachen Vorwölbungen sind 3 kräftige Zähne befestigt, von denen der Mittelzahn etwas tiefer als die übrigen inserieren.”

⁷¹ “Primitive” refers only to the number of teeth.

⁷² The original uses the phrase “penetrate the bursa velum outwardly.”

⁷³ The original has *R. conica*, which was shown by Sudhaus (1985a) to be a junior synonym of *R. parateres*.

mains peloderan and normally developed, and three teeth are present on each metarhabdion.

Rhabditis stammeri, which is aberrant in various respects, raises some questions.⁷⁴ Besides some special characters that are of no interest here, the lips of this species are not offset, the glottoid apparatus is inconspicuous, and the pharynx is anguilluloid.⁷⁵ Actually, these are primitive characters and therefore should be attributed to the ancestor of *Pelodera*. At least the “absence” of a glottoid apparatus feigns a more primitive situation if one does not wish to accept that a glottoid apparatus evolved convergently within *Rhabditis*.⁷⁶ (In comparison, a glottoid apparatus is missing secondarily in the dauer larvae of *R. inermis* and *R. plicata* as well, whereas it is formed in the other ontogenetic stages of these species.) The opinion about the other characters is not so indisputable,⁷⁷ particularly in the case of pharynx shape. Up to now, not a single example could be demonstrated of a reversal of the change from an anguilluloid pharynx to a rhabditoid pharynx with a median bulb. As long as one does not wish to assume that *R. stammeri* evolved completely independently and homeomorphically to the species of the *Teres* group of *Pelodera*, one must infer that the ancestor of *Pelodera* maintained an anguilluloid pharynx. From this it follows that a median bulb arose repeatedly within this group.

The subgenus *Pelodera* can be subdivided into two natural groups, the *Coarctata* group and the *Teres* group (cf. Osche, 1952b). The crucial changes leading to the *Coarctata* group are (cf. Fig. 10) the formation of a closed bursa, the more distinct metarhabdion teeth, and the greater cuticularization of the telorhabdions. Furthermore, this *Coarctata* group is characterized by a general trend to a sexual dimorphism of the lips, the formation of a pharyngeal sleeve and median bulb, a slight widening of the posterior part of the buccal tube, and by waving juveniles. There are several reasons for a separation of this group before the divergence between the *Teres* and *Strongyloides* groups. Although no apomorphies are known for the last mentioned species group (called the *Teres* group *sensu lato* [i.e., *Teres* group *sensu stricto* + *Strongyloides* group]), it is inappropriate to regard it only as a paraphyletic group. This opinion could be supported by the fact that all *Pelodera* species exhibit a pharyngeal sleeve (except *R. strongyloides* and *R. punctata*, which must then have branched off earliest). However, such a derived state⁷⁸ demonstrably occurred of-

ten and independently within *Rhabditis*. The [phylogenetic] value of this character is therefore not sufficient for making such a decision.⁷⁹

The *Teres* group [*sensu lato*], characterized by a pleiomorphically open bursa and regarded as “presumably monophyletic” (though no apomorphies can be given) consists of two subgroups (Fig. 10). One group [the *Teres* group *sensu stricto*] (*R. stammeri*, *R. teres*, *R. parateres*⁸⁰) has three precloacal papillae and a pharyngeal sleeve. The species of the second group [the *Strongyloides* group] (*R. strongyloides*, *R. punctata*) have spicules fused more than half their length and a median pharyngeal bulb, yet remain primitive with regard to the other characters: only two precloacal papillae, absence of a [pharyngeal] sleeve, and the valved [terminal] bulb with a double haustulum. As previously mentioned, a conical female tail originated convergently by pedomorphism in *R. punctata* and *R. parateres*⁸¹ (see also *R. litoralis*). Moreover, a median bulb must have evolved independently in each of the *Strongyloides*, *Teres*, and *Coarctata* lineages, insofar as the speculations regarding *R. stammeri* are correct.⁸² (The formation of three precloacal papillae within the *Teres* group [*sensu lato*] apparently occurred in a manner different from that in *R. tretzeli* and *R. par* of the *Coarctata* group, in which the third papilla was simply shifted anteriorly to form a group with the other two precloacal papillae. Rather, it appears that an “intermediate stage” with 11 bursal papillae existed [in the ancestral lineage of the *Teres* group *sensu stricto*] such that a new papilla emerged far anterior to the papilla that was previously the first. Such a stage exists cryptotypically within the *Teres* group [*sensu lato*] and is observed in rare aberrations. In *R. strongyloides* and *R. teres*, variations with 11 papillae (3 precloacal) are known to have occurred (Reiter, 1928; Schuurmans Stekhoven and Teunissen, 1938; Völk, 1950; pers. obs.). Furthermore, *R. litoralis* was described with 11 papillae (perhaps an error of observation?) and Osche (1952b) depicted *R. stammeri* with 11 papillae on one side.⁸³ Because a maximum of 10 pairs of papillae appears to be a fairly rigid constancy

⁷⁴ The discussion in this paragraph is obsolete because *R. stammeri* does not belong to *Pelodera*.

⁷⁵ That is, a median bulb is missing.

⁷⁶ That is, the absence of a glottoid apparatus in *R. stammeri* appears to be a reversal, not a truly retained, primitive feature, under the assumption that it is unlikely a glottoid apparatus arose convergently within this species group.

⁷⁷ That is, it is by no means certain if the other characters of *R. stammeri* (e.g., the anguilluloid pharynx) are truly primitive (retained) or only apparently primitive (convergences or reversals).

⁷⁸ i.e., presence of a pharyngeal sleeve.

⁷⁹ That is, the existence of a pharyngeal sleeve is insufficient information for determining if the *Teres* group *sensu stricto* is the sister group of the *Coarctata* group (with the pharyngeal sleeve as a synapomorphy) and therefore if the *Teres* group *sensu lato* (i.e., *Teres* group *sensu stricto* + *Strongyloides* group) is paraphyletic.

⁸⁰ The original has *R. conica*, a junior synonym of *R. parateres* (Sudhaus, 1985a).

⁸¹ The *R. conica* in the original is a synonym of *R. parateres* (Sudhaus, 1985a).

⁸² Actually, the speculations regarding *R. stammeri* are not correct.

⁸³ [Footnote 3 in the original text.] *Rhabditis litoralis* was too poorly described by Skwarra (1921). A relationship [between the described species and] *R. teres* or *R. strongyloides* appears to exist. On the basis of the conical female tail, synonymy with one of these species can be ruled out. However, it may be an as yet unknown aberration of *R. punctata*. In the *Coarctata* group, 11 papillae are unknown as well as aberrations. Only Völk (1950) illustrated *R. cylindrica* [*cylindrica* lapsus in the original] with 11 papillae without discussing this separately in the text. Presumably, [this implies that] the depiction is erroneous. Within other *Rhabditis* groups, 11 papillae occur in *R. (Pellioditis) fruticicolae* and as a rare aberration in *R. (Rhabditella) axei*. [In the original footnote, “*R. (Rhabditella) pseudoelongata*” is used, but this is synonymous with *R. axei* (Sudhaus, 1980).]

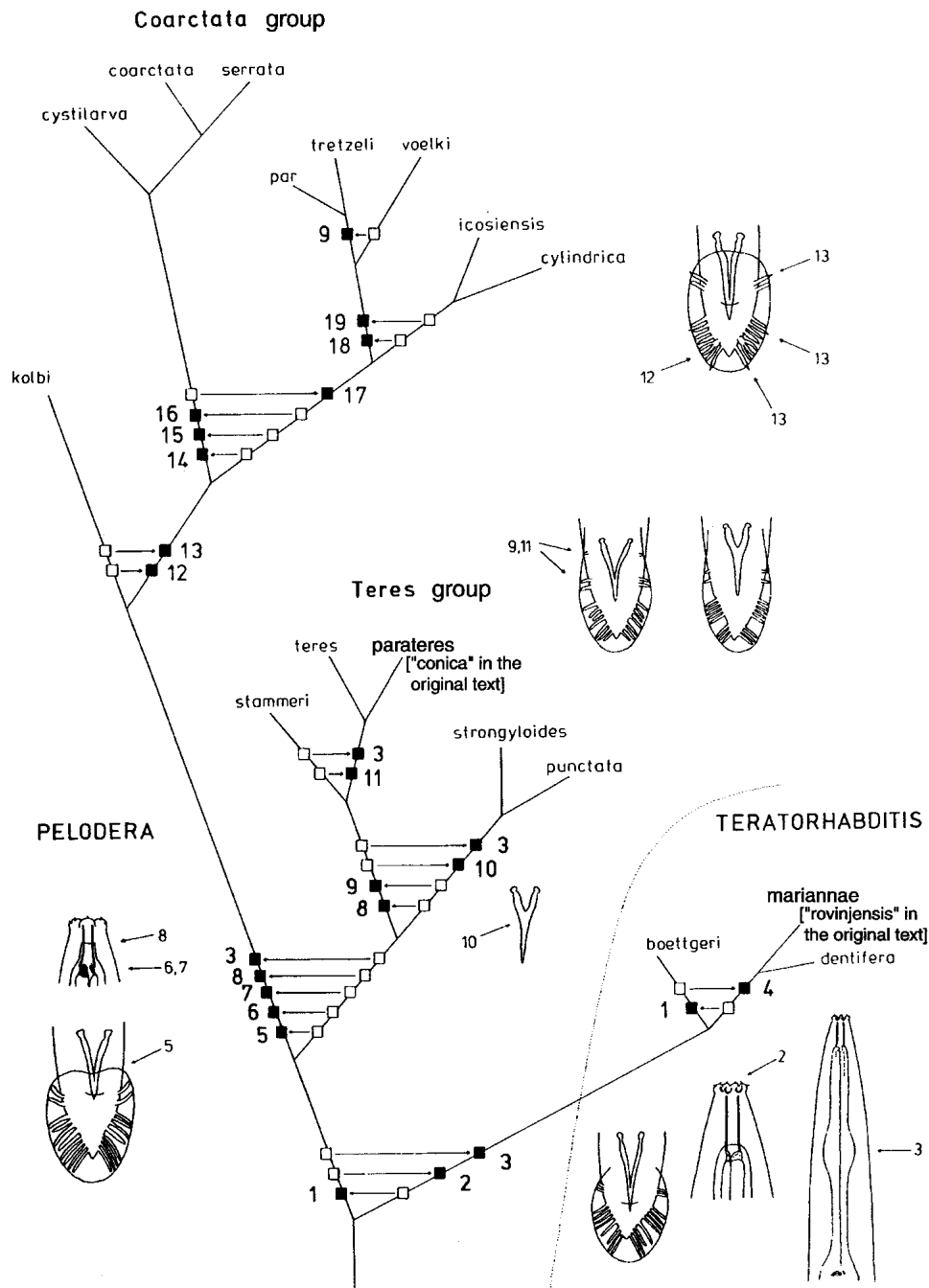


FIG. 10. Cladogram of *Teratorhabditis* and *Pelodera* (except *R. (Pelodera) litoralis* and *R. (P.) operosa*). The numbers denote the following apomorphies: (1) median vulva and amphidelphic ovaries; (2) lip margins cuticularized like *Teratocephalus*; (3) median bulb present; (4) median bulb thickened; (5) bursa closed; (6) metastomal teeth stronger; (7) telorhabdions more strongly cuticularized; (8) pharyngeal sleeve formed; (9) 3 preloacal papillae; (10) spicules fused by more than 50% [of their length]; (11) papilla arrangement (1+2/1+3+3); (12) papillae 7-9 fused basally; (13) papillae 1, 4, and 10 protrude from bursa margin; (14) third papilla thickened; (15) cuticle of the dauer larva heavily sculptured; (16) dauer larvae make cysts; (17) bursa velum structured; (18) bursa narrower at the point of the cloaca opening; (19) lips in males not set apart. Includes figures from Sachs (1950), Hirschmann (1952), Osche (1952b), and Sudhaus (1974b).

[restriction?] in Rhabditinae (presumably due to underlying "morphogenetic fields"; see in general the "rules" for "fixation by chance," Steiner, 1955), [it is likely that] a posterior papilla has been lost in conjunction with the appearance of a new papilla in the anterior position. Actually, the papilla that is lost seems to be the fourth papilla from the last (i.e., the papilla that

was originally the seventh [counting from anterior to posterior]), as is evidenced by a comparison of *R. teres* and *R. parateres*⁸⁴ with *R. strongyloides* and *R. punctata*

⁸⁴ *Rhabditis conica* in the original is synonymous with *R. parateres* (Sudhaus, 1985a).

and from the previously mentioned aberration of papillae in *R. stammeri*. (Compare Chapter II.)⁸⁵

To subdivide the *Coarctata* group *sensu lato*, Osche (1952b) suggested a division into two groups, later named “*Coarctadera*” and “*Cylindridera*” by Dougherty (1953), based on an undulating or smooth bursa margin. As already pointed out by Andr ssy (1962), such an action does not appear to be justified. A smooth bursa margin is a symplesiomorphy, and thus not appropriate for defining a [monophyletic] group. Also, a wavy bursa margin could have originated convergently easily with the enlargement of the bursa. Besides, the undulation of the bursa margin is neither emphasized nor clearly depicted in every description of the species united to the *Coarctata* group.

²⁵ Looking for apomorphies for species within the *Coarctata* group, a group is found with all papillae situated within the bursa (the plesiomorphic state) with the tips of papillae 1, 4, and 10 opening dorsally, and moreover with papillae 7, 8, and 9 fused basally (Fig. 10). *Rhabditis kolbi* falls outside this combination of characters. Its first papilla lies anterior of the bursa (i.e., is prebursal), papillae 7–9 are not joined basally, and papillae 4 and 9 (instead of 4 and 10) open dorsally on the bursa. Within the group separated from *R. kolbi*, there is a clear bipartition. One subgroup (with *R. cystilarva*, *R. serrata*, and *R. coarctata*) exhibits a conspicuously thicker third bursal papilla. Also, the dauer larvae possess a strongly sculptured cuticle and are able to attach to transporting animals with their anterior ends, thereby forming “cysts.” In the other subgroup (*R. cylindrica*, *R. icosiensis*, *R. tretzeli*, *R. par*, and *R. voelki*), these characters are absent (the plesiomorphic state) and all these species instead have a bursa conspicuously structured by longitudinal and transverse striae. Within the cyst-forming group, *R. coarctata* and *R. serrata* are closely related and exhibit a sexually dimorphic lip region, corresponding to a trend that has repeatedly occurred within the entire group. *Rhabditis cystilarva* (= *R. acarambates*) possesses a relatively long tail thread in the female and a forked gubernaculum. Within the second subgroup, *R. voelki*, *R. tretzeli*, and *R. par* are the most closely related; their bursa is slightly cinched in [i.e., is narrower] at the level of the anus, the male is much smaller than the fairly large female (often by nearly a factor of 2), and the lips are not offset in the paedomorphic male (and in the female of *R. voelki*). In *R. tretzeli* and *R. par*, the third bursal papilla is shifted anterior of the cloaca. No synapomorphies can be named

for *R. cylindrica* and *R. icosiensis*, but the bursae of the males resemble one another enough to cause confusion.

One problem arises for *R. kolbi*, the species that diverged earliest in the *Coarctata* group. It has one pair of prebursal papillae, the formation of which could have occurred in two possible ways to be discussed. First, the first papilla has been shifted far anterior before a proximal [anterior] closure of the bursa occurred. This would mean that in [the lineage to] this species, the closure of the bursa took place independently from the other species, although this could be treated as a “common trend” of a monophyletic group. Alternatively, the first papilla was removed from a bursa that had already become closed. This possibility must indeed be strongly considered because in Strongylyna, [species of] which display closed bursae, there is frequently a prebursal papilla (= a first papilla) that has been removed from the bursa (see Osche, 1958).⁸⁶

h. Subgenus *Teratorhabditis* Osche, 1952

Despite its heterogeneity, this species group was united by Osche (1952b) on the basis of the strongly cuticularized lip edges like those in *Teratocephalus*. If this feature (quite certainly an apomorphy) is examined in more detail, however, it can be shown that this cuticularization is very similar in only three species. These species (*R. dentifera*, *R. boettgeri*, *R. mariannae*)⁸⁷ represent the subgenus *Teratorhabditis* in the sense used here.⁸⁸ The other two species (*R. coronigera*⁸⁹ and *R. chitinolabiata*) fail to fit with regard to numerous characters and are reminiscent of the subgenus *Cephaloboides*, and will be discussed in the section on *Diploscapteroides*.

Currently, the **diagnosis** for *Teratorhabditis* must be as follows: relatively large species (665–1,551 µm) with an ungainly body form and annulated cuticle, lip edges strongly cuticularized as in *Teratocephalus*, buccal tube with three denticles or prominent warts per metarhabdion, a pharyngeal sleeve lacking, median [pharyngeal] bulb present, terminal bulb with a double haustulum, an [anteriorly] open and peloderan bursa with 10 bursal papillae (2 of which are precloacal and numbers 3 and 8 pointing dorsally), long spicules (47–59 µm) that are fused nearly halfway, vulva usually⁹⁰ far posterior (though midbody in *R. boettgeri*, with correspondingly amphidelphic ovaries), and a female tail that is cupola

⁸⁵ From ontogenetic comparisons between *R. teres* and *R. strongyloides* using anti-adherens junction antibody as a marker of apical cell boundaries, it is clear that there was no evolutionary gain-and-loss of papillae. Rather, the differences in bursa arrangements arises from morphogenetic repositioning of the papilla precursor cells during development of the last juvenile stage (J4). Additionally, the seventh papilla in most cases investigated belongs to the phasmid; there are therefore a constant number of nine bursal “ray” papillae (Fitch and Emmons 1995; Fitch et al., unpubl.).

⁸⁶ That is, this second alternative possibility could have occurred in the lineage to *R. kolbi*.

⁸⁷ In the original text, the name *R. rovinjensis* was used. However, this is a junior synonym of *R. mariannae* (see Sudhaus, 1980:328).

⁸⁸ This was previously suggested by Farkas (1973:62), who also excluded *R. boettgeri*. *Rhabditis boettgeri* probably belongs to subgenus *Diploscapteroides* (see Sudhaus, 1985b:219).

⁸⁹ The original used the name “*R. coroniger*,” which was emended by Farkas (1973:62).

⁹⁰ “Usually” should be replaced by “always” if it is correct that *R. boettgeri* does not belong to *Teratorhabditis*.

shaped with a [short] spike or (in *R. dentifera*) short and dagger shaped.

The species of *Teratorhabditis* are similar to those of *Pelodera* with regard to several **plesiomorphic** characters (absence of a sleeve, existence of three teeth per metarhabdion, a double haustulum at the terminal bulb, structure of the bursa, number and arrangement of the papillae) as well as important **apomorphic** characters (body size and shape, fusion of the long spicules, cupola-shaped female tail) (Fig. 10). All of these characters have originated repeatedly and independently within *Rhabditis*. However, it is only in *Teratorhabditis* and *Pelodera* that this combination of characters is found. This appears to be reason enough to regard these characters as synapomorphies resulting from a phylogenetic relationship. *Teratorhabditis* diverged from *Pelodera* before a median vulva evolved in the latter lineage.⁹¹ The median vulva in *R. boettgeri* and the median bulb of the *Teratorhabditis* species developed convergently [with equivalent characters] in *Pelodera*.⁹² The divergent conical tail of *R. dentifera* can easily be explained by paedomorphism. A correspondence between the apomorphies of *Teratorhabditis* and *Cruzinema* cannot be demonstrated.

Of the three *Teratorhabditis* species, *R. mariannae*⁹³ and *R. dentifera* are the most closely related. *Rhabditis dentifera* appears to be a "successor species"⁹⁴ with a non-gonochoristic mode of reproduction originating by paedomorphism (female tail conical, lips not offset). *Rhabditis boettgeri* is known only vaguely (from only one female).

i. Subgenus *Caenorhabditis* Osche, 1952⁹⁵

Apomorphies of *Caenorhabditis* include a certain increase in body size (603–1,850 µm), the setiform apical labial sensilla, the formation of a median [pharyngeal] bulb, the midbody position of the vulva and corresponding paired ovaries, the nearly closed bursa (produced by enlarging the proximal parts of the velum), the reduction to nine bursal papillae⁹⁶ arranged in the order (2 / 4 + 3), the flask-shaped appearance of some of these papillae (especially the thickened sixth) due to their basal swelling, the seventh of which is bent dorsally and opens on the dorsal surface of the bursa ve-

lum, and the bent, knife-like gubernaculum. Which of the original 10 bursal papillae was lost during evolution is unknown. **Symplesiomorphies** of the species are the light, transversely striated cuticle, the closed lips that are not offset, the terminal bulb with a double haustulum, the peloderan bursa with two precloacal papillae, the separate dagger-like spicules of medium length (27–52 µm, enlarged only in *R. plicata* and *R. avicola* to 54–95 µm), the invariably conical female tail, and the H-shaped excretory system. Furthermore, the following characters appear to be displayed by all members of this group: the margin of the bursa is slightly pleated and serrated, the anterior cloacal lip bears an anteriorly directed process,⁹⁷ the buccal tube of the juvenile is anisotropic (slightly longer dorsally), and the dauer larvae are unsheathed.⁹⁸ Until these characteristics are actually shown to be universally valid [for these species], they may be proposed as apomorphies for *Caenorhabditis*.

Accordingly, *Caenorhabditis* certainly represents a natural group. The species that belong to this group so far are all very closely related ("a jam of forms," Osche, 1952b⁹⁹). They are fairly slender and very agile. *Rhabditis plicata* plays a key role in the derivation of the *Caenorhabditis* taxon (Fig. 11) in that it is (in my view) the most primitive. Unlike the other *Caenorhabditis* species, *R. plicata* bears three barely projecting ridges on each metarhabdion, a pattern to be assumed as plesiomorphic for *Rhabditis*, and from which came the characteristic metarhabdion teeth of the *Pelodera* group, for instance¹⁰⁰ (Osche, 1952b). Osche placed *R. plicata* as an appendix to the *Teres* group of *Pelodera*. But it does not fit into the constitution of those characters typical [to the *Teres* group]. Since having three metarhabdion teeth in this simple pattern is interpreted as plesiomorphic by Osche, this feature cannot be treated simultaneously as an apomorphy for an entire group. Consequently, some aberrant species must be removed from the *Pelodera* group as it was originally defined (see p. 20). Disregarding the metarhabdion teeth, *R. plicata* shares numerous features with *Caenorhabditis*. Of particular importance in this context is the formation of a nearly closed bursa, the arrangement of the nine bursal papillae, and the shape of the separate spicules. Primitive characters are triply ridged metarhabdions, a slight pharyngeal sleeve, and the proximally slightly open bursa. Apomorphic characters include the increased body length (1,013–1,850 µm) and correspondingly increased spicule length (54–62 µm), the shortened con-

⁹¹ What is actually meant is that the stem species split into two species that were ancestral to the sister groups *Teratorhabditis* and *Pelodera*.

⁹² This statement is not very clear with respect to the evolution of the median bulb of the pharynx. As discussed above, a median bulb evolved in three different lineages within *Pelodera*. This scenario is obsolete with the exclusion of *R. stammeri* from *Pelodera*.

⁹³ Again, *R. mariannae* is the senior synonym for *R. rovinjensis* cited in the original.

⁹⁴ Although the term "*Folgeart*" is used in the original, the author now disregards (except perhaps in rare cases) this type of sympatric speciation in which the stem species (here *R. mariannae*) survives unaltered and another species (here *R. dentifera*) diverges as an offshoot.

⁹⁵ A more comprehensive and revised phylogenetic analysis, which includes newly described species, has recently been accomplished (Sudhaus and Kiontke, 1996; see Appendix 1 for a cladogram).

⁹⁶ "Reduction" in the sense of the loss of one pair of papillae.

⁹⁷ This structure is also known as the "hook."

⁹⁸ Although *R. briggsae* was cited as an exception in the original text (after Yarwood & Hansen, 1969), dauer juveniles of this species also appear unsheathed.

⁹⁹ The word "*Formenstau*" (a "jam of forms") coined by Osche was not subsequently used and is not a fruitful concept.

¹⁰⁰ That is, the metarhabdion embellishments of *Pelodera* species are one instance of how the plesiomorphic metarhabdion conserved in *Caenorhabditis plicata* has evolved.

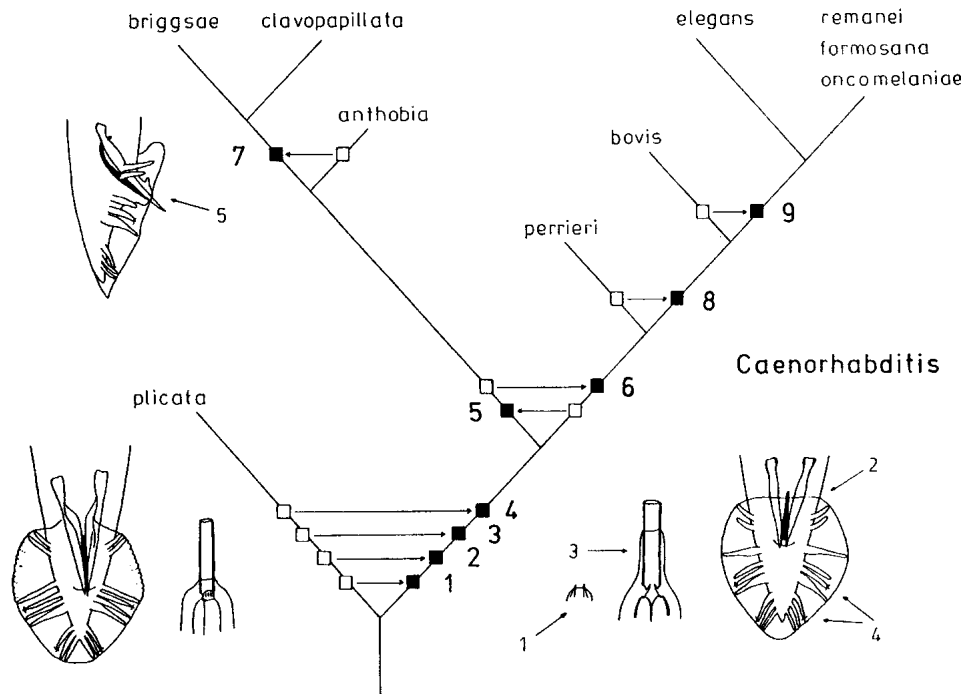


FIG. 11. Cladogram of *Caenorhabditis* (except *R. avicola*, *R. craspedocerca*, and *R. genitalis*). The numbers denote the following apomorphies: (1) two teeth per metarhabdion [an error, see footnote 101]; (2) bursa closed; (3) [pharyngeal] sleeve covers half the buccal tube; (4) fifth and seventh papillae open dorsally ["outwardly" in the original]; (5) third papilla reduced (only eight papillae present) [erroneous, since this proposed change was based on the erroneous observation of only eight papillae in the derived species; see footnotes 105-107]; (6) papilla arrangement (2/1+3+3); (7) papillae shortened and thickened; (8) female tail elongated; (9) bursa form and arrangement [of papillae] correspond. Includes figures from Nigon and Dougherty (1949) and Sudhaus (1974c).

cal tail of the female, and the lack of a tail tip in the male such that the last papillae meet at their bases (see Fig. 11).

That *R. plicata* has three ridges per metarhabdion supports the hypothesis that the two pointed and hollow metarhabdion teeth projecting into the lumen as described for *Caenorhabditis*¹⁰¹ are derivable from the three-ridged morphology. That *Caenorhabditis* and *Mesorhabditis* share this double-toothed metarhabdion feature must therefore have resulted by convergence, an inference that is further supported by the differences in the special quality of this structure between the two groups.¹⁰² A direct phylogenetic connection also cannot be established with *Pellioiditis*, which shares with *Caenorhabditis* closed lips, a peloderan bursa, separated spicules, a midbody vulva, formation of a pharyngeal sleeve (except *R. plicata*) and the nearly complete reduction of the 10th bursal papilla.¹⁰³ The latter three features represent derived states, although independent transformations to these states have occurred frequently in the *Rhabditis* group. Both *Pellioiditis* and *Caenorhabditis* differ considerably in crucial characters such

that a closer relationship is unlikely. A metarhabdion type with two teeth such as appears again in *R. (Pellioiditis) dolichura* (which will be discussed later with the subgenus *Pellioiditis*) does not suggest in my view a phylogenetic relationship with *Caenorhabditis*.¹⁰⁴

In the group of *Caenorhabditis* species that diverged from *R. plicata*, two evolutionary trends can be observed that correspond to two divisions of the group (see Fig. 11).¹⁰⁵ Beginning with the primitive bursal type (2 / 4 + 3) with a group of four postcloacal bursal papillae (as still expressed in *R. plicata*), the first group contains derived forms in which the third papilla was reduced [i.e., lost] or was fused with its posterior neighbor, thus resulting in only eight papillae in a (2 / 3 + 3) arrangement (*R. anthobia*,¹⁰⁶ *R. briggsae*,¹⁰⁷ *R. clavopapillata*). In the second group, the third papilla shifted anteriorly, thus setting it off from the neighboring posterior group of three, to produce the pattern (2 / 1 + 3 + 3). This trend culminated in *R. craspedocerca* and *R. perrieri* where the third papilla was even shifted precloacally,

¹⁰¹ The older observation of two hollow teeth per metarhabdion is an error. For the other *Caenorhabditis* species, there is generally a single, triangular flap or "tooth" per metarhabdion (Baird et al., 1994; Sudhaus and Kiontke, 1996).

¹⁰² This statement is obsolete (see previous footnote).

¹⁰³ In *Caenorhabditis*, there is no "remnant" of a 10th papilla. It should be noted, however, that one *Caenorhabditis* species (strain PS1010) displays 10 pairs of papillae; the most posterior pair are the phasmids that extend into the bursa velum. This state is uncharacteristic for most *Caenorhabditis*, where the phasmids in the tail tip generally do not extend into the velum.

¹⁰⁴ This statement is obsolete (see footnote 101).

¹⁰⁵ The first "trend" mentioned is erroneous, since the inference is based on erroneous observations of only eight papillae in *R. anthobia*, *R. briggsae*, and *R. clavopapillata*, as detailed in the following two footnotes.

¹⁰⁶ A reexamination of type material showed that third papillae are actually present in *R. anthobia*, bringing the total number of papillae in this species to nine pairs (Fig. 6 of Sudhaus and Kiontke, 1996).

¹⁰⁷ Note that, at least in *R. briggsae*, this fusion (not loss) of the third and fourth papillae occurs only in a fraction of wild type populations and often occurs on only one side of the animal (see Fig. 1 of Fitch and Emmons, 1995).

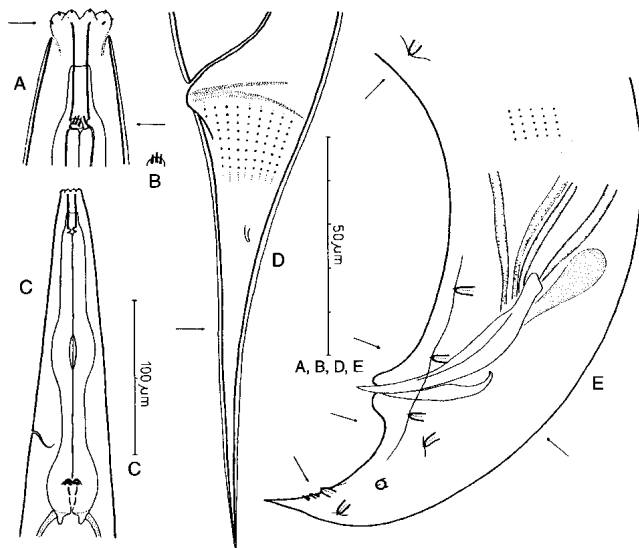


FIG. 12. *Rhabditis (Rhabditoides) inermiformis* Osche, 1952. A) Anterior end and buccal tube, ventral view. B) Metarhabdion. C) Anterior end and pharynx, lateral view. D) Posterior end of the female, lateral view. E) Posterior of the male, lateral view.

forming a group with the first two: (3 / 3 + 3). In the remaining species, the female tail was elongated. Of these species, *R. remanei* and *R. elegans* are distinguishable almost solely by their mode of reproduction (complementary species).

j. Subgenus *Rhabditoides* T. Goodey, 1929

Features that are shared by species within this taxon are closed lips, a long pharyngeal sleeve enveloping 50–85% of the buccal tube, metarhabdions with three small denticles arranged in a triangle, the formation of a median bulb, a midbody vulva, and a conical female tail. Except for the first and last, these characters are **apomorphies**. The body length in each case is about 1 mm (420–2,000 μm). Furthermore (although not known for the non-gonochoristic *R. helversenorum*¹⁰⁸), the open and leptoderan bursa is reduced to a narrow velum and the arrangement of the papillae is radial (see Fig. 12). Typically, there are 10 usually stocky bursal papillae (only 6–7 are described for *R. incisocaudata*¹⁰⁹ and only five for *R. macroura*) of which three stand precloacally (except that the number of precloacal papillae in *R. giardi* is supposedly four, two in *R. frugicola*, and one in *R. incisocaudata*). The first papilla, which is usually far from the proximal end of the spicules, is easily overlooked. Papillae four and five generally stand very close together; papillae five and seven are positioned sublaterally. The 20–57-μm-long spicules are separate. In addition to the apomorphies listed above, characters essential for supporting the unity and monophyly of the group include the construction of

the bursa and the arrangement of the papillae. Because of the three precloacal papillae, *Rhabditoides* is closely allied with those groups united as “*Eurhabditis*.” The warts on the metarhabdions of “*Eurhabditis*”¹¹⁰ may have originated from denticles [like those in *Rhabditoides*].

A subdivision of *Rhabditoides* is not possible with any certainty, since some of the species are insufficiently known. Therefore, only some presumed evolutionary trends will be pointed out. In the arrangement of bursal papillae, *R. inermis* seems to be primitive. Starting from such a form, an elongation of the conical tail in both sexes can be observed. Because of this elongation, some of the papillae of the first and second group are set widely apart. The species concerned (particularly *R. longispina*) attain a high degree of similarity to Diplogastridae with regard to the arrangement of papillae, the extensive reduction of the bursa velum, and the thread-like tail. The most derived in this respect is *R. helversenorum*, with its extremely long female tail. Starting with a spoon-shaped gubernaculum (in *R. incisocaudata*¹¹¹), the distally more-or-less forked gubernacula of *R. inermis*, *R. longispina*, and *R. inermiformis* can be derived. This species group is united by slightly strengthened telorhabdions as well. The lips, originally not distinct at the anterior end and closed, can become more or less prominently set apart (*R. inermiformis*, *R. helversenorum*). In *R. inermis*, the rounded anterior end (with only faintly distinct lips) could likewise represent a derived situation, but in the opposite direction. With respect to this feature, *R. resistens* is similar, but is placed in this group only supplementarily, because it supposedly bears small warts on the glottoid apparatus and has no pharyngeal sleeve (the latter feature being completely atypical for this group). It should be noted that the metarhabdion structures are not simply uniform within *Rhabditoides*. The central tooth always stands slightly higher (in a triangular pattern). However, whereas the longer denticles in *R. inermiformis* (Fig. 12A, B) are clearly bent and the central denticle in *R. longispina* has a specially structured base in contrast to the lateral ones, the denticles in *R. helversenorum* are simply wart-like. Used in this sense, the term “wart” (used with *R. resistens*) applies well within this framework.

Subgroup “*Eurhabditis*”¹¹²

This extensive species group—referred to here as “*Eurhabditis*”—unites the five subgenera that are discussed below [Sections 4k–o] and that share the follow-

¹⁰⁸ Males of this species have now been found (W. Sudhaus, pers. obs.); the same circumstances apply.

¹⁰⁹ Sudhaus (1980) placed this species in the *Rhabditis (Poikilolaimus)* taxon.

¹¹⁰ Erroneously “*Rhabditis*” in the original.

¹¹¹ Because of its revised position in subgenus *Poikilolaimus* (Sudhaus, 1980), a forked gubernaculum can be hypothesized as an apomorphy of *Rhabditoides*.

¹¹² By using quotation marks, the author signifies that this name does not refer to a genus- or subgenus-level taxon, but rather to a species group at an intermediate level.

ing characters: a leptoderan bursa (except in *Pellioiditis* and two species of *Cephaloboides*, which are secondarily peloderan) that is open nearly without exception (but closed in the large *R. dubia* and *R. maxima* as well as in *R. dacchensis*), separate spicules (uncertain exceptions include *R. ciliata*, *R. dudichi*, *R. maxima*, and *R. dubia*¹¹³), always a midbody vulva, a glottoid apparatus with warts on the metarhabdions (except *R. oxycerca*, *R. jodhpurensis*, *R. dolichura*, and *R. rara*), and a pharyngeal sleeve that surrounds 50–80% of the buccal tube length (missing in *R. chitinolabiata*¹¹⁴). Nearly all species possess 10 bursal papillae. However, the 10th [i.e., the most posterior] may be more or less reduced.¹¹⁵ Finally, *Pellioiditis* species nearly always have only nine papillae. Primitively, three papillae were situated precloacally, spaced nearly evenly at first. In some species, the metastom is anisotopic and anisomorphic.

Very few characters of “*Eurhabditis*” are ubiquitously represented. With respect to the extensive pharyngeal sleeve, the midbody vulva, the leptoderan bursa, and the three precloacal papillae, the group shares features with *Rhabditoides* that I interpret as synapomorphies resulting from monophyletic evolution. Informally, then, the metarhabdion warts of “*Eurhabditis*” can be derived from three denticles arranged in a triangle as in *Rhabditoides*—ultimately evolving from a prototype with metarhabdions bearing three ridges each. These warts are therefore the only apomorphy of “*Eurhabditis*” and are furthermore not displayed in two species groups (see previous paragraph).

k. Subgenus *Rhabditella* Cobb, 1929

This group includes only two species (*R. axei*¹¹⁶ and *R. octopleura*).¹¹⁷ Besides the characters typical for “*Eurhabditis*,” *Rhabditella* species have a strongly reduced and radially arranged bursa with 9–10 papillae, the arrangement of which $(1 + 2 / 1 + x)$ is reminiscent of the subgenus *Cephaloboides*. Papillae one, four, and nine are placed laterally. The tail is exceedingly long in both sexes, often giving the impression that the species are *Diplogaster*-like (see Fig. 13). The lips are closed and not distinct, the buccal tube is long and more or less anisotopic, and a median bulb is present. The distal tips of the reflexed ovary reach the level of the vulva. The spicules, measuring 30–50 μm , are strongly arched, distally shaped like a probe, and possess a dorsal thorn. The body size can be considerable, 570–2,900 μm [in

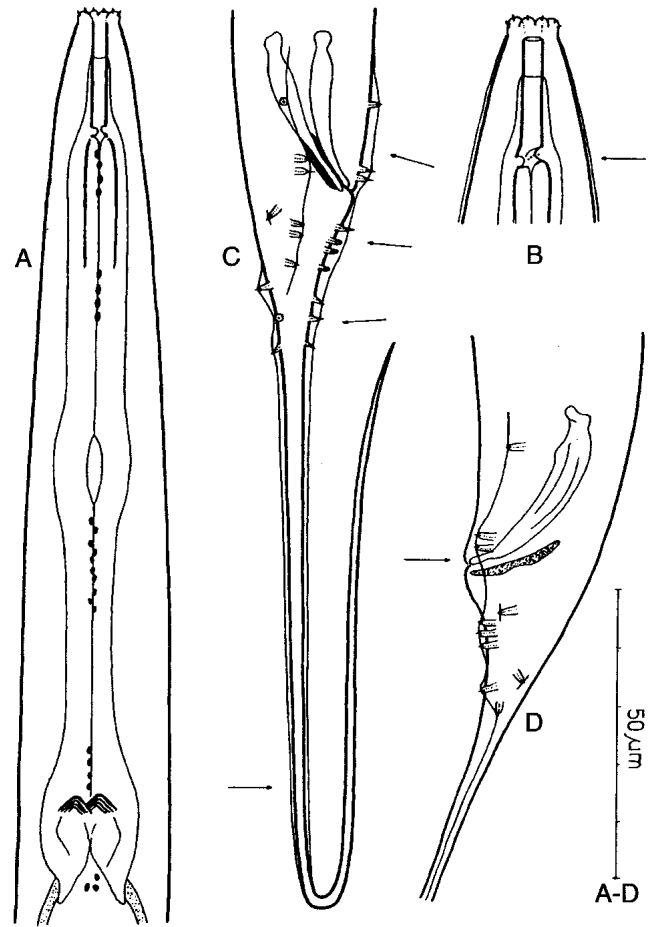


FIG. 13. *Rhabditis (Rhabditella) octopleura* [?] Steiner, 1929. [Note that the species identity of the particular specimen depicted is actually unknown (see Kiontke, 1999:90).] A) Anterior end and pharynx with corpuscular food particles. B) Anterior end and buccal tube. C) Posterior end of male, subventral view. D) Posterior end of male, lateral. Material from J. Weiser (Prague) from dead larvae of the moth *Diatraea lineolata* [Pyralidae] from the vicinity of Havana, Cuba.

length] when nutrient levels are good. The species are gonochoristic. The [dauer] juveniles display *Röhrenwinken* [a waving behavior in a tube of unsloughed cuticle from the previous molt]. The noteworthy similarity of *Rhabditonema* (= *Termirhabditis*) *fastidiosa* (Massey, 1971) is probably due to convergence.

l. Subgenus *Diploscapteroides* Rahm, 1928

*Rhabditis coronigera*¹¹⁸ and *R. chitinolabiata* have been excluded from the *Teratorhabditis* group (p. 23) because no substantial corresponding similarities can be observed with those species. The cuticularization of the edges of the lips is superficially similar (and *Teratocephalus*-like), but such similarity also holds for several other nematode genera), emphasizing the probability that such a structure evolved convergently. On the other hand, these species, in common with *R. brevicauda* and

¹¹³ Actually, the spicules have now been observed to be fused in *R. ciliata*, *R. dudichi*, *R. dubia*, and *R. maxima* (W. Sudhaus, pers. obs.; for *R. dubia*, see Sudhaus and Kühne, 1990).

¹¹⁴ A pharyngeal sleeve is present in the type specimens recently examined (Sudhaus, pers. obs.).

¹¹⁵ This “reduced 10th papilla” is in nearly all cases the phasmid (Kiontke and Sudhaus, 2000).

¹¹⁶ In the original text, this species is called *R. pseudoelongata*, which is synonymous to *R. axei* as demonstrated by Sudhaus (1980:332).

¹¹⁷ See Kiontke (1999) and Fig. 34 (Appendix 1) for an update on this species group and descriptions of new species.

¹¹⁸ The name used in the original, *R. coroniger*, has since been emended to *R. coronigera*.

R. dacchensis, display characters typical of “*Eurhabditis*”: a leptoderan bursa, separated spicules, a midbody vulva, and a pharyngeal sleeve enveloping half of the buccal tube (the latter presumably overlooked in *R. chitinolabiata*¹¹⁹ and *R. brevicauda*). The metarhabdion structures have not been described.

- [32] The independence of this species group is supported by the following characters (Fig. 23): the lips are offset, the lip edges are strongly cuticularized such that the cheilostom and buccal tube look like a question mark in optical [sagittal] section, a median bulb is present, the female tail is conical and generally relatively short, the bursa is minimized, all papillae are positioned post-cloacally, the 29–48- μ m-long spicules proximally possess a ventral projection¹²⁰ and are distally thickened or broadened, and the gubernaculum is triangular. The body length generally remains less than 1 mm (410–1,687 μ m). In particular, the formation of the lips and the organization of the bursa are considered **apomorphies** of *Diploscapteroides*. In the postcloacal arrangement of all the bursal papillae, these species are reminiscent of *R. nidrosiensis* of subgenus *Cephaloboides*. In this species, a strengthened cheilostom also forms,
- [33] which is partly similar to that of *Diploscapteroides*. The extent to which this similarity reflects a relationship is discussed in the next section.

The following combination of characters appears to support a close phylogenetic relationship between the subgenera *Diploscapteroides* and *Cephaloboides*: the strongly reduced bursa with a similar arrangement of the papillae (for the moment excluding from consideration that the papillae of *Diploscapteroides* begin posterior of the cloaca) with the first traces of a radial organization (papillae four and eight placed sublaterally?), and perhaps the offset lips and thick cuticle. However, these species groups clearly differ in other characters. Above all, there is as yet¹²¹ no cupola-shaped tail formed in *Diploscapteroides*.

As all of the *Diploscapteroides* species are known but vaguely, their classification cannot be clearly outlined. A close relationship seems to exist between *R. dacchensis* and *R. brevicauda*, which display a tooth-like protrusion of the dorsal buccal tube wall. In addition, their bodies are longer [than those of other *Diploscapteroides* species] (greater than 1 mm). *Rhabditis dacchensis* is distinguished by its proximally closed bursa. A detailed investigation of this group should probably determine, for example, whether the radial arrangement and strong reduction of the bursa could actually be apomorphic for [the stem species of] *Cephaloboides* and *Rhabditella* (as supposed here) or if they are convergent.

m. Subgenus Cephaloboides Rahm, 1928

The species belonging to this group have the characters of “*Eurhabditis*,” namely an open and (as a rule) leptoderan bursa, separated spicules, a midbody vulva, a pharyngeal sleeve around 50–70% of buccal tube length, and usually metarhabdion warts. Apart from these features, they possess a cupola-shaped tail in both sexes, nearly always a very thick cuticle, and a more or less strongly reduced and radially arranged bursa generally with three precloacal papillae, with papillae one, four, and eight in sublateral position. Usually, a median bulb is conspicuously formed, the terminal bulb has a double haustrulum, and the distal ends of the flexed ovaries reach the level of the vulva. The species are generally compactly cylindrical, the body length varies between 460 and 1,890 μ m, and the spicule length is 22–72 μ m. The following can probably be regarded as original: the (1 + 2 / 1 + 3 + 3) bursal arrangement, the arched and dagger-shaped spicules, and a “triangular,” distally rounded gubernaculum. Particularly because of the formation of a cupola-shaped tail in both sexes, this group is distinguishable as a natural unit, separate from both *Diploscapteroides* and *Rhabditella*.

The question raised in Section 41 regarding the possible derived status of several characters in *R. nidrosiensis* and the species of subgenus *Diploscapteroides* (i.e., the shifting of all bursal papillae to positions posterior of the cloaca and the strong cuticularization of the edges of the lips) is difficult to answer in view of the little knowledge of the species involved. I give greater weight to the formation of cupola-shaped tails in both sexes and the typical (1 + 2 + 1 + 3 + 3) arrangement of the papillae in *R. nidrosiensis* (Fig. 14) as apomorphic characters shared with the *Cephaloboides* group, such that the previously mentioned characters must be convergences with *Diploscapteroides*. At least, these parallelisms, by not occurring elsewhere in *Rhabditis*, certainly appear to support a phylogenetic relationship as do, for example, the convergent trachea that frequently evolved in arthropods, yet are known exclusively in arthropods.

The reduction of the bursa and its radial arrangement—at least the “trends” toward these states—should be viewed as apomorphies for [the stem species of] *Rhabditella* and *Cephaloboides*, an elucidation of which is hoped will come from a detailed study of the *Diploscapteroides* species. These characters thus cannot be used redundantly in the systematization of *Cephaloboides* itself. Therefore, both the larger bursa and partially radial arrangement of the papillae in *R. valida* appear to be secondary changes. In the formation of its bursa, this species is reminiscent of *Pellioiditis* (see below [Section 4o]). (*Rhabditis ciliata* should belong to the subgenus *Rhabditis*, where it is discussed in this text.)

Within *Cephaloboides*, two species diverged from the lineage to a species group united by a distally forked gubernaculum. The gubernaculum of these two species

¹¹⁹ A pharyngeal sleeve is actually present in *R. chitinolabiata* (W. Sudhaus, pers. obs.).

¹²⁰ “*Ventralzahn*” (“ventral tooth”) is used in the original.

¹²¹ By using this phrase with a temporal connotation, the author is expressing the use of polarity information in the reconstruction (where a conical tail is inferred to be plesiomorphic).

Cephaloboides

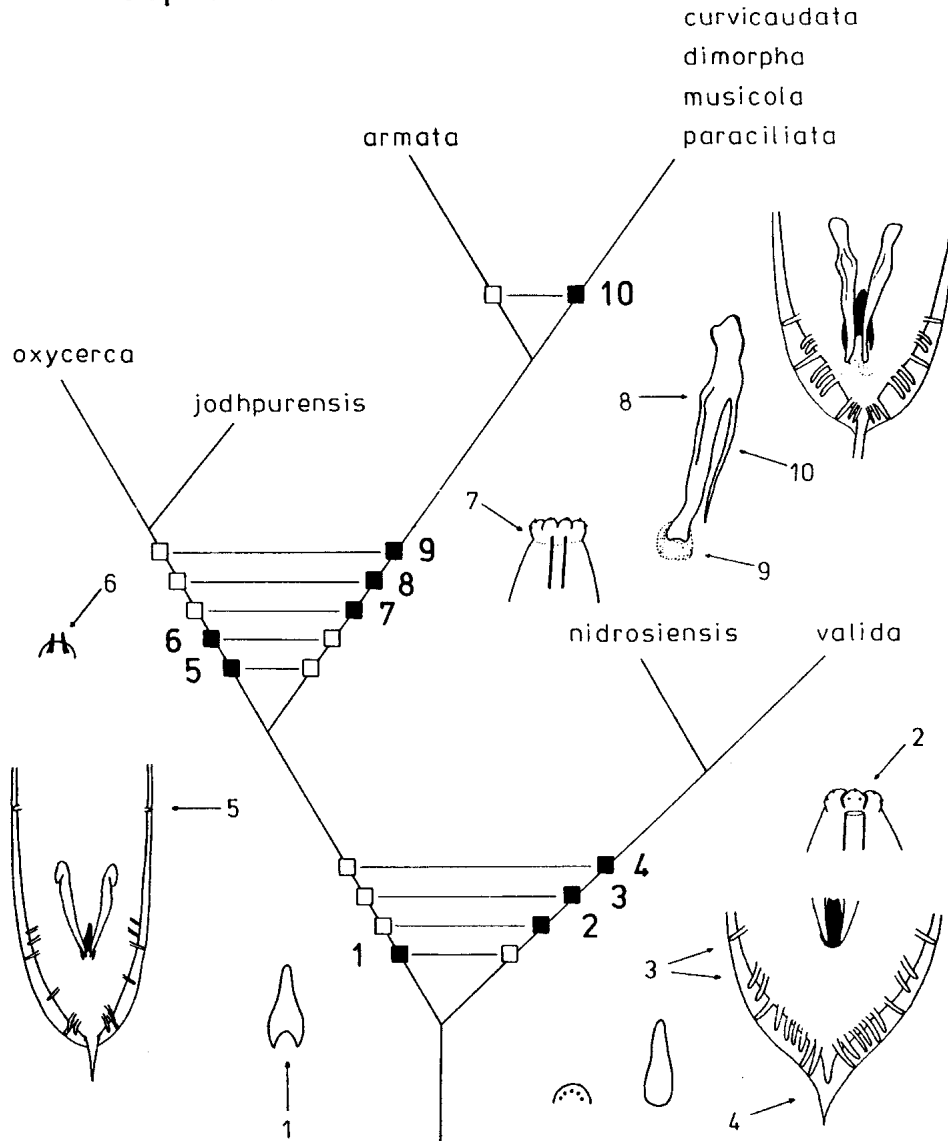


FIG. 14. Cladogram of *Cephaloboides*. The numbers denote the following apomorphies: (1) gubernaculum distally forked; (2) lip margins heavily cuticularized; (3) bursal papillae moved to postcloacal positions; (4) transition to peloderan bursa; (5) first papilla is shifted prebursally; (6) metarhabdion teeth formed; (7) ball-like lips set apart; (8) spicule thickened, with a ventral projection and a blunt end distally; (9) spicule with cap of secretion; (10) spicule with dorsal thorn. Includes figures from Osche (1952b) and Sudhaus (1974a).

remains plesiomorphically shaped like a spatula or shoehorn; as in *Diploscapteroides*, however, the edges of the lips became quite strongly cuticularized and all of the bursal papillae (or all but one of the papillae) shifted posterior of the cloaca (see Fig. 14). Of these species, *R. nidrosiensis* has nearly retained the original arrangement of the 10 bursal papillae (1 + 2 + 1 + 3 + 3). In *R. valida*, presumably the seventh (or sixth) papilla was reduced and the resulting nine papillae became arranged into three clusters of three papillae each. The radial arrangement was reversed; however, the first, fourth, and third from the last papillae still open on the dorsal surface of the velum. It is significant that the bursa of *R. valida* became peloderan and included [surrounded] the tail [tip], such that the entire

bursal structure is strongly reminiscent of the species in subgenus *Pellioiditis*. This trend is already found in *R. nidrosiensis*, in which a transition from a leptoderan to a peloderan tail and bursa can be observed as intraspecific variation such that *R. valida* is by no means unique in subgenus *Cephaloboides* with regard to this character.

Within the species that have a forked gubernaculum (although this is not known for *R. jodhpurensis*), *R. oxycerca* (Fig. 14) and *R. jodhpurensis* remain primitive in the sense that their lips are closed and not offset and their spicules are nearly dagger shaped and pointed. Both species are also exceptional in having only a weak median bulb and *R. oxycerca* in having the remains of transverse ridges in the anterior part of the pharynx. Characters that must be considered derived in these

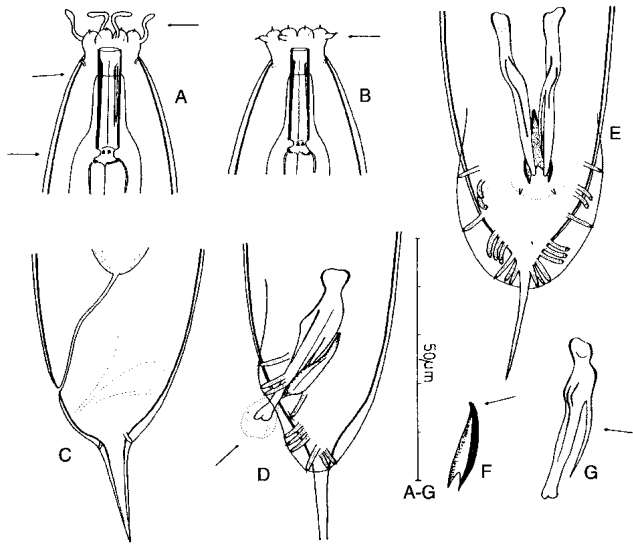


FIG. 15. *Rhabditis (Cephaloboides) dimorpha* n. sp. A) Anterior end and buccal tube of female, lateral view. B) Anterior end of male, lateral. C) Tail of female, lateral. D) Posterior end of male, lateral. E) Bursa of male, ventral. F) Gubernaculum subventral. G) Spicule, lateral view. From wood pulp of a plane [sycamore] tree [most likely *Platanus orientalis*] in Asprovalta on the Gulf of Strimón in Macedonia [Greece] (sampled by P. Miotk).

species include the shift of the first papilla to a position anterior of the proximal end of the spicules, the reduction and alteration in the arrangement of the papillae, and the formation of metarhabdion teeth (in *R. oxycerca* each metarhabdion bearing two delicate, protruding teeth, and in *R. jodhpurensis* each bearing one large plate-like tooth). These animals are able to retract their anterior and posterior ends into the inflatable cuticle.

The other species are similarly characterized by distinctly offset, almost ball-shaped lips and an alteration of the dagger-shaped spicules to become stouter and thickened proximally and distally; the spicules also display a distal cap of (mucosal) secretion (Fig. 14). At this point, a group of four¹²² species diverged, the spicules of which share the peculiarity of a dorsal prong.¹²³ Within this group of species, *R. paraciliata* and *R. musicola* appear to be the most closely related because of their spicule morphology and possibly [because of] the anisotropic buccal tube [i.e., metarhabdions].

Unusual features of this group not yet mentioned include the “cilia-like” bristles on the lips of *R. paraciliata*, the lateral sensilla extending like tentacles from the (sexually dimorphic!) lips of females of *R. dimorpha* n. sp. (Fig. 15A), a buccal tube in *R. musicola* that is bent with a tooth-like projection, and the position of the phasmids in [the females of] *R. armata* and *R. curvicauda* on the tail spike itself and distal from the dome.¹²⁴

n. Subgenus *Rhabditis* Dujardin, 1845

Currently, there is no convincing reason to split “*Eurhabditis*” into two natural subgroups corresponding to the *Maupasi* and *Longicaudata* groups of Osche (1952b) or the subgenera *Rhabditis* and *Choriorhabditis* of Dougherty (1955), much less [an additional split into] a third group (*Ablechroiulus* Andrassy, 1966). As one can easily see in a comparison of the corresponding species, an informal division into one “short-tailed” and one “long-tailed” species group is not possible. Clear apomorphies have not been demonstrated for any of the named subgroups, which may be due in part to the unsatisfactory state of research of this particular group of species. Since it is not known whether the “*Eurhabditis*” ancestor had a long or short conical female tail, tail length is unsuitable for differentiating one group from the other. Also, the theoretical consideration that a leptoderan bursa probably could emerge only in parallel with the extension of the female tail from an ancestral form with a peloderan bursa in [the genus] *Rhabditis*, and consequently that a longer female tail would have to have originally existed in leptoderan *Rhabditis*, scarcely provides further support [for such a separation into short-tailed and long-tailed groups within the subgenus *Rhabditis*]. It is conceivable that, in the evolution of the species group, the tail length was easily changed convergently in one direction or the other and surely has changed repeatedly (as can be shown for subgenus *Pellioiditis*, treated in the following section). The *Longicaudata* and *Maupasi* groups therefore are combined at present (as subgenus *Rhabditis*), emphasizing the necessity for intense comparisons involving all species in this morphologically diverse and species-rich group.

As **symplesiomorphies**, the representatives¹²⁵ of this subgenus certainly show the typical characters of “*Eurhabditis*”: a well-formed bursa that is not radially arranged, leptoderan, and open as a rule, spicules that are nearly always separated, a median vulva with correspondingly amphidelphic gonads, a glottoid apparatus with 2–5 warts [per metarhabdion], and a pharyngeal sleeve enveloping half or more of the buccal tube. Each of the closed lips bears two sensilla, the excretory system is H-shaped, and the cuticle is gently striated transversely. Furthermore, 10 bursal papillae are plesiomorphic, of which three are precloacal. However, the 10th papilla is not well developed, but is vestigial or entirely missing.¹²⁶ The original state [i.e., 10 bursal papillae] was retained only in *R. gracilicauda* and *R. producta*.¹²⁷ Also plesiomorphic in this group are an anguilluloid

¹²² Not three, as erroneously stated in the original text.

¹²³ This divergence can no longer be upheld because a dorsal prong also exists on the spicules of *R. armata* (W. Sudhaus, pers. obs.).

¹²⁴ Because the separate systematic position of *R. armata* is no longer justifi-

fied, this last feature may be a synapomorphy for establishing *R. armata* and *R. curvicauda* as sister species.

¹²⁵ i.e., the species.

¹²⁶ In many cases, the 10th papilla is actually the phasmid, which is not always conspicuous (Fitch, 1997; Kiontke and Sudhaus, 2000).

¹²⁷ Sudhaus and Kühne (1990) showed that *R. dubia* also has 10 bursal papillae.

pharynx,¹²⁸ a double haustulum in the terminal bulb, a conical female tail, an oviduct that is bent like a U, weakly curved and dagger-shaped spicules, a gubernaculum probably shaped like a spatula or spoon, and a relatively small body size (less than 1 mm), which subsequently increased many times¹²⁹ ([resulting in a broad range of] 500–3,744 μm).

The question must be discussed whether the typical, nonradially arranged bursa was primitive in this species group. There is the possibility that a leptoderan tail evolved along with a reduction of the bursal velum, the evolution of a radial arrangement of the bursal papillae, and a change in copulatory behavior from the parallel form to the spiral form. The radial formation of the bursa would then be a synapomorphy of *Rhabditoides* and “*Eurhabditis*” and a plesiomorphy within “*Eurhabditis*.” The “alteration” of this bursa type [i.e., to non-radially arranged (flat) or only partially radially arranged] in subgenus *Diploscapteroides* and *Cephaloboides valida* as well as the species to be treated here (i.e., subgenus *Rhabditis*) would have to be interpreted as convergences (cf. p. 28). For the moment, I consider this scenario speculative.¹³⁰ The formation of a normal bursa¹³¹ with a large velum is certainly a primitive character for [the genus] *Rhabditis*. It seems more likely to me that a leptoderan, non-radially arranged bursa could be derived from such a [peloderan, “normally” arranged] bursa than from a radially arranged and already strongly reduced bursa. Additionally, the radially arranged bursae of *Rhabditoides* and *Rhabditella* or *Cephaloboides* are too different in their details to suggest a common origin without difficulty. Therefore, I propose that the normally arranged, leptoderan bursa was plesiomorphic at this branch of the *Rhabditis* tree,¹³² and that the radially arranged bursae derived from such a form evolved in independent lineages. Because of this, it is not possible to observe a shared apomorphy in a form of the bursa that is typical of subgenus *Rhabditis* [leptoderan and normally arranged] that could be used to support the monophyly of this group.

Clear **apomorphies** cannot be given for subgenus *Rhabditis*, suggesting the possibility that this group is paraphyletic (cf. p. 38). A notable [trend] is the reduction of the 10th bursal papilla.¹³³ This papilla is never particularly well developed. All stages of this reduction can be observed within the species group, down to a tail knot¹³⁴ (Fig. 16) or even complete disappearance.

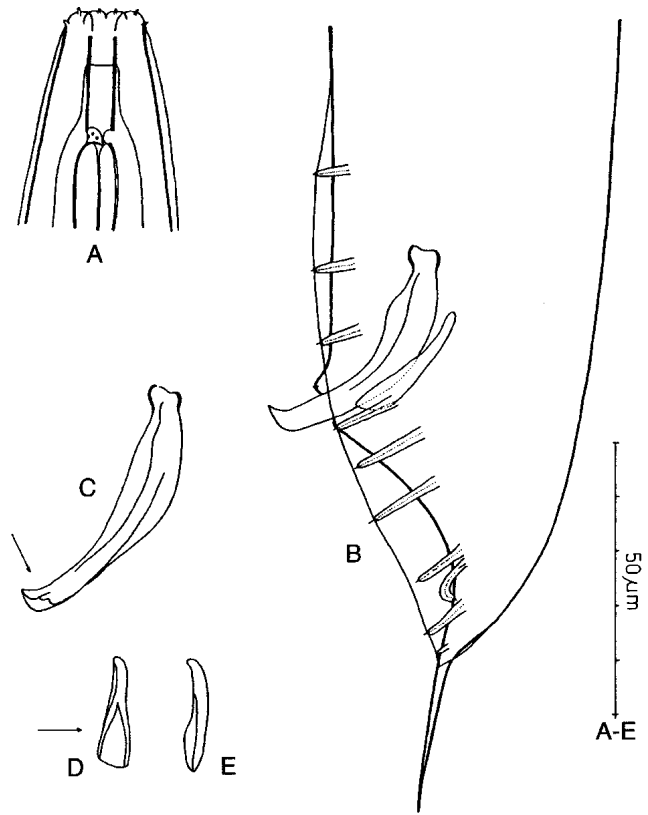


FIG. 16. *Rhabditis (Rhabditis)* sp., a species of the *Brassicae* group [*R. broughtonalcocki*] in the original text has since been synonymized with *R. brassicae*. A) Anterior end of male. B) Posterior end of male, lateral view. C) Spicule, lateral view. D) Gubernaculum, subventral view. E) Gubernaculum, lateral. Discovered in compost-like material washed up on the edge of the dunes of Bottsand, Kieler Aussenförde [Germany]. Female unknown.

However, because such a trend toward reduction appears to exist generally in “*Eurhabditis*,” considering this feature a shared apomorphy may be criticized, particularly because (as already mentioned) the 10th papilla in two species of this subgenus is present in fairly typical form and reaches the edge of the bursa velum. I would also view the fact that papillae five and eight open on the dorsal surface of the velum as a presumably primitive feature within subgenus *Rhabditis*. Perhaps this feature was characteristic for the stem species, and therefore may be considered an apomorphy of the group, even if this character is not present in all extant species. A (secondary) transformation in the *Gracilicauda* group, which is certainly monophyletic on the basis of other shared characters, possibly occurred in two steps: first, the fourth instead of the fifth papilla opened dorsally on the bursa velum, and then the seventh instead of the eighth [opened dorsally], such that both papillae four and seven now open dorsally on the velum.

Therefore, the unity of this group [subgenus *Rhabdi-*

¹²⁸ i.e., a pharynx without a median swelling.

¹²⁹ i.e., in different evolutionary steps in lineages to different species.

¹³⁰ In the original text, the word “hypothetical” is used instead of “speculative.”

¹³¹ i.e., with a well-developed and peloderan bursa containing papillae arranged in a flat as opposed to radial arrangement.

¹³² i.e., the lineages to *Rhabditoides* + “*Eurhabditis*” and “*Eurhabditis*” alone (cf. Fig. 24).

¹³³ Again, in most cases investigated within this subgenus, this papilla is actually the phasmid (see Fig. 17B, C).

¹³⁴ “*Schwanzknoten*” or “tail knot” refers to the appearance of this “reduced

10th papilla” (often the phasmid) as a small tubercle at the tail tip. The term was also used by previous authors.

tis], in the sense of a monophyletic group, cannot be proven with the current information. It shall be considered here, with all due caution, as a closed group that has a number of shared characters that are plesiomorphic for "*Eurhabditis*." Typologically, this group has a basal position within "*Eurhabditis*," probably from whence two special lineages emerged, the subgenera *Cephaloboides* and *Pellioiditis*.

A natural division of this species group (a portion of which includes species that are extremely similar) is very difficult, particularly because some species descriptions are too vague. Three main evolutionary lineages can be observed, although it is not obvious how these lineages are related (cf. Fig. 18). In one lineage, a median bulb [of the pharynx] developed and the 10th bursal papilla was reduced to a tubercle on the tail. However, the arrangement of the bursal papillae into three loose groups of three [papillae each] remained largely as in the ancestor. From this branch of the possibly paraphyletic *Maupasi* group (in the narrow sense) that displays many plesiomorphies, a species group containing *R. brassicae*¹³⁵ diverged, which is distinguished by strongly curved and often distally notched spicules and a trough-shaped gubernaculum (Figs. 16, 18). Possibly in this lineage, the female tail was at first cupola shaped, with a long spike, and became conical again in some species by "paedomorphism." Within the group containing *R. maupasi*, males of which are distinguished by a relatively short tail spike, the conical female tail became shorter. By reducing the threadlike tail tip, which is still relatively long in *R. terricola*, for example, the phasmids became positioned relatively far back on the [female] tail, especially in *R. maupasi* itself. The general trend in this group for the first bursal papilla to move a little away from the other ones was especially intensified in *R. acris* and *R. fertilior*. In *R. aberrans* and *R. reciproca*, only eight well-developed papillae are present, two of which are precloacal. In *R. reciproca*, the third papilla was shifted postcloacally and the seventh was lost, whereas in *R. aberrans*, which is not described precisely enough to make such "speculations," the first papilla may have become lost. The tendency to lose the seventh papilla in this group is also displayed by an aberration of *R. maupasi* that I found, in which the seventh papilla was missing on one side. Compared with *R. reciproca*, an additional papilla was shifted posterior to the cloaca in *R. guignardi* (Fig. 17) such that only one papilla is positioned precloacally. The rectal glands at the rectum of females [of the *Maupasi* group] appear to contain two nuclei. In this group several species are found that abandoned the gonochoristic mode of reproduction. The current information does not al-

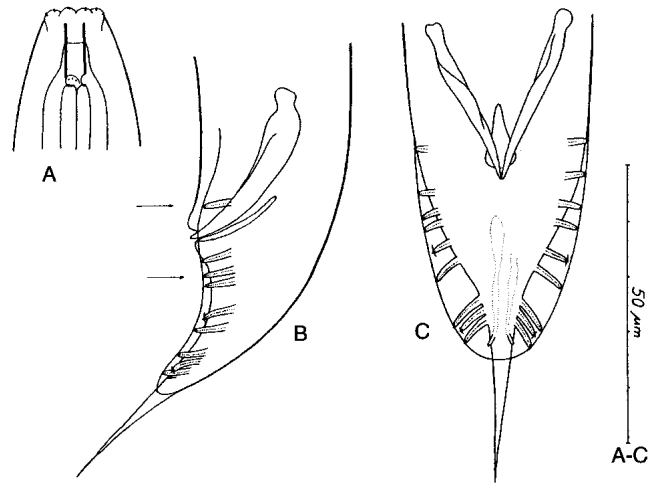


FIG. 17. *Rhabditis (Rhabditis) guignardi* Maupas, 1900. A) Anterior end of male. B) Posterior end of male, lateral view. C) Bursa of male, ventral. Apparently a rare *Rhabditis* species. Found for the first time in 74 years in the "yellow bodies" of a small earthworm from a compost heap in Kiel [Germany].

low one to portray the changes described above for this [*Maupasi*] group in a phylogenetic model.

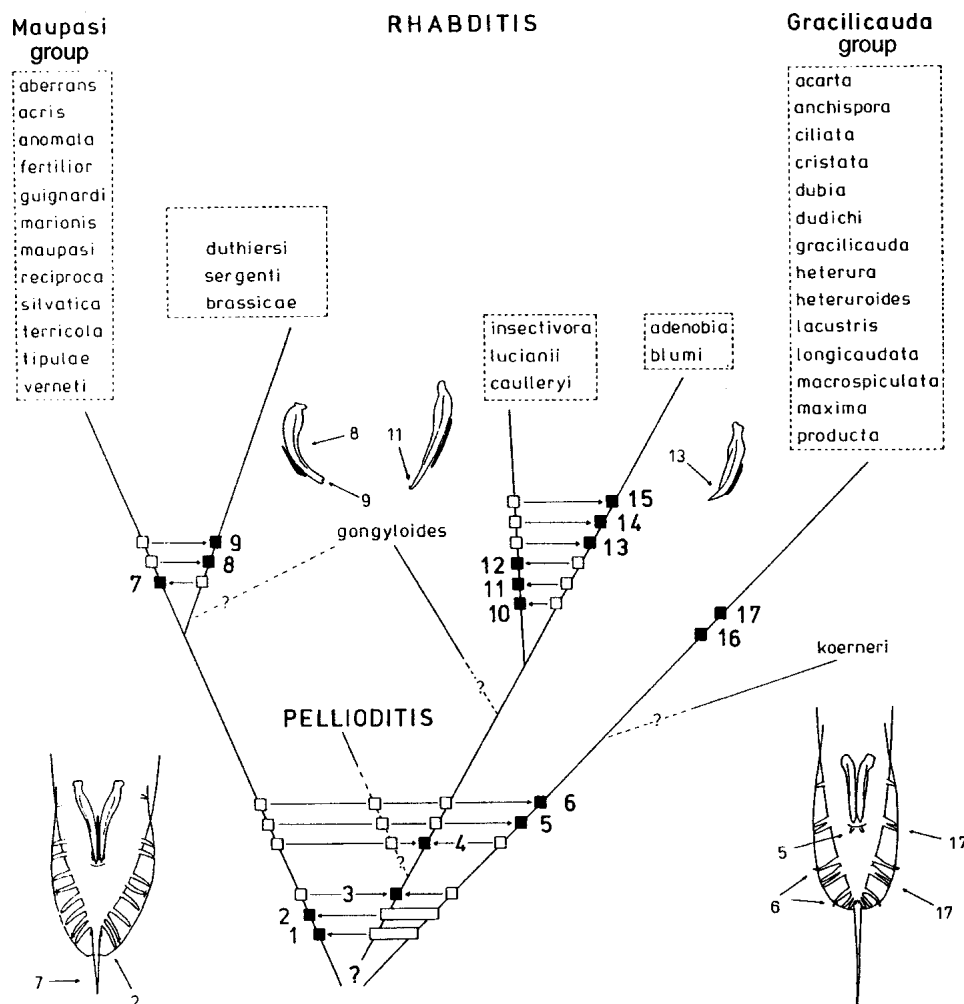
In another evolutionary lineage, it can be established that the spaces between the three precloacal bursal papillae increased equally, whereas the postcloacal papillae moved closer together into two groups of three each. In this group, the anguilluloid pharynx and the conspicuously developed but reduced 10th bursal papillae remain plesiomorphic.¹³⁶ This lineage diverged into two distinct species groups: one containing *R. insectivora* with a long rectum in the female and with spicules distally hooked like a crochet needle (Fig. 18), and the other containing *R. adenobia*, in which the spicules are distally saber shaped (Fig. 18) and the seventh pair of papillae was lost (convergently with that in *R. reciproca*) such that only eight fully developed bursal papillae are present. The last point can be demonstrated because only the fifth and seventh, and not the fifth and eighth, open on the dorsal surface of the velum, whereas the strongly reduced posteriormost papilla (here the ninth) is a homolog of the original 10th papilla.¹³⁷ *Rhabditis gongyloides* may have branched off before the divergence of these groups. According to the illustration of Reiter (1928), the fifth and seventh papillae of *R. gongyloides* open on the dorsal surface of the bursa and only nine papillae are present.¹³⁸ This may indicate that in this evolutionary lineage, the seventh

¹³⁶ The original has "*Schwanzpapillen*" (tail papillae) as Reiter (1928) called both the bursal papillae and the phasmids of the female tail. The "10th papillae" are indeed the phasmids in these species (Fitch, 1997; Kiontke and Sudhaus, 2000).

¹³⁷ Indeed, the cell lineages producing the seventh papilla (in this case ray homolog 8; see Appendix 3) in the other *Rhabditis* species do not occur in *R. blumi*, and the posterior papilla is the phasmid (Fitch and Emmons 1995).

¹³⁸ This species has since been found (W. Sudhaus, pers. obs.). It has nine bursal papillae, and prominent phasmids lie anterior to papilla eight. Papillae four and seven, not five and seven, open on the dorsal surface of the bursa.

¹³⁵ In the original text, this species was called *R. broughtoncocki*, which is a junior synonym of *R. brassicae* (Sudhaus, 1991).



41 FIG. 18. Cladogram of subgenus *Rhabditis* (except for the insufficiently described *R. erschowi*, *R. gurneyi*, *R. succaris*, and *R. uliginosa* [and *R. broughtonalcoki*, listed in the original but now synonymized with *R. brassicarum*]). The numbers denote the following apomorphies: (1) median bulb distinguishable; (2) 10th papilla reduced to a tail knot; (3) papilla arrangement (1+1+1/3+3+r); (4) postcloacal papillae form two closely packed groups of three; (5) males with strong cloacal tubercles; (6) fourth and seventh papillae open dorsally ["outwardly" in original]; (7) tail thread in males very reduced; (8) spicule strongly bent; (9) spicule is distally notched; (10) female with a very long rectum; (11) spicule shaped distally like a crochet needle; (12) tail in both sexes shortened; (13) spicule sabre shaped; (14) seventh pair of papillae lost; (15) haustulum simplified; (16) bursa arrangement (1+2/3+3+r); (17) papillae two and three, five and six, eight and nine, respectively, placed closely together and (partially) fused at their bases. Includes figures from Buckley (1931), Hirschmann (1952), Körner (1954), and Sudhaus (1974c).

papilla was also lost, whereas what was previously the 10th papilla remained conspicuous.¹³⁹ If this is correct, the loss may not have occurred independently from that in the lineage leading to *R. blumi* and *R. adenobia*.

Finally, the species group that includes *R. gracilicauda* must be discussed. This group includes (among others) the majority of species that have been placed by Andrassy (1966) into a separate genus with the unfortunate name *Ablechroiulus*. Likewise, the species that belong in this group are for the most part too little known to facilitate a phylogenetic interpretation. Most of these species remain relatively small. The bursal arrangement changed first (Fig. 18), such that the first papilla moved

sometimes quite far from the next posterior one in a way that always produces a clear arrangement of papillae according to the formula (1 + 2 / 3 + 3 + r).¹⁴⁰ In particular, papillae pairs two and three, five and six, and eight and nine drew closer to the extent that they grow together basally in a fair number of species (*R. cristata*, *R. dubia*, *R. dudichi*, *R. gracilicauda*, and *R. heteruroides*). The lips have been repeatedly (and only in the *Gracilicauda* group) offset in a conspicuous manner at the anterior end; a median bulb is missing or at best weakly developed; the tail thread is usually long in both sexes (a plesiomorphy?), independent from the tail shape in the female; the males always have prominent

¹³⁹ As evidenced by the previous footnote, it is clear that no papillae have been lost in the lineage to *R. gongyloides*.

¹⁴⁰ "r" denotes a small (reduced) papilla that in some of these species is the phasmid (Kiontke and Sudhaus, 2000).

cloacal tubercles that are rather long in *R. dubia*. Perhaps as a result of two independent evolutionary steps (previously discussed [on p. 31]), the fourth and seventh papillae open on the dorsal surface of the bursa velum, whereas in all [other] lineages discussed so far, such a characteristic is always displayed by papillae numbers five and eight (considered here the plesiomorphic state). This behavior of the fifth and eighth papillae occurs despite manifold alterations of the bursa, in particular the postcloacal shift of anterior papillae or the loss of individual pairs of papillae. An example of the first step is *R. longicaudata* [in which the fourth instead of the fifth papilla opens dorsally].

The formation of a cupola-shaped female tail could be viewed as primitive for the *Gracilicauda* group, with a conical shape derived by means of "paedomorphism." In opposition to this [scenario], however, is the fact that conical tails frequently exist only in those species in which the lips are offset at the anterior end, whereas generally in *Rhabditis* [*sensu lato*, i.e., the genus], paedomorphism affects tails and lips to the same extent (see Osche, 1954). In some species, the cuticle of the "prostom"¹⁴¹ is conspicuously reinforced in contrast to the portion of the buccal tube that is enveloped by a very long pharyngeal sleeve. In addition, most of these species (except *R. gracilicauda*) bear groups of bristles on the lips (see Fig. 26), although these were described in a very similar way for *R. brassicae*¹⁴² as well (Buckley, 1931). Andr ssy (1966) observed that these easily missed structures correspond with those of such species as *R. ciliata* which fit quite well with the character assemblage (bursa organization, spicule form, etc.) of the *Gracilicauda* group. It thus seems justified to exclude this species from subgenus *Cephaloboides*, in which it could be classified only with difficulty. I would like to counter the suggestion that the subgenus *Cephaloboides* could be related to such species of the *Gracilicauda* group that have offset lips and a cupola-shaped tail. The reasons are, first, that the 10th bursal papilla is only vestigial in the last-mentioned species in contradistinction to *Cephaloboides*, and second, that the evolution of a radially arranged bursa from here¹⁴³ would have constrained papillae one, four, and seven to take a sublateral position and not papillae one, four, and eight as in *Cephaloboides*.

In the species with offset lips, the terminal bulb is generally angular. The spicules are nearly straight, often distally possessing a small hook, and are usually so close together that they can hardly be separated (Fig. 18). It is therefore difficult in specific cases to decide if the spicules are even fused, as noted for *R. ciliata*, *R.*

dubia, *R. dudichi*, and *R. maxima* as well. In *R. dubia*, the spicules are described as separate by Bovien (1937) and as fused by Osche (1952b).¹⁴⁴ In *R. maxima*, the spicules are parallel and appear to be fused along their entire length, entirely uncharacteristic for *Rhabditis*. The gubernaculum is often forked distally. In two species (*R. maxima*, *R. dubia*), the bursa has been proximally closed, evidently resulting from independent events. The extremely large *R. maxima*, which is aberrant in many features, is also reminiscent of the *Maupasii* group in other features: the blunt conical female tail with very posteriorly positioned phasmids, the development of a median bulb, and perhaps the arrangement of the bursa. In this species, the first papilla is anterior of the bursa (resembling *Pelodera kolbi*), contrasting with that in *R. dubia*, which has a long tail and an anguilluloid pharynx.¹⁴⁵ This [separation between the species] is consistent with the independent evolution of a closed bursa [in the lineages leading to *R. maxima* and *R. dubia*]. *Rhabditis dubia* is closely related to *R. cristata* and *R. dudichi* as suggested by the conspicuous fusion of bursal papillae two with three, and five with six.

After enumerating the important character changes that have occurred in the [evolution of] the *Gracilicauda* group (changes that have not explicitly occurred simultaneously as far as is known), it is evident that a good many apomorphic features in this group must have evolved independently¹⁴⁶ and others have been secondarily reversed. Characteristics such as the reinforcement of the "prostom"¹⁴⁷ portion of the buccal tube and the formation of delicate bristles on the lips have certainly been overlooked from time to time. On the other hand, one must really take into account the secondary loss of such bristles (e.g., in *R. gracilicauda*). The result of such a reversal cannot then be distinguished from the original condition, hindering a clear recognition [of phylogenetic relationships] in this area. The same goes for the alteration of the shape of the female tail. Because of poor knowledge in the details, a finer subdivision of this group is not advisable at this time.

Significant characters have already been referred to that evolved convergently within the subgenus *Rhabditis* itself. The most important features that must be denoted as **convergences**¹⁴⁸ according to the phylogenetic connections sketched above are summed up as follows. A closed bursa has evolved independently in *R. dubia* and *R. maxima*. Both these species are the only

¹⁴⁴ The spicules are fused in *R. ciliata*, *R. dubia*, and *R. dudichi* (W. Sudhaus, pers. obs.).

¹⁴⁵ i.e., a pharynx without a well-developed median bulb.

¹⁴⁶ Whereas the original uses the term "polyphyletically," this term should be reserved for species groups, not for individual characters; the term "independently" has therefore been substituted.

¹⁴⁷ "Gymnostom" in the nomenclature of De Ley et al. (1995).

¹⁴⁸ The term "analogy" used in the original is not specific enough and is here replaced by "convergence," which is a special form of analogy (see Sudhaus and Rehfeld, 1992:85).

¹⁴¹ "Gymnostom" in the nomenclature of De Ley et al. (1995).

¹⁴² The original has *R. broughtonalcoki*, which is synonymous with *R. brassicae* (Sudhaus, 1991).

¹⁴³ i.e., from an ancestral arrangement of the bursal papillae typical for the *Gracilicauda* group.

leptoderan *Rhabditis* species besides *R. dacchensis* that exhibit a closed bursa. The first bursal papilla has been shifted anterior of the proximal end of the spicules independently in *R. gongyloides*, *R. acris*, and the *Gracilicauda* group. Independently in *R. adenobia*/*R. blumi*, *R. reciproca*, and *R. aberrans*, one bursal papilla was completely reduced (usually number seven), so that only eight pairs of bursal papillae are well developed.¹⁴⁹ In contrast to the view of Andr  ssy (1966), bristles on the lips evolved independently in *R. gongyloides*, *R. brassicae*,¹⁵⁰ and the *Gracilicauda* group. A median bulb has been developed in the lineage to the *Maupasi* group and probably repeatedly within the *Gracilicauda* group. The female tail became dome shaped, possibly several times, within the *Gracilicauda* group as well as in *R. brassicae*.¹⁵¹

o. Subgenus Pellioditis Dougherty, 1953

By possessing a large pharyngeal sleeve, normally three or five warts on each metarhabdion (with the exception of *R. dolichura* and *R. rara*, see below [p. 39]), a median vulva, three precloacal papillae on the open bursa, and separate spicules, the members of the subgenus *Pellioditis* are to be viewed as typical representatives of "Eurhabditis." They present an exception in but one important character, namely in their peloderan (tail-encompassing) bursa form. Furthermore, only nine bursal papillae are nearly always found; a short 10th papilla (designated the "phasmid") still appears¹⁵² on the tail only in the clade containing *R. papillosa*. (Ten papillae have also been described for *R. incilaria*, and *R. fruticicolae*¹⁵³ supposedly bears 11 pairs of bursal papillae and distinct phasmids (Kreis, 1967), an entirely unusual situation for Rhabditinae. Assuming that the observation has not been erroneous, the only possible explanation, by comparison with the similar *R. incilaria*, is that a duplicated papilla has been inserted into the interesting region between the fifth and seventh papillae.) Both of these characters (the peloderan bursa and extensive reduction of the 10th papilla, with regard to which *R. fruticicolae* and *R. incilaria* cannot be considered due to insufficient knowledge) define the only known **apomorphies** for this group. The ancestral form of *Pellioditis* furthermore possessed an anguilluroid pharynx¹⁵⁴ with a double haustulum at the terminal bulb, an H-shaped excretory system, a conical and relatively short female tail, an arrangement of the bursal papillae as (3/ 3+3+ r) or (1+1+1/ 3+3+ r) in which the fifth and the dorsally pointing eighth papilla

opened on the dorsal surface of the bursa velum, dagger-shaped spicules, and a gutter-shaped gubernaculum. The body size of *Pellioditis* species varies between 298 and 3,400 μm ; some forms (like *R. rara*, Fig. 19) are secondarily diminutive.

On the basis of the exceptionally similar pair of species *R. dolichura* and *R. pseudodolichura*, Osche (1952b: 215) attempted to derive the *Rhabditis* species that have metarhabdion warts from the *Caenorhabditis* group by a degradation of their two metarhabdion teeth. Other than the two teeth per metarhabdion in *R. dolichura* and five warts per metarhabdion in *R. pseudodolichura* and the occurrence or absence, respectively, of waving juveniles, the differences between these two species are so minute that one could doubt that these are really

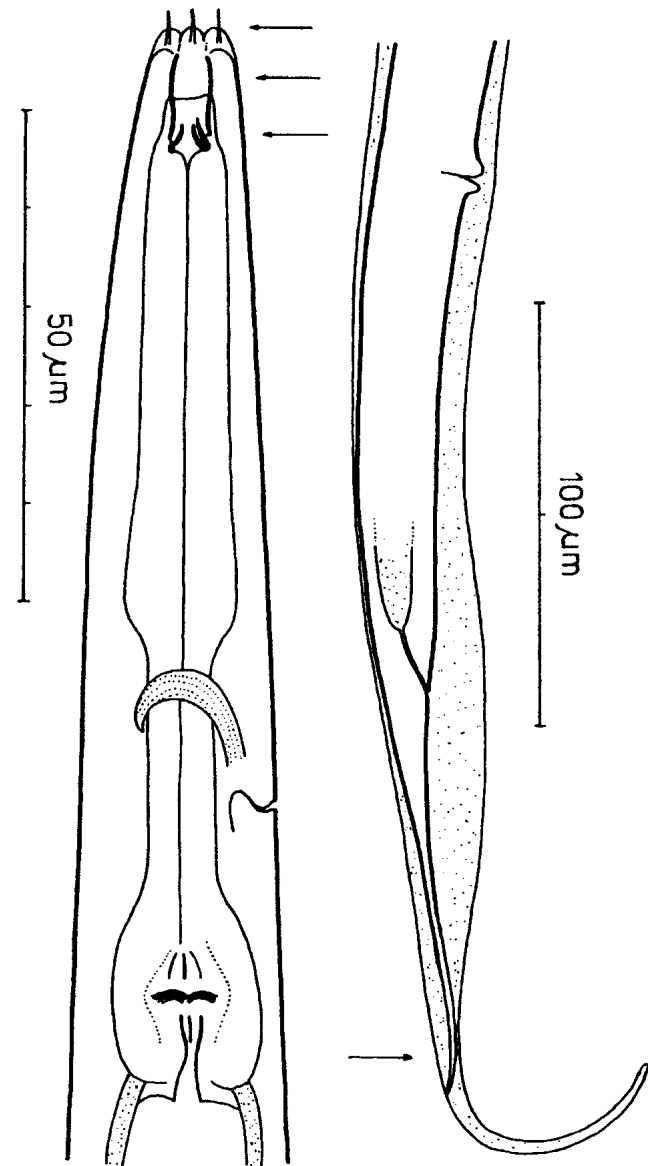


FIG. 19. *Rhabditis* (*Pellioditis*) *rara* K  rner, 1954. A) Anterior end, buccal tube, and pharynx of the female form. B) Vulval region and tail (at the last molt).

¹⁴⁹ See footnote 137 concerning additional cellular evidence for this statement.

¹⁵⁰ The original has the synonymous *R. broughtonalcocci*.

¹⁵¹ The original has the synonymous *R. broughtonalcocci*.

¹⁵² By using "still appears," the author connotes that a 10th papilla in these species is conserved from the pattern in the stem species.

¹⁵³ *R. fruticicolae* Kreis, 1967, is now interpreted as a synonym of *R. incilaria* Yokoo and Shinohara, 1955.

¹⁵⁴ i.e., without a median bulb (see Fig. 19).

different species.¹⁵⁵ To put [these two species] into two different subgenera based on their different metarhabdion structures seems absurd. Whether this implies an easy transformation from *Caenorhabditis* to *Pellioiditis* (as Osche suggested) is certainly debatable (see below [pp. 36, 43]). The reverse transformation, namely the derivation of *Caenorhabditis* from *R. dolichura* ancestors, likewise seems improbable if one considers the entire suite of characters. It is also here that yet another convergence is observed: *Rhabditis oxyerca* (from subgenus *Cephaloboides*) also bears two teeth on each metarhabdion.¹⁵⁶ The problem of convergence will again be discussed in Chapter II in the section (Section 3) on the variation of metarhabdion structure.¹⁵⁷

The first important question considered here is whether the peloderan bursa of the subgenus *Pellioiditis* within "*Eurhabditis*" could not be a primitive state, especially since a hypothetical ancestor with a peloderan bursa is presumed for the genus *Rhabditis*. In this context, possible similarities with subgenus *Cruznema* need to be verified: *Cruznema* has a small pharyngeal sleeve, still separated spicules, and an open peloderan bursa with only nine bursal papillae. A connection between the subgenera *Pellioiditis* and *Cruznema* is refuted, however, by the (2 / 2 + 5) arrangement of the papillae in *Cruznema*, which allows only with great difficulty a transition to the (3 / 3 + 3) arrangement of papillae that is normal in *Pellioiditis*. Furthermore, the reduction to nine bursal papillae by itself cannot be considered a shared derived character of these two groups since 10 pairs of fully developed papillae must be postulated in basal "*Eurhabditis*" groups, as can be shown for the *Papillosa* group (at least as vestiges).¹⁵⁸ A close relationship with *Cruznema* can thus be rejected. A similar situation arises from a comparison of *Pellioiditis* with the subgenus *Xylorhabditis*, which also exhibits separate spicules and only nine bursal papillae; although the ninth papilla has already been strongly reduced, the papilla arrangement characteristic of *Pellioiditis* species could be easily

derived from the kind of bursal arrangement exhibited in *Xylorhabditis*: (2 / 1 + 3 + 3).

The same objections may be levied against a close connection between *Pellioiditis* and *Caenorhabditis* (cf. p. 25), which also presents no evidence of a former 10th bursal papilla.¹⁵⁹ At any rate, the bursal organization (2/1+3+3) of species in part of the *Caenorhabditis* group (including *R. elegans* and *R. remanei*), in which the third papilla is separated from the adjacent triplet of papillae, easily allows the origin of three precloacal papillae and the *Pellioiditis* bursa (3/3+3) by an antieriad shift of the third papilla (cf. *R. perrieri*). A similar hypothetical stage must also be inferred for the ancestor of *Rhabditoides* and "*Eurhabditis*," but (in contrast to *Caenorhabditis*) still with an open bursa and a posterior quartet of papillae: (2/1+3+4).

Although *Pellioiditis* cannot be derived from any of the extant peloderan *Rhabditis* subgenera without great difficulty, nothing has yet been presented against the possibility that a peloderan bursa could be just a plesiomorphy for "*Eurhabditis*." However, a second important character of *Pellioiditis* argues against this possibility, namely the reduction of the 10th bursal papilla. The primitive state of a peloderan bursa could be demonstrated only if at least one species of this group had all 10 bursal papillae fully developed, as is the case in other "*Eurhabditis*" groups. (Perhaps such representatives were found in *R. inciliaria* and *R. fruticicolae*.¹⁶⁰ It was already pointed out, however, that these species are not sufficiently known and it is suspected that they show a secondary increase in papilla number.) Since this is not the case, *Pellioiditis* is connected to subgenus *Rhabditis* with its trend toward the reduction of the tail tip and the 10th papilla as a final step in this string of reductions. The development of a peloderan bursa in *Pellioiditis* is thus in all probability a secondary change in which the trend toward the reduction of the tail tip finds its conclusion. An argument in favor of this possibility is that a leptoderan tail is observed as a rare aberration in representatives of *Pellioiditis* (see below [the following two paragraphs]).

Once it has been recognized that the absence of a well-developed 10th bursal papilla and the peloderan shape of the bursa are products of a process of reduction, the question is raised whether such a reduction could have arisen convergently within the subgenus *Rhabditis* several times. If so, the *Pellioiditis* group would not be a monophyletic unit. Independent origins for a peloderan bursa must be considered, especially since there are indications that such a stage can nearly be reached within the variation exhibited by extant species

¹⁵⁵ Enough additional differences (body color, corpus shape, female tail, lateral field) have now been found to distinguish these two species easily (see Sudhaus and Hooper, 1994).

¹⁵⁶ "Metastom" is used in the original.

¹⁵⁷ The translation of this section is on p.45.

¹⁵⁸ In 1976, the author was fairly certain that 10 bursal papillae was a plesiomorphic state not only for "*Eurhabditis*" but also for Rhabditidae. Because one of these papillae is the phasmid in every species with 10 papillae investigated so far, it would be more accurate to separately trace the evolution of the phasmids and the other papillae, which can be differentiated as the "ray" papillae (see Appendix 3). The "reduction" to nine bursal papillae usually reflects a change in the conspicuousness and (or) placement of the phasmid, although in some species (e.g., *R. blumi*), a ray papilla has been lost. In this view, nine ray papillae could be plesiomorphic for Rhabditidae (and for "*Eurhabditis*"). Alternatively, because species in the related families Panagrolaimidae and Cephalobidae have fewer than nine "genital" papillae (7-8) (Kiontke and Sudhaus, 2000), the plesiomorphic state for Rhabditidae could have been fewer than nine. In any case, a similarity in the number of papillae shared between *Cruznema* and *Pellioiditis* still cannot be used to support a close relationship between these groups, since this similarity is due to plesiomorphy. However, there are further complications emerging in this story. First, one of the nine bursal papillae described for *R. (Cruznema) tripartita* is the phasmid, so there are only eight ray papillae. Second, preliminary molecular analyses suggest that *Cruznema* is actually related to the "*Eurhabditis*" group (see Appendix 1).

¹⁵⁹ It must be recognized, however, that the inconspicuous phasmid of *Caenorhabditis* is clearly homologous to the slightly extended phasmid (i.e., 10th bursal papilla) of *Pellioiditis*.

¹⁶⁰ *Rhabditis fruticicolae* Kreis, 1967 is interpreted as a synonym of *R. inciliaria* Yokoo and Shinohara, 1955.

[45] (*R. insectivora*) in the leptoderan subgenus *Rhabditis*. The possibility that a peloderan bursa could have arisen several times from a leptoderan one is further suggested by a certain similarity between some of the species or groups of species placed in *Pellioiditis* and those that have been placed in the subgenus *Rhabditis*. In this regard: (1) the species of the *Dolichura* group and those of the *Insectivora* group share the anguilluloid pharynx, the similar bursal arrangement, and (apomorphically) a long rectum in the female.¹⁶¹ (2) A great similarity seems to me to exist between *R. reciproca* (from the *Maupas* group) and the peloderan *R. seurati*, as far as this can be determined from the inadequate and unillustrated description of *R. seurati* (correspondences appear in the anomalous bursal arrangement [2 / 3 + 1 + 2], the particularly thick cuticle, the measurements, the non-gonochoristic mode of reproduction, and the rare occurrence of “dwarf males”). Leptoderan individuals have been observed as aberrations in *R. seurati* (Maupas, 1916). (3) In the species group that includes *R. buetschlii*, the fourth and seventh bursal papillae open dorsally on the bursa velum,¹⁶² whereas the fifth and eighth behave this way in (several) other species of *Pellioiditis*, a feature that must certainly constitute a plesiomorphy (especially considering the equivalent situation in subgenus *Rhabditis*). This special bursal arrangement of the *Buetschlii* group is reminiscent of the *Gracilicauda* group of subgenus *Rhabditis*, with which these species also share a relatively long female tail or (as in *R. buetschlii* itself) a cupola-shaped tail with a long tail spike. Such differences exist between these groups with regard to other characters (bursal organization, shape of the buccal tube, construction of the pharynx, possibly the bristles on the lips, and shape of the spicules) that a common phylogenetic¹⁶³ basis appears unlikely. It also appears extremely unlikely that a peloderan bursa form could have been derived from very long-tailed forms (*Buetschlii* group).

If a peloderan bursa evolved convergently within “*Eurhabditis*,” it might be expected that such a derived stage was reached at different times during phylogenesis. If so, the recent evolution of peloderan species would allow a greater probability of the disjunctive, atavistic appearance of leptoderan bursae within *Pellioiditis*. There is hardly any reliable piece of evidence for such an atavism. Only Maupas (1916), a very careful observer who is held in high esteem, noticed “leptoderan” individuals as aberrations in *R. seurati* and *R. dolichura*.¹⁶⁴ Such atavisms demonstrate quite clearly that *Pellioiditis*

species descended from leptoderan ancestors.¹⁶⁵ As already discussed with regard to other characters, both of these species support the possibility that a direct connection exists between them and leptoderan species of subgenus *Rhabditis* (in the *Maupas* or *Insectivora* species groups).

The significant question whether a peloderan bursa could have evolved convergently within leptoderan lineages of subgenus *Rhabditis* cannot be answered yet with certainty because other definite apomorphies are lacking for the groups of species that have been united as *Pellioiditis*. The only indisputable case of an independent origin of a peloderan bursa within “*Eurhabditis*” is in subgenus *Cephaloboides* in the closely related species *R. nidrosiensis* and *R. valida* (p. 29).¹⁶⁶ After only a cursory investigation, *R. valida* especially would have been classified with *Pellioiditis* (as occurred previously with *R. nidrosiensis*), demonstrating the difficulty in obtaining insightful information in this field of microsystematics. It is hoped that painstaking comparisons of species within subgenera *Pellioiditis* and *Rhabditis* may yet settle the question whether a peloderan bursa evolved independently¹⁶⁷ within “*Eurhabditis*.” At the moment I think it is most probable that a peloderan bursa evolved very rarely within this taxonomic group and most (or even all) of the species that have been united as *Pellioiditis* are in fact a monophyletic unit. Here this group will be sustained, even though its unity cannot be proven, because there are even fewer arguments for dissolving the group. In particular, this long discussion should draw attention to the potential for errors not considered until now.

The next question deals with the precise position of *Pellioiditis* in the “*Eurhabditis*” system. In this regard, the question is whether this group branches off outside of, or from within, subgenus *Rhabditis*, which in the latter case would only be paraphyletic. The procedure of exclusion can be taken here: *Pellioiditis* cannot be derived [46] from the *Maupas* group because the pharynx of these species has already developed a median bulb. Likewise, it cannot be derived from the *Gracilicauda* group, an argument supported by the organization of the bursa and the positioning¹⁶⁸ of papillae four and seven in the *Gracilicauda* group. On the other hand, there is a good resemblance between *Pellioiditis* and the species of the

¹⁶¹ Both of these groups (*Insectivora* and *Dolichura*) have been united under the subgenus *Oscheius* within the genus *Rhabditis* by Sudhaus and Hooper (1994) with the consequence that *Pellioiditis* in the original sense is not monophyletic.

¹⁶² In the original, these papillae were described as “pointing outwardly.”

¹⁶³ i.e., monophyletic.

¹⁶⁴ Such aberrations have since been found in *R. dolichuroides* and one closely related unnamed species of the *Dolichura* group (Sudhaus and Hooper, 1994: 526). Note also that leptoderan mutants in *C. elegans* have been induced chemi-

cally and map to several different genetic loci (Y. Yang, T. Del Rio, C. Nguyen, and D. Fitch, unpubl.).

¹⁶⁵ An alternative interpretation might simply be that leptoderan bursae are derivable from peloderan bursae. If several loci affect the same morphological character, variants that might appear to be “atavisms” may not necessarily arise from reversals of evolutionary changes, but could involve novel changes (as indeed suggested by a cell-level study of tail tip evolution; D. Fitch, 2000). However, as demonstrated here, the body of evidence strongly suggests multiple independent changes to both leptoderan and peloderan forms.

¹⁶⁶ *R. valida* may actually belong to the *Pellioiditis* group.

¹⁶⁷ The word “independently” has been substituted for “polyphyletically” in the original text, since the latter term should be used only for groups and not for characters.

¹⁶⁸ The original had “behavior.”

Insectivora and *Adenobia* groups, especially with respect to the organization of the bursa and the long papillae on the tail¹⁶⁹ as well as plesiomorphies such as the anguilluloid pharynx. Moreover, *R. insectivora* is a species that occasionally produces individuals that appear nearly peloderan (Körner, 1954, and pers. obs.). Certain features shared between species of the *Insectivora* group and particular representatives of *Pellioiditis* (such as the short buccal tube in the *Papillosa* group or the long rectum in the females of the *Dolichura* group¹⁷⁰) must, however, be interpreted as convergences if reversions [in other characters] should not be considered.

There is thus a certain probability that *Pellioiditis* is an offshoot of the branch leading to the *Insectivora* and *Adenobia* groups and took part in their common evolution, though without showing the special differentiations of either of these groups. The alternative possibility, that *Pellioiditis* had already diverged earlier, before the origin of subgenus *Rhabditis* (which would require that the correspondences with the *Insectivora/Adenobia* branch—in the organization of the bursa—be explained as convergences), can be discussed only with difficulty insofar as no clear apomorphies can be shown for subgenus *Rhabditis*. The only candidates, namely the extensive reduction of the 10th papilla and the dorsal opening of papillae five and eight (see p. 31), were present in the progenitor of *Pellioiditis* and must therefore be postulated for the common ancestor of *Pellioiditis* and *Rhabditis*. With the current state of knowledge, I maintain that it is most probable that *Pellioiditis* is the sister group of the *Insectivora/Adenobia* group and therefore that the subgenus *Rhabditis*, consisting of three distinct evolutionary lineages, is a paraphyletic group (see Fig. 18). In view of the very hypothetical nature of this statement, however, I do not feel that it is appropriate yet to dissolve the subgenus *Rhabditis*.

A more detailed subdivision of the subgenus *Pellioiditis*, which is characterized by a peloderan bursa, depicts four different species groups (see Fig. 22). (1) The *Papillosa* group still possesses a vestigial 10th papilla (or “tail” papilla)¹⁷¹ and also remains primitive in its bursal arrangement as $(1 + 1 + 1 / 3 + 3 + r)$ (Fig. 20). In *R. fruticicolae* and *R. incilaria*, which should probably be placed in this group, it appears that the number of papillae in the first postcloacal group increased such that *R. fruticicolae* with its species-specific pattern of 11 pairs of bursal papillae does not fit within the typical pattern of Rhabditinae (see footnote 83). (A thorough investigation of these species will hopefully provide an answer to the question whether the last papilla has been reduced in the evolution of *Pellioiditis* as supposed

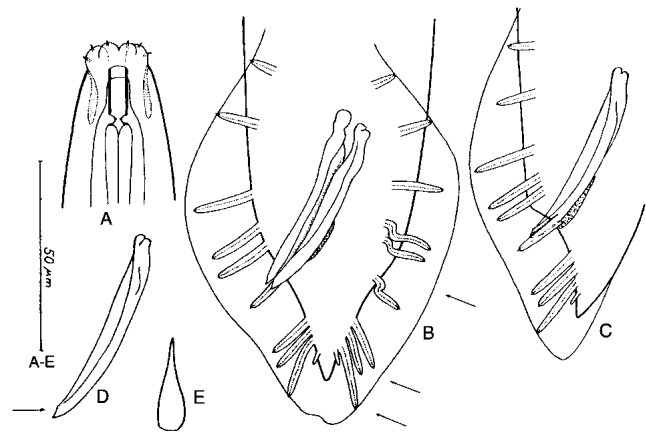


FIG. 20. *Rhabditis (Pellioiditis) hermaphrodita* (Schneider, 1859). A) Anterior end of male. B) Posterior end of male, ventral view. C) Posterior end of male, lateral view. D) Spicule, lateral view. E) Gubernaculum, ventral view. This represents the fifth time this species has been found—this one in forest soil in Corsica, in which were three slugs that died during transport. A rare “snail nematode” [associated with slugs].

here.) The buccal tube in the species of the *Papillosa* group is short and wide and provided with a large glottoid apparatus. A median bulb is present. The body size has increased (902–3,400 μm); the spicule length is 54–85 μm . In *R. pellioidis* males, no tail [tip] papillae [i.e., 10th papillae] can be demonstrated. These papillae remained in the other species; most of the postcloacal papillae do not reach the margin of the bursa. The phasmids of the females are also quite pronounced. With their cupola-shaped female tails, *R. papillosa*, *R. fruticicolae*, and *R. incilaria* differ somewhat from other members of subgenus *Pellioiditis* (Fig. 22); this feature is found again only in *R. buetschlii*, though shaped a bit differently. One may assume, however, that the stem species of the group including *R. papillosa* had a cupola-shaped tail that was reversed [to a conical female tail] by pedomorphism in *R. neopapillosa*¹⁷² and its complementary species *R. hermaphrodita* (see Osche, 1954). *Rhabditis mairei* is but insufficiently known; it shows resemblances with *R. pellioidis* and *R. papillosa*.

(2) The following three species groups all have entirely lost the 10th papillae,¹⁷³ and only in *R. bengalensis* does the stub-shaped papilla remain as a remnant (though a similar situation is found in some other species as atavisms; e.g., *R. typica*, *R. pellioides*). It is by no means certain that this loss occurred only once.¹⁷⁴ Using reductions for ascertaining phylogeny is problematic in general. With respect to bursal organization (1 +

¹⁶⁹ i.e., the phasmids.

¹⁷⁰ The elongated female rectum was interpreted as a synapomorphy for the *Insectivora* and *Dolichura* groups and thus an apomorphy for the subgenus *Oscheius* (Sudhaus and Hooper, 1994).

¹⁷¹ This papilla is actually the phasmid (D. Fitch, unpubl.; Kiontke and Sudhaus, 2000).

¹⁷² In the original, the term “Folgeart” was applied to *R. neopapillosa* and *R. hermaphrodita*, implying a concept of a speciation event that has since been revised.

¹⁷³ These sensilla, the phasmids, have not actually been lost, but are inconspicuous instead of papilliform.

¹⁷⁴ “Monophyletically” is applied to this character loss in the original text, but such a term should be reserved for species groups, not characters.

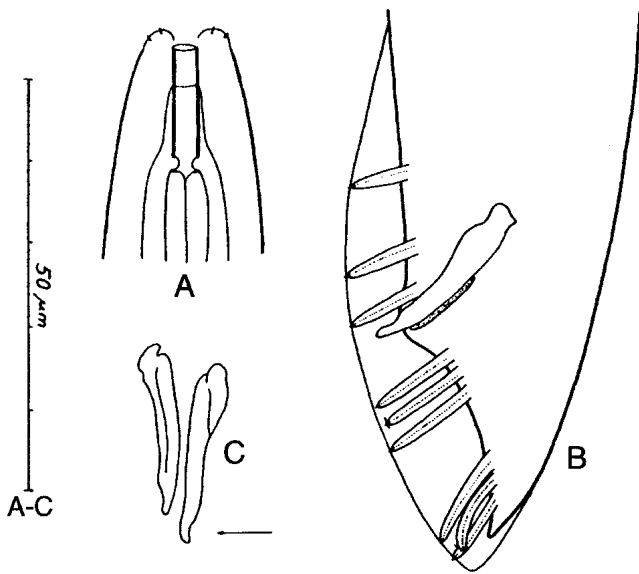


FIG. 21. *Rhabditis (Pellioiditis) sechellensis* Potts, 1910. A) Anterior end of male. B) Posterior end of male, left lateral view. C) Spicule, ventral view. Found for the first time in 62 years in a blue-algal covering on a moist boulder in Freiburg (Schloßberg) [Germany].

1 + 1 / 3 + 3), the *Dolichura* group must be closely connected with the *Papillosa* group. This feature, as well as the retained anguilluloid pharynx in this group, must be regarded as plesiomorphic. In the species of the *Dolichura* group, the rectum of the females is nearly always very long and conspicuously expandable in the proximal portion like a bladder¹⁷⁵ (see Fig. 22). In the view taken here, the rectum must have been shortened again in *R. rara* (Fig. 19) and *R. carpathica*. The dagger-shaped, 26–39 μm -long spicules are swollen distally and rounded like a probe (Fig. 22). Closely related (if not identical) are *R. pseudodolichura* and *R. sechellensis* (Fig. 21), whose spicules always seem to be of different length and show a small notch at the distal and ventral edge. In the lineage to *R. dolichura* and *R. rara* (Fig. 19), two pointed and hollow teeth have evolved on each metarhabdion, the apical lip sensilla are setiform and point forward, and the buccal tube is relatively wide. In *R. carpathica*, metarhabdion structures are unknown, but metarhabdion teeth might be expected, since this species is very similar to *R. rara* with regard to the wide buccal tube, which has walls that are slightly curved like the walls of a barrel. *Rhabditis bengalensis* should be one of the most basally diverged species of this group. Moreover, it is the only known gonochoristic species of this group.

(3) The following two species groups (like the *Papillosa* group) have formed a median bulb. It is not certain if this character can be interpreted as a synapomorphy. The group that includes *R. marina* and *R. typica* (i.e.,

the *Typica* group) unites those species whose precloacal papillae (primarily) were arranged as 1 + 2 (Fig. 22), thereby following an evolutionary trend that can be observed repeatedly within *Rhabditis* (see also the *Gracilicauda* group). Tail [tip] papillae [i.e., 10th papillae] in the male can arise atavistically (*R. typica*). Of the several uncertain species that presumably belong to this group, *R. viguieri* has only one precloacal papilla due to a [posterior] shift in papilla positions.

(4) The last species group (the *Buetschlii* group), which includes *R. buetschlii*, contains three species that are quite similar with respect to the organization of the bursa as (3 / 3 + 3), in the structuring of the spicules, and the (apomorphic) formation of a very long female tail (Fig. 22). A median bulb is developed, the metarhabdions bear five or two (*R. friderici*) warts, precloacally there is a group of three closely spaced papillae, and papillae one, four, and seven open dorsally on the bursa velum with number seven being turned dorsad. This last feature and the long, whip-like female tail are reminiscent of the *Gracilicauda* group.

The following special structures within the *Pellioiditis* group have not yet been addressed. Convergently in *R. marina* and *R. bengalensis*, the tail terminus of juveniles and females is slightly clavate, which is presumably an adaptation to the same habitat. Similar tails, though less consistent, have also been observed as aberrations in cultures of *R. neopapillosa* by Osche (1954). How far this could be an expression of cryptotypic specification for a cupola-shaped tail that was retained in the genome is not known, at least as far as *R. bengalensis* of the *Dolichura* group is concerned, because there is not a trace of cupola-shaped tails in this group. The spicules are distally forked in *R. marina* and *R. neopapillosa*; they have a dorsal prong in *R. marina mediterranea* and *R. buetschlii*. The residual males of *R. viguieri* and *R. seurati* are only about half the size of the [hermaphroditic] females.¹⁷⁶ Undoubtedly, secondary dwarfism can be observed in *R. rara* and *R. carpathica*.

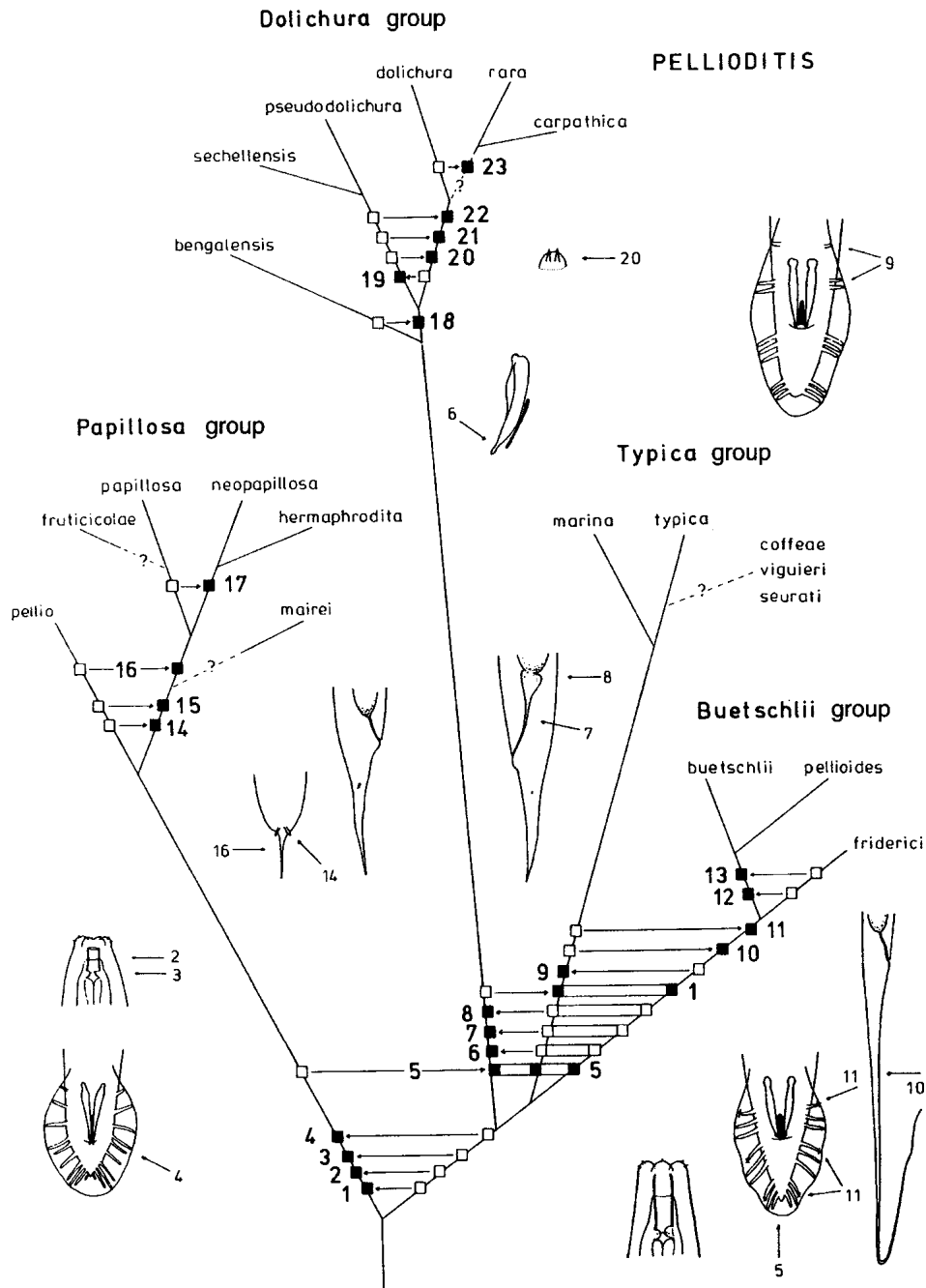
p. Relationships within the "Eurhabditis" group

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A summary of the preceding sections (k–o) is depicted in the following phylogenetic diagram (Fig. 23), which presents what I consider to be the most likely phylogenetic connections within the extensive group "Eurhabditis" with its five subgenera accepted in this work. Two clear evolutionary lineages can be distinguished. First, in the lineage leading to *Cephaloboides*, the tail thread has apparently been lengthened or has remained long in both sexes, the bursa arrangement has become fixed as (1 + 2 / 1 + x), a median bulb has become differentiated, and the bursa has become more and more reduced and radially organized. The original

¹⁷⁵ In the original text, Sudhaus used the term "pre-rectum" for this bladder-like part of the rectum. It is left out here because for other nematodes, this term specifically refers to a posterior subdivision of the intestine.

¹⁷⁶ The original text just encloses "females" in quotation marks to indicate that these individuals of female morphology are generally selfing hermaphrodites.



49 FIG. 22. Cladogram of *Pellioditis* (except *R. incilaria* and *R. voighti*). The numbers denote the following apomorphies: (1) median bulb formed; (2) buccal tube shortened and widened; (3) very large glottoid apparatus; (4) fourth and fifth papillae closely apposed; (5) 10th papilla entirely reduced; (6) spicule distally swollen and probe-like; (7) female rectum very long; (8) female rectum widened like a bladder; (9) papilla arrangement (1+2/3+3); (10) female tail threadlike and long; (11) first, fourth, and seventh papillae open dorsally ["outwardly" in the original] (the seventh bent dorsally); (12) spicule with a dorsal velum or dorsal thorn; (13) buccal cavity prismatic; (14) female phasmids very distinguishable; (15) most postcloacal papillae fail to reach the edge of the bursa; (16) female with cupola-shaped tail (?); (17) female tail secondarily conical; (18) nongonochorism; (19) spicules of uneven length; (20) two hollow, pointed teeth per metarhabdion ["metastom" in original]; (21) apical lip sensilla bristle-like; (22) relatively broad buccal cavity; (23) buccal tube with curved walls like a barrel. — Depiction using figures from Hirschmann (1952), Osche (1952b, 1954), Mengert (1953), and Sudhaus (1974a, 1974c).

10 bursal papillae have been retained. On the other hand, in the lineage leading to *Pellioditis*, the tail thread presumably has first been shortened, the 10th [papilla] has become more reduced, and the fifth and eighth papillae open on the dorsal surface of the bursal velum.

Here, the primitive anguilluloid pharynx and lepto-deran (but not radially arranged) bursa have been retained. In the *Cephaloboides* lineage, a divergence has resulted in [one group of] species with elongated, slender bodies with long whip-like tails in both sexes and a

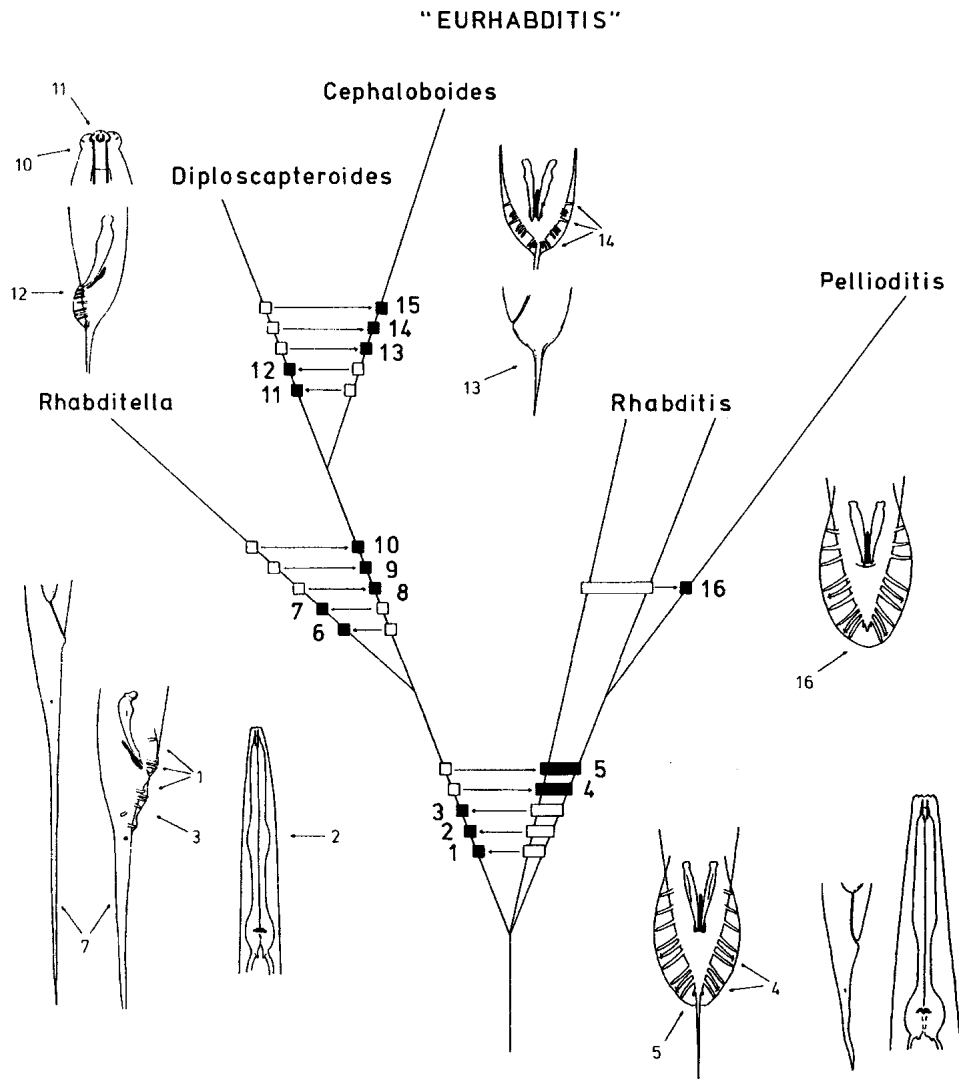


FIG. 23. Cladogram of "Eurhabditis." The numbers denote the following apomorphies: (1) papilla arrangement (1+2/1+x); (2) median bulb distinguishable; (3) trend toward reduction and radial organization of the bursa; (4) fifth and eighth papillae open dorsally on the bursa ["penetrate outwardly" in the original]; (5) reduction of the 10th papillae to tail papillae; (6) long, slim body shape; (7) whip-like tail in both sexes; (8) cylindrical body shape; (9) thickening of the cuticle; (10) trend toward offset lips; (11) lip margins heavily cuticularized; (12) all bursal papillae lie postcloacally; (13) cupola-shaped tail in both sexes; (14) papillae one, four, and eight lie in a sublateral position; (15) thick cuticle; (16) bursa peloderan. Includes figures from Reiter (1928), Cobb (1929), Osche (1952b), Körner (1954), and Timm (1959). The two lineages that lead to the subgenus *Rhabditis* suggest that it is presumably a paraphyletic group.

strongly reduced bursa (e.g., the subgenus *Rhabditella*), and [another group of] rather stout,¹⁷⁷ shorter-tailed species with thickened cuticles and possibly offset lips. The latter lineage forked once more to produce the subgenus *Diploscapteroides*, characterized by strongly cuticularized lip edges and a shift of all bursal papillae to positions posterior of the cloaca, and the subgenus *Cephaloboides*, the representatives of which are distinguished by a cupola-shaped tail in both sexes and the special bursa arrangement with papillae one, four, and eight placed sublaterally. Second, in the other evolu-

tionary lineage (i.e., the *Pellioditis* lineage¹⁷⁸), three different evolutionary directions can be observed [i.e., the *Maupasi/Brassicacae* group, the *Insectivora/Adenobia* group, and the *Gracilicauda* group], which still did not lead to clearly distinct types [except *Pellioditis* itself]; all are therefore classified within subgenus *Rhabditis*. At most, one long-tailed group (the *Gracilicauda* group) and two short-tailed groups (the *Maupasi-Brassicacae*¹⁷⁹ and the *Insectivora-Adenobia* groups) can be distin-

¹⁷⁸ This could be misleading; it would be better to call this the *Rhabditis-Pellioditis* lineage.

¹⁷⁹ The original text uses "*Broughtonalcocci*" in the name of this species group, but *R. broughtonalcocci* is a junior synonym of *R. brassicae* (see Sudhaus, 1991); the group name was thus also changed to reflect this synonymization.

¹⁷⁷ "Walzenartig" is used in the original text, meaning "like a fat cylinder."

guished. Presumably, the lineage leading to the subgenus *Pellioiditis*, which is characterized by the evolution of a peloderan bursa, branched off from the *Insectivora-Adenobia* lineage within the subgenus *Rhabditis*, which is thereby paraphyletic.

5. Relationships of the groups within Rhabditinae sensu lato

The following characters of the Rhabditinae appear to be **symplesiomorphies** by comparison and therefore are of no value for assessing connections between the different groups (genera, subgenera, species groups): closed lips that are not offset at the anterior end, absence of a glottoid apparatus as well as a pharyngeal sleeve and a median bulb, differentiation of a transverse ridging in the inner wall of the corpus, a double haustulum [posterior of the valves] in the terminal bulb, an H-shaped excretory system, a posteriorly situated vulva with a correspondingly unpaired gonad, a (short) conical female tail, an open bursa with 10 bursal papillae (two of which are situated precloacally), separate spicules, paired blind sacs at the vas deferens, and a relatively small body size (less than 1 mm). Osche (1952b: 210) previously incorporated nearly the same characters into one form, thus obtaining a hypothetical "*Urform*"¹⁸⁰ of the Rhabditinae.

In individual cases, some of the traits mentioned could even turn out to be [secondarily] derived, namely cases in which the reversibility of the formation of a character could be established by comparison with immediately related species. Such reversibility can be shown to have occurred repeatedly within *Rhabditis* by paedomorphosis; e.g., in the evolution of lips that are not offset from lips that were offset and of conical female tails from cupola-shaped tails (cf. Osche, 1954). By loss or change in position of papillae, a secondary change from three back to two precloacal papillae is possible (*R. aberrans*, *R. reciproca*, *R. seurati*). A glottoid apparatus nearly disappears in *R. stammeri*, and body size is secondarily reduced (cf. *R. rara*). Such secondary "simplifications" (reversals) cannot always be distinguished from the original character formations, but are revealed only in a group of very closely related species.

According to my ideas about the evolution of the bursa, the hypothetical ancestor of the Rhabditidae primarily¹⁸¹ possessed a leptoderan bursa with a tail thread that jutted beyond the velum. It is difficult to resolve the question whether the leptoderan bursa of extant species ("*Eurhabditis*," *Rhabditoides*, and possibly *Mesorhabditis*) is a primitively retained character. In support of this notion, there are a few species within the

Mesorhabditis group¹⁸² that remain primitive and apparently have the leptoderan type of bursa. The leptoderan *Rhabpanus ossicula* likewise exhibits many plesiomorphic characters. Inconsistent with this hypothesis¹⁸³ is the fact that the most basally derived groups of Rhabditinae¹⁸⁴ have an exclusively peloderan bursa (e.g., *Parasitorhabditis*, *Protorhabditis*, and others such as *Cruznema* and *Teratorhabditis* that have such primitive features as a posterior vulva). The arguments against [a stem species bearing a leptoderan bursa] seem to outweigh [those that support such an ancestral character], so that one must agree with Osche (1952b), who assumes a peloderan bursa for the prototype¹⁸⁵ of extant groups of Rhabditinae. The other possibility, that the leptoderan "*Eurhabditis*" and *Rhabditoides* groups branched off earlier from the other Rhabditinae, is excluded as long as the formation of the glottoid apparatus at the base of the buccal tube in *Rhabditis* is regarded as having occurred only once.¹⁸⁶

The formation of a leptoderan bursa as a secondary change apparently correlates with a lengthening of the tail by spreading from the female to the male.¹⁸⁷ That a peloderan bursa could evolve secondarily is demonstrated in subgenus *Pellioiditis*. That three bursal papillae now lie in a precloacal position is linked with the evolution of a leptoderan bursa, whereas all other groups retained the original two precloacal papillae, almost without exception (secondary alterations in *Caenorhabditis perrieri* and *Pelodera*; see p. 21). These questions are discussed again in connection with the evolution of the bursa (Chapter II, Section 7). The correlation of three precloacal papillae with a leptoderan bursa might support a common ancestry of *Rhabditoides* and "*Eurhabditis*."

The formation of a glottoid apparatus from three glottis-like arches projecting into the lumen of the buccal tube is regarded as an apomorphy because of the same "specific quality." Because of this, the following groups are to be considered a monophyletic unit: *Mesorhabditis*, *Crustorhabditis*, *Operculorhabditis*, *Cruznema*, *Rhabpanus*, *Xylorhabditis*, *Pelodera*, *Teratorhabditis*, *Caenorhabditis*, *Rhabditoides*, and "*Eurhabditis*" (this last being the union of *Rhabditella*, *Diploscapteroides*, *Cephaloboides*, *Rhabditis*, and *Pellioiditis*). Treated as genus *Rhabditis*, these groups will be contrasted with the genera *Parasi-*

¹⁸² i.e., the *Monhystera* group, which branched off first (see Fig. 8).

¹⁸³ i.e., inconsistent with the hypothesis that a leptoderan bursa existed in the stem species of the Rhabditinae.

¹⁸⁴ The original erroneously has "*Rhabditis*," which of course does not include *Parasitorhabditis* or *Protorhabditis*.

¹⁸⁵ This may now be interpreted as "the stem species."

¹⁸⁶ The original used the term "monophyletic" with regard to this concept of a character change, but this term should be reserved for taxa.

¹⁸⁷ That is, a long tail tip selected for in females is expressed apomorphically for males. However, male tails are developmentally derived from juvenile tails that are usually similar in both sexes. A leptoderan tail is more likely a retained juvenile state than a sexual transformation (see Fitch, 1997; Nguyen et al., 1999).

¹⁸⁰ This term actually implies an ancestral form. However, this hypothetical form is typological, not ancestral.

¹⁸¹ This character description is meant to refer not to the most recent common ancestor (i.e., stem species), but to an earlier species in the lineage ancestral to the stem species of Rhabditidae.

torhabditis, *Protorhabditis*, and *Prodontorhabditis*, in which a glottoid apparatus is absent. Certainly, the glottoid apparatus has exhibited structure since its origin, as stated by Osche (1952b:211): “probably even structures like ridges and teeth already existed [rudimentarily] in the corresponding place before a typical glottoid apparatus had developed.” This is suggested by such structures (or similar structures) established in *Parasitorhabditis* and *Protorhabditis*. To subdivide the genus *Rhabditis* into the subgenera mentioned, the question concerning the nature of these metarhabdion structures becomes important. Several different types [of such structures] exist. For example, three teeth appear on each metarhabdion as in *Pelodera*, *Cruznema*, *Xylorhabditis*, and the basally derived [in the *Caenorhabditis* group] *Caenorhabditis plicata*. Sometimes they can be modified to appear wart-like, as in *Teratorhabditis* and *Rhabditoides*. In other groups, two teeth are formed on each metarhabdion as in *Mesorhabditis*, *Rhabpanus*, and *Caenorhabditis*,¹⁸⁸ or only one tooth, as in *Operculorhabditis*.⁵⁴ Finally, two, three, or five warts per metarhabdion may be found as in “*Eurhabditis*.” Because denticles are already found in this position (one or two at each position) in some *Parasitorhabditis* species (but in the absence of a glottoid apparatus) and are also found in other groups such as Diplogastriidae and Panagrolaimidae, the formation of such denticles may be assumed to be a plesiomorphic trait. Additional support is suggested by the fact that metastomal teeth are widespread within *Rhabditis*.

On the other hand, it is more difficult to answer the question of whether the number of teeth per metarhabdion in *Rhabditis* was primitively two or three. An argument¹⁸⁹ for three is the broad distribution of this number within *Pelodera*, *Cruznema*, *Teratorhabditis*, *Rhabditoides*, and “*Eurhabditis*.” Additional support [for this hypothesis] is suggested because reductions (from three to two) appear to be easier than building corresponding novel structures. Evidence against [this hypothesis] would be that only two teeth occur per metarhabdion just within the primitive¹⁹⁰ subgenera *Mesorhabditis* and *Rhabpanus*, although this may be connected with the small size of the metastom. Moreover, there are a few species within “*Eurhabditis*” (*R. oxyerca*, *R. dolichura*, *R. rara*) that exhibit two teeth per metarhabdion (perhaps by activation of a latent potency). However, a derivation of this group from species¹⁹¹ with only two teeth per metarhabdion as in *Ca-*

*norhabditis*¹⁹² (see Osche, 1952b:215) appears unlikely if one wishes to suggest a common origin for *Rhabditoides* and “*Eurhabditis*” on the basis of three precloacal papillae. Because *Rhabditoides* displays three wart-like denticles, it is more likely that three warts are primitive¹⁹³ in “*Eurhabditis*” as well, and that their number has been changed secondarily. This alteration could just be connected with the size of the glottoid apparatus. Indeed, species with an unusually large glottoid apparatus (like *R. koerneri*, *R. papillosa*, and *R. buetschlii*) have five warts on each metarhabdion, whereas *R. cristata*¹⁹⁴ and *R. gracilicauda*, which bear only two warts on each metarhabdion, are relatively small species with a correspondingly small glottoid apparatus. This character [i.e., the reduction in the number of structures on the metarhabdion with a reduction in size of the metarhabdion] could be used to argue for the derivation of two teeth on a *Mesorhabditis* metarhabdion from a reduction of a median tooth.¹⁹⁵ The present state of knowledge conforms with the assumption of Osche (1952b) that three teeth per metarhabdion¹⁹⁶ is most likely ancestral in Rhabditinae that have a glottoid apparatus (genus *Rhabditis*).

If one attempts to organize a phylogenetic system from what has been recognized so far, the resulting picture of the large-scale grouping is not very satisfying. Once again, the difficulty and hypothetical nature of the attempt to infer phylogenetic order are particularly well exemplified here. Only in a few lucky cases can the course of evolution be traced with a certain degree of confidence (see Fig. 24). Here, four phases of adaptive radiation can be distinguished. Within the¹⁹⁷ radiations, the individual—presumably dichotomous—divergences cannot (yet) be demonstrated on morphological grounds. The first [radiation] led to three groups (*Parasitorhabditis*, *Protorhabditis*, and *Rhabditis*). The precise relationships among these groups cannot be determined because of the lack of synapomorphies. The second [radiation] led to the different types of *Rhabditis*. Likewise, [the data] scarcely allow a plausible branching order of these groups to be inferred. At best, a common root can be assumed for *Mesorhabditis* and *Cruznema* / *Rhabpanus* because of the offset lips and the formation of a median bulb, just as [a common root can be inferred] for *Caenorhabditis* and *Rhabditoides* / “*Eurhabditis*” on the basis of the median vulva and an arrangement of papillae in *Caenorhabditis* that supports

¹⁸⁸ This is based on a faulty observation for *Caenorhabditis* as described in the section on *Caenorhabditis*; most of these species bear a single “tooth” (actually more like a flap) in the place of each “metarhabdion.” *Rhabditis plicata* has three denticles per metarhabdion.

¹⁸⁹ The plural, “arguments,” was used in the original, but there appears to be only one argument.

¹⁹⁰ i.e., primitive with regard to the plesiomorphic state of other characters.

¹⁹¹ Of course, only a single lineage (not many species) is meant as an ancestor to this (presumably) monophyletic group.

¹⁹² Proposing a derivation of “*Eurhabditis*” from a lineage shared recently with *Caenorhabditis* would appear even more unlikely on the basis of this argument, since *Caenorhabditis* does not have two teeth per metarhabdion.

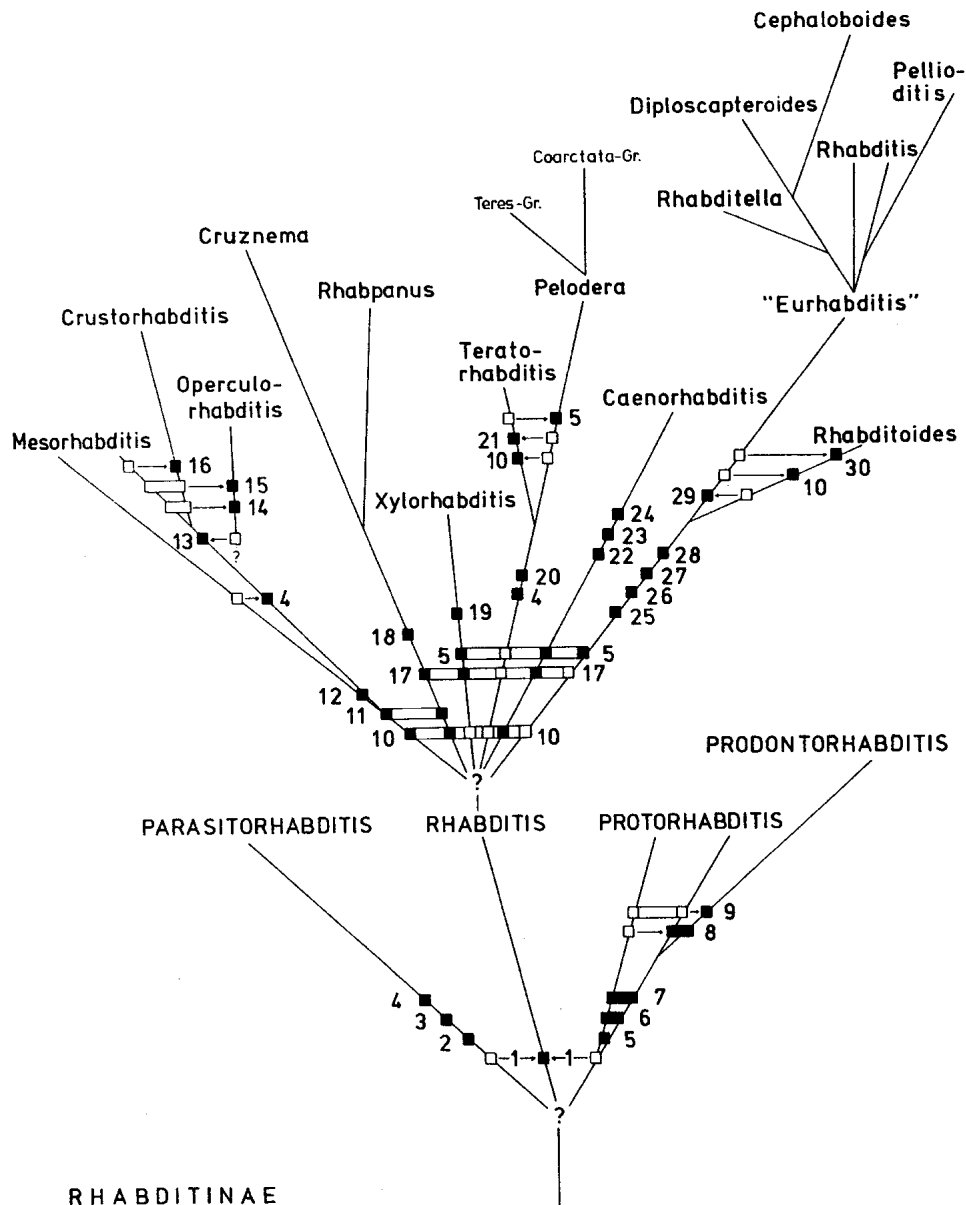
¹⁹³ “The most primitive” is written in the original text, but “primitive” alone suffices to describe the ancestral trait.

¹⁹⁴ Unpublished results suggest this name is a junior synonym of *R. lacustris*.

¹⁹⁵ That is, from the reduction of the middle of 3 teeth on each metarhabdion.

¹⁹⁶ “3 Metastomzähne” in the original.

¹⁹⁷ “First two” should perhaps be added at this point, since only the first and second radiations in Fig. 24 bear question marks.



53 FIG. 24. Cladogram of Rhabditinae *sensu lato*. The numbers denote the following apomorphies: (1) glottoid apparatus formed with three ridges; (2) female tail short and plump; (3) sixth bursal papilla short and thickened; (4) spicules fused distally; (5) vulva midbody; (6) 10th papilla lost; (7) fifth and seventh papillae open dorsally; (8) bursa closed; (9) "prodonty"; (10) median bulb formed; (11) lips set apart; (12) two teeth per metarhabdion; (13) third papilla opens dorsally; (14) one tooth per metarhabdion; (15) cuticular vulval flap apparent; (16) spicules fused along 2/3 their length; (17) reduction of a bursal papilla (but which, and always the same?); (18) third and ninth papilla open dorsally; (19) last papilla stumpy; (20) cupola-shaped female tails; (21) lip margins heavily cuticularized; (22) bursa nearly closed; (23) some papillae swollen at their bases; (24) seventh papilla opens dorsally; (25) pharyngeal sleeve covers half the buccal tube; (26) bursa leptoderan; (27) three precloacal papillae; (28) metastomal teeth in a triangular arrangement; (29) metastomal warts; (30) bursa reduced and radially arranged. ■ = homomorphic apomorphies, for which uncertainty exists regarding synapomorphic status (cf. p. 6). Genus *Protorhabditis* and subgenera *Mesorhabditis* and *Rhabditis* are paraphyletic groups, which are depicted by two lineages leading to each taxon.

the derivation of a bursa with three precloacal papillae [as in *Rhabditoides*/*Eurhabditis*]. Such an opinion, however, can in no way be entirely convincing.

The third phase led to a further branching of the *Mesorhabditis*, *Cruzanema* / *Rhabpanus*, *Pelodera* / *Teratorhabditis*, and *Rhabditoides* / "*Eurhabditis*" lineages into the respective, typical subgroups. Finally, a fourth

phase is recognized in which further branching occurs in *Pelodera* and to a larger extent in the "*Eurhabditis*" group. From the viewpoint of both the diversity of types and species, "*Eurhabditis*" is the most successful group. In all four phases [of radiation], the formation of various types is first observed, from which one or a few lineages were then capable of further, richer subdivi-

sion, whereas other groups that have diverged closer to the root have led to only minor alteration and modest diversification into the extant species.

II. CHARACTER EVOLUTION IN RHABDITINAE

3. Metastomal structures

The systematic significance of the ornamentation of the metastom and its alterations (which could be neutral because they have no function¹⁹⁸) was first recognized and consequently used by Osche (1952b) after previous authors had observed these structures now and then (Maupas, 1919; Fuchs, 1931; Chitwood and Chitwood, 1950; Völk, 1950; Sachs, 1950). (The earliest observation of metastom denticles was made by Schneider [1866:152] with regard to the "vestibule" of *Pelodera*: "there are three very small denticles at its posterior end," which he could have observed only in *P. strongyloides* or *P. teres*.) A short overview of these important transformation series follows.

There is good reason to assume that the newly evolved glottoid apparatus in the genus *Rhabditis* already had three tooth-like structures on each metarhabdion (p. 43). As suggested by Osche (1952b), these can be derived from a triply ridged metarhabdion (three strongly cuticularized ridges without anterior projections), as it exists in a similar manner in *R. plicata* (cf. Fig. 26). The slight differentiations of three somewhat wartlike denticles in *Cruzinema*, *Xylorhabditis*, *Teratorhabditis*, and the *Pelodera-Teres* group were suggested as symplesiomorphies or the similarities [among these taxa] were interpreted as results of parallel changes from a triply ridged metarhabdion. In the *Pelodera-Coarctata* group, the three ridges became three strong teeth of nearly equal height projecting into the lumen (Fig. 25 H-L). In another lineage the middle tooth first grew larger, then shifted forward and projected into the lumen farther than the more posterior teeth on either side (cf. *R. longispina*, Fig. 25B). Finally, this led to a triangular arrangement of the (altogether smaller) teeth (*Rhabditoides*, and according to Osche, also in *Teratorhabditis*). Three such structures are thus conserved in all of the species of the aforementioned groups.

In "*Eurhabditis*" (convergently with *Teratorhabditis*), the teeth were eventually reduced to warts (i.e., to more strongly cuticularized bumps on the weakly cuticularized glottoid apparatus) (Fig. 26). Three warts on each metarhabdion appear to be plesiomorphic, typically arranged in a triangle like the denticles in *Rhabditoides*. Such an arrangement could have given rise to a further reduction or a secondary increase in the number of warts with, respectively, a reduction or enlargement of

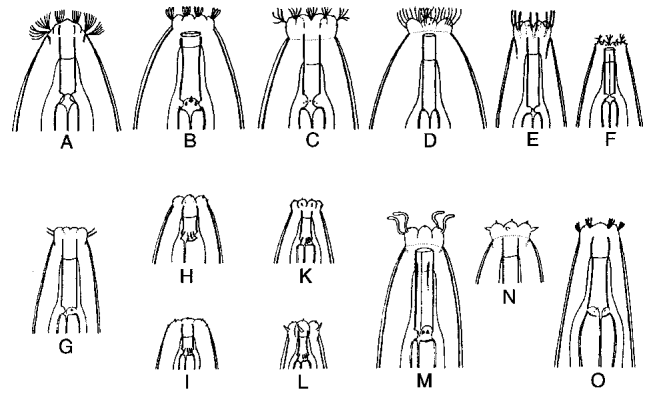


FIG. 25. [Fig. 26 in original.] Formation of lip bristles and sexually dimorphic lip variants: A) *Matthesonema tylosa* (from Osche, 1955b). B) *Rhabditis longispina*. C) *Rhabditis paraciliata*. D) *Rhabditis ciliata* (from Fuchs, 1931). E) *Rhabditis cristata* (from Hirschmann, 1952). F) *Rhabditis brassicae* [in the original, the synonym *R. broughtonalcocki* was used] (from Buckley, 1931). G) *Rhabditis* sp. (*lacustris*?). H, I) *Rhabditis tretzeli* female (H) and male (I). K, L) *Rhabditis coarctata* female (K) and male (L) (from Sachs, 1950). M, N) *Rhabditis dimorpha* n. sp. female (M) and male (N). O) *Rhabditis anchispora* (from Andrassy, 1966) (B, C, G-I, M, N: drawings by the author).

the glottoid apparatus (cf. p. 43). In *Pellioditis typica*, of the three metarhabdion warts, the two lateral ones are more strongly developed than the middle one. From this type of arrangement, a type with two warts can be easily derived by a complete reduction of the middle bump, as has occurred in this species group in *P. friederici*. Convergently, two metarhabdion warts are also found in *R. gracilicauda* and *R. cristata*. For most of the species it is not known for sure if there are three or five (or a different number) warts per metarhabdion. However, both types [three or five warts] are often found within the same group of closely related species; one must therefore presume a frequent change in the number of warts. According to Osche (1952b), the warts on the dorsal (anisomorphic) metarhabdion are fused into

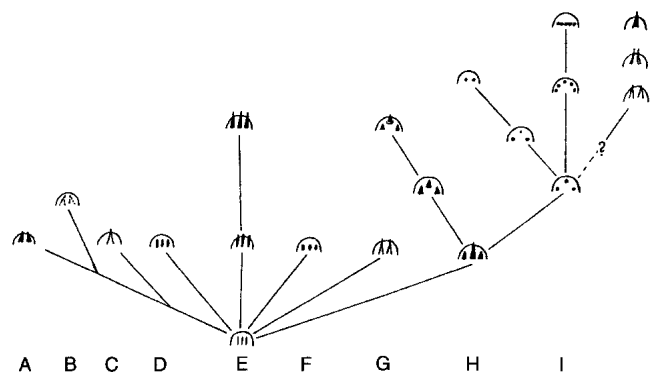


FIG. 26. [Fig. 28 in original.] Transformations of metastomal structures (the arrangement corresponds to the cladogram [of Rhabditinae]; cf. Fig. 24). Metarhabdions depicted are representative of those of [the following species groups]. A) *Mesorhabditis*. B) *Crustorhabditis*. C) *Operculorhabditis*. D) *Cruzinema*. E) A "triply ridged metarhabdion" (*R. plicata*) and its transformations within *Pelodera*. F) *Teratorhabditis*. G) *Caenorhabditis*. [Should actually show a single flap on the metarhabdion; see footnote 101.] H) *Rhabditoides*. (I) The changes within "*Eurhabditis*" (details in the text).

¹⁹⁸ The author now believes it is impossible to show these structures are functionless.

a [transverse] ridge in *R. musicola* and *R. typhae*.¹⁹⁹ In *R. dudichi*, although the subventral metarhabdions each bear three small warts, a pointed tooth may occur on the dorsal metarhabdion (Andrássy, 1970).

⁶³ The reverse change, from warts to teeth, is also possible. For example, within the “*Eurhabditis*” group, which is characterized by metastomal warts, there are two lineages of species with metastomal teeth (*Cephaloboides oxyerca* and *C. jodhpurensis*; *Pellioiditis dolichura* and *P. rara*), most with two as is typical for *Caenorhabditis*.²⁰⁰ This fact still cannot be satisfactorily explained (cf. pp. 36, 43). According to the previously presented view, a metarhabdion with three bumps must be assumed for the ancestor of “*Eurhabditis*.” These teeth, found again only in these two evolutionary lineages, must therefore be an evolutionary novelty and convergent with *Caenorhabditis*.²⁰¹ (Fig. 26). In this case a parallel change²⁰² can be excluded because the extant *Caenorhabditis plicata* with its triply ridged metarhabdion clearly shows that the *Caenorhabditis* ancestor did not have metastomal warts, in contrast to [the metarhabdion] of the “*Eurhabditis*” ancestor.

Besides *Caenorhabditis*, there are also two metarhabdion teeth known for *Rhabpanus*, *Mesorhabditis*, and *Crustorhabditis* (which is derived from *Mesorhabditis*). They are especially clear in *Mesorhabditis monhystera*, *M. longespiculosa*, and *M. irregularis*, where they project obliquely into the buccal cavity. They are less impressive in the other species of this group and sometimes appear to be completely absent (*R. spiculigera*). The formation of two metarhabdion teeth must be interpreted in this case as a convergence with *Caenorhabditis*,²⁰³ and can easily be derived from three teeth as a reduction of the middle tooth. In the details, these two teeth have different “specific qualities” in each lineage; i.e., they are strongly cuticularized in *Mesorhabditis*, hollow and pointed projections of the metarhabdions that extend relatively far into the buccal cavity in *Caenorhabditis* species and *Pellioiditis dolichura*, or very long and thin processes in *Cephaloboides oxyerca* (Osche, 1952b). A further reduction to but a single metarhabdion tooth is observed independently in *Operculorhabditis* (which was presumably derived from an ancestor within *Mesorhabditis*) and *Cephaloboides jodhpurensis* (closely related to *C. oxyerca*). Also here are important differences in the details: the metarhabdion tooth in *Operculorhabditis* is hollow and pointed, and plate-like and strengthened in *Cephaloboides jodhpurensis*. In *R. dudichi* of the *Rhabditis-Gracilicauda* group, there is a relatively strong and

pointed tooth on the dorsal metarhabdion instead of warts as on the other metarhabdions, beautifully demonstrating the transition from warts to teeth, as only inferred for other species groups.

7. Bursa formation and its transformations²⁰⁴

a. Peloderan and leptoderan bursa types

It may be assumed that in the evolution of the Rhabditinae, the males originally had a conical tail (like the females) with a certain number and order of sensory papillae (cf. Fig. 27). Cuticular lateral “wings”²⁰⁵ then developed at the posterior end (caudal alae), which presumably promoted better adherence during copulation. Such cuticular seams may have appeared at first on the female tail as well, where they are to be found at present as reduced features in a few representatives of some *Rhabditis* subgenera. The sensory papillae are now included within the caudal alae, such that this cuticular structure may be ultimately supported and stretched from the papillae²⁰⁶ (which may have adopted this as a new function).²⁰⁷ To be able to use this structure as a *bursa copulatrix*, the tail [tip] had to be reduced more and more, so that it protruded only slightly beyond the [posterior edge of the] bursa or not at all.²⁰⁸ The last step of this evolution was the formation of a peloderan bursa type.

It was already discussed on p. 42 that a peloderan bursa might be assumed for the ancestral form of the Rhabditinae, although this has by no means been shown with absolute confidence, and according to our hypothetical scenario above, an even earlier ancestor should have had a leptoderan bursa. The peloderan bursa is then a symplesiomorphy that is characteristic for most of the groups of Rhabditida. Again it should be especially noted that the peloderan bursa type of *Pellioiditis* and *Cephaloboides nidrosiensis* / *C. valida* (and possibly also of *Cruznema*) arose convergently from a leptoderan bursa. In the transformation series through the

²⁰⁴ In this case, “bursa formation” refers mostly to the formation of the bursa velum (sometimes called “caudal alae” or the “fan”) and the form of the tail tip. The patterning of the bursal papillae is covered in Section 8.

²⁰⁵ Not in quotation marks in the original, which uses the word “*Seitenflügel*.”

²⁰⁶ Some mutants of *C. elegans* that lack rays can still bear a velum (e.g., reduced-function mutations in the gene *lin-32*; Zhao and Emmons, 1995), suggesting that rays are not required to support this structure.

²⁰⁷ [Footnote 6 in the original text.] Up to now, nothing has been said about whether such a bursa was just acquired in the lineage leading to *Rhabditis* or whether it was acquired much earlier near the origin of Secernentea (regarded by all authors as a natural taxonomic unit). In support of the latter are the major correspondences between the bursa of *Rhabditis* with the monhysterids *Diplolaimelloides* Meyl, 1954, and *Monhystrium* Cobb, 1920. For *Monhystrium wilsoni* (Baylis, 1915), even 10 pairs of bursal papillae are described, two of which are preloacal (cf. Riemann, 1969). The resulting difficulty that faces us is thus [how to explain] the loss of a bursa and completely different papilla numbers (and order) that would have to be derived in the Cephalobidae (a group closely related to Rhabditidae).

²⁰⁸ This statement should be taken to mean that tail-tip reduction was likely to be a preadaptation to the copulatory behaviors generally associated with males bearing broad bursae (e.g., parallel instead of spiral search patterns). On the other hand, mating efficiency tests with some mutants of *C. elegans* that bear different lengths of leptoderan tail tips show that leptoderan tail tips per se may not interfere with such behaviors (D. Fitch, unpubl.).

¹⁹⁹ *Rhabditis octoppleura* in the original; the population studied by Osche was more likely *R. typhae*, a species in the *R. octoppleura* species complex (see Kiontke, 1999).

²⁰⁰ *Caenorhabditis* is now known to have only one large projection per metarhabdion (see footnote 101).

²⁰¹ See previous footnote.

²⁰² See previous footnote; there is no such parallel change with *Caenorhabditis*.

²⁰³ See previous footnote.

forms of the *Gracilicauda*, *Maupasi*,²⁰⁹ and *Pellioiditis* species groups, a gradual reduction of the tail thread²¹⁰ of the males can be followed that ultimately ends at a peloderan stage. This transformation series also serves as a model for the origin of a peloderan bursa for the ancestor of the Rhabditinae. Conversely, all the evidence supports the scenario that a leptoderan bursa arose from a peloderan bursa only twice; namely in *Rhabpanus* and in the ancestor of *Rhabditoides* / “*Eurhabditis*.” Apart from this, there is also within *Mesorhabditis* a group (*R. monhystera*, Fig. 7, *R. paucipapillata*) that displays a reduced and what may be considered by some authors a “leptoderan” bursa.

At this point, one must ask about the conditions under which selection could cause the replacement of an evidently optimal tail-encompassing (peloderan) bursa by a leptoderan one. For this, three possible assumptions must be examined:

1. Prerequisite to the development of a leptoderan bursa is an extension of the female tail.
2. The leptoderan bursa form is correlated with a reduction of the bursa.
3. The leptoderan bursa form proceeds with (or is the consequence of) a radial arrangement of the bursa.²¹¹

The first possibility appears in all likelihood to be correct, if one assumes that the long tail thread of the female, which emerged under certain selection conditions, can be passed to the male.²¹² An argument for this is that the most primitive²¹³ representatives of “*Eurhabditis*,” namely the subgenera *Rhabditella* and *Rhabditis* (*Gracilicauda* group), have long-tailed forms in both sexes. For *Rhabditoides*, however, this would not apply, since it has already been concluded that an extension of the tail in all probability occurred within this

group itself (p. 26). This question²¹⁴ cannot be resolved, since the common leptoderan stem species cannot be sufficiently reconstructed. On the other hand, there are also rhabditid groups in which peloderan bursae are conserved and throughout which females often display especially long tails (*Protorhabditis*, *Prodontorhabditis*, *Caenorhabditis*, *Pellioiditis*).²¹⁵ The latter case may also serve as an indication that the origin of a leptoderan bursa from a peloderan one is apparently not easy, especially since a selective force prevents such a transformation, thereby raising the systematic value of this feature. The question will be of interest to us again in a discussion of copulatory behavior (Chapter VI, Section 9).

The second and third possibilities considered to explain the formation of a leptoderan bursa in connection with a reduction and (or) radial arrangement of the bursa should be discussed here jointly because both tendencies appear to be mutually dependent and stabilizing. Thus, there are also species of peloderan rhabditid groups known to have bursae that are in part greatly reduced and display a weak or a [more derived] strong radial organization of the papillae (*Protorhabditis parvovellata*, *Mesorhabditis irregularis*, and possibly *M. monhystera*). *Mesorhabditis labiata* and *M. paucipapillata* also have a narrow and apparently reduced bursa; for the latter, Paetzold (1955) even described a slightly leptoderan bursa, although this [description] is doubted by other authors (Meyl, 1960; Loof, 1964). The bursae of these species, however, still show no indication of radial arrangement, so that one would like to propose the reduction of the bursa velum as the first step for the development of this syndrome,²¹⁶ especially since no example of a radially arranged bursa with a well-developed velum is known within *Rhabditis*. For the species mentioned, there is no case in which the female tail is especially long (for *Protorhabditis parvovellata* and *Mesorhabditis irregularis* it is even slightly cupola shaped). Possibly, this facilitates an explanation for why a leptoderan bursa did not appear in these cases (with the uncertain exception of *R. paucipapillata* and *R. monhystera*), despite a reduction and radial arrangement of the bursa.

For the leptoderan *Rhabditoides* / “*Eurhabditis*” group, the bursa is often greatly reduced and radially arranged, as in all species of *Rhabditoides*, *Rhabditella*, *Cephaloboides*, and probably (at least in initial evolutionary stages) in *Diploscapteroides*. However, the reduced and radially arranged bursa can be viewed only partly as

²⁰⁹ “*Maupassi*” in the original text is a misspelling.

²¹⁰ The shape of an extended tail tip is described as “threadlike” (*Schwanzfaden*) in the original, but has also been described as a “tail spike” in some other publications. A peloderan shape in each case studied so far (*Caenorhabditis*, *Crustorhabditis*, *Cruzema*, *Pellioiditis*, *Pelodera*, *Tevatorhabditis*) results from a morphogenetic “retraction” of the tail-tip cells in the latter portion of the last juvenile stage. Until this developmental stage, the tail-tip cells are morphologically similar between the sexes. The shape of the female tail tip and that of leptoderan males usually results from a retention of the juvenile developmental state of these cells, although this is not always the case (Nguyen et al., 1999).

²¹¹ i.e., with papillae arranged dorsally and ventrally around the tail instead of being confined, in-line, to the lateral plane of a broad, flat bursa velum. The pattern of papilla precursor cells in the J4 stage entails both anteroposterior and dorsoventral distributions of precursor cells in the lateral fields. In animals with significant bursa morphogenesis, this pattern is almost completely flattened into the bursa itself, whereas this (“radial”) pattern is largely maintained in animals with little bursa morphogenesis.

²¹² That is, given unnamed selective conditions that allow it, leptoderan tail tips can arise only in peloderan lineages in which females already possess long tail tips. Actually, it is not the shape of the adult female tail that is the important prerequisite for the pointy shape of leptoderan tails, but rather the shape of the juvenile tail. This is because leptoderan tails result from failure of the tail-tip cells (which are homologous between males and females) to retract during male tail morphogenesis (Fitch, 1997; Nguyen et al., 1999).

²¹³ i.e., basally diverged in the “*Eurhabditis*” group.

²¹⁴ i.e., concerning how a leptoderan tail tip evolved in *Rhabditoides*, where extension of the female tail tip is the first step in this evolutionary transformation.

²¹⁵ i.e., a long female tail is not sufficient for the evolution of a leptoderan tail tip. Given the phylogeny presented in Appendix 2 (Fig. 37), however, it can be inferred that the leptoderan tails of *Rhabditoides* species are plesiomorphic, whereas those of *Rhabditella* and *Rhabditis* species are probably apomorphic.

²¹⁶ i.e., a radially arranged bursa in which the papillae are connected with a narrow velum.

an apomorphy for these groups (namely within “*Eurhabditis*” for *Rhabditella*, *Diploscapteroides*, and *Cephaloboides*) since other “*Eurhabditis*” groups have a normally developed leptoderan bursa. At this time, there is no support for an assumption that this [well-developed leptoderan bursa in these other “*Eurhabditis*” groups] is itself a derived condition, such that one must assume that the ancestor of the *Rhabditoides*/“*Eurhabditis*” group still had a well-developed leptoderan bursa with papillae arranged in-line and probably a long tail thread. Reduction and radial arrangement of the bursa in *Rhabditoides* and *Rhabditella* are therefore convergences.²¹⁷

⁷² A consequence of this discussion is that one cannot use reduction and (or) radial arrangement of the bursa as a [necessary] cause or precondition for the formation of a leptoderan bursa. One may say, however, both [a reduction of the bursa and a radial arrangement of the papillae] evolved more often and apparently more easily in species with a leptoderan bursa than in species with a peloderan bursa. Accordingly, the “spreading” of the extended tail of the female to the male²¹⁸ remains as the only explanatory principle for the origin of a leptoderan bursa from a peloderan one.

If one proceeds on the assumption that the bursa of rhabditids should make possible an attachment of the male to the side of the female body²¹⁹ in a manner similar to the action of a suction cup (i.e., copulation according to the “parallel form”), the sensory papillae, now spanning and supporting the velum, must all be at an equal level ventrolaterally. A radial bursa organization, in which the papillae protrude at different angles (Reiter, 1928), would have to impair the suction cup effect, although it would favor the sensory function of the papillae, which would come to lie along a broader front. The stabilization of the “suction-cup bursa” through these selection conditions therefore explains why there are no peloderan or leptoderan *Rhabditis* species with both a well-developed bursa velum and a radial organization of papillae.²²⁰ A compromise is reached to satisfy the selection forces for the two different papilla functions, insofar as certain papillae (different [papillae] in different [species] groups) only proximally support the bursa and at their distal end

open toward the inside (ventrally) or toward the outside (dorsally).²²¹ When the mode of attachment is changed (e.g., winding around the female in accordance with the “spiral form” [of copulatory behavior]), the suction cup effect of the bursa can be abandoned and the bursa velum is narrowed as the first step and a radial bursa arrangement arises [as the second step]. As already mentioned, there are indications of this process in peloderan *Protorhabditis* and *Mesorhabditis* and in a greater degree in leptoderan *Rhabditoides* and “*Eurhabditis*.” In the latter, the extreme radial arrangement (in which the sensory papillae are fully employed) appears to be necessary for copulation according to the “spiral form.” With this type of copulation, however, the selection pressure for a bursa velum is relaxed, and the bursa velum is gradually reduced in these lines. However, there is no reduction [of the bursa velum] in *Rhabditis* as extensive as in the Diplogastridae, where it has often disappeared almost entirely.

b. Open and closed bursae

The last item in this section involves the alteration of an open to a proximally closed bursa. The open bursa type, in which the proximal edge of the bursa merges with the body cuticle, prevails as a symplesiomorphy in almost all rhabditid groups. A closed bursa (i.e., a plate-like bursa) originated independently from [an open one] several times, likely by an enlargement of the proximal portion of the velum (cf. *R. plicata*) that finally united [anteriorly]; this occurred in the peloderan forms once in the ancestor of the *Protorhabditis-Oxyuroides* group and of *Prodontorhabditis*, once in *Pelodera* (*Coarctata* group), and once in *Caenorhabditis*. In leptoderan forms, however, a closed bursa occurs only in *R. dubia* and *R. maxima*, both quite large species (possibly also in *R. dacchensis*). Their formation seems to have occurred independently. Therefore, a closed bursa has independently arisen at least five times in Rhabditinae, an indication of the strong selection pressure favoring strong suction²²² during copulation with a closed suction cup-like bursa as opposed to an open bursa. Because adherence is particularly difficult in large forms, the largest leptoderan *Rhabditis* species (*R. dubia*, *R. maxima*) are typically equipped with a closed bursa. There is no known example of an open bursa having developed secondarily from a closed bursa.

²¹⁷ Given the phylogeny presented in Appendix 2 (Fig. 37), a rudimentary velum and radial arrangement of the papillae would be considered plesiomorphic in *Rhabditoides* and a reversal in *Rhabditella*.

²¹⁸ The term, *das Übergreifen*, is used in the original and is here translated as “the spreading.” This is meant only in the metaphorical sense that whatever mechanism is responsible for expressing an extended tail tip in the female is also required for the expression of a leptoderan tail tip in males. Again, it is important to stress that the prerequisite for a leptoderan tail tip is really the pointy shape of the *juvenile* tail tip (which tends to be inherited by both sexes).

²¹⁹ Here, “side” is used figuratively, not in the literal sense of “lateral,” since males actually attach to the ventral “side.”

²²⁰ An alternative interpretation is that the morphogenetic process by which a bursa velum arises does not allow for a case in which a broad bursa velum is formed without the papillae being drawn into the plane of the bursa velum. That is, a “developmental constraint” may exist from the ontogenetic correspondence between the degree of morphogenetic “retraction” and the degree to which papillae are drawn into the plane of the bursa velum.

²²¹ Again, the alternative explanation for the dorsoventral pattern of ray openings on the surface of the velum is one of developmental “constraint.” In every case, the cuticular fold that results in the velum margin is near the dorsoventral midline; during bursa morphogenesis, the dorsoventral distribution of papilla precursors is “translated” into the dorsoventral pattern of papillae in the velum as the lateral field of cuticle (and papillae) is folded to make the velum. Naturally, this does not obviate the probable maintenance of the dorsoventral distribution of papilla precursors in the J4 lateral field by selection on the adult pattern. But consideration of this process does suggest that it is not necessary to infer a secondarily derived compensatory mechanism causing papillae to open dorsally or ventrally once they are in a broad, flat bursa velum.

²²² i.e., adherence.

73 8. Number and arrangement of the bursal papillae
a. Papilla number

Schneider (1866:23) recognized the systematic significance of tail papillae in nematodes: "Where papillae exist, it has been established that the number and position follow the same law for a larger and otherwise similar group. Either the total number is the same, or just a certain number is constant; e.g., the number of the preanal papillae is usually constant, while the number and positions of the postanal papillae vary the most." To illustrate this [law],²²³ he mentioned that all species in the genus "*Leptodera*"²²⁴ have three precloacal papillae (Schneider, 1866:156).

It must be assumed that, ancestrally in the Rhabditiinae, 10 pairs of bursal papillae (2 lying precloacally) developed at approximately equal intervals [apart from one another] by "chance fixation" (cf. Fig. 27). More than 10 papillae, namely 11, have been known only as individual aberrations in *Pelodera*, *Rhabditella axei*²²⁵ (Reiter, 1928), and *Cephaloboides curvicaudata*, a situation that will be discussed further at length below, and otherwise only in species that have been described quite inaccurately, and in this respect presumably incorrectly (an alleged 11 papillae in *R. fruticolae*, Kreis, 1967, and 12 papillae in *R. silvatica*,²²⁶ Volz, 1951; 11-13 papillae in *R. inermis*, *R. axei*,²²⁷ *R. strongyloides*, *R. teres*, and "*R. producta*" in Schuurmans Stekhoven & Teunissen, 1938). In some groups (*Parasitorhabditis*, *Operculorhabditis*, *Pelodera*, *Teratorhabditis*), all the species hold surprisingly tenaciously to the type with 10 bursal papillae, which can be found in all groups, at least as vestiges. In several lineages, however, reductions occurred and led at first to nine papillae. It is thereby demonstrated, that in most cases (but not always), the last (10th) papilla is involved in the reduction, such as in *Protorhabditis* (where aberrations of *P. oxyuroides* show the remnants of a 10th papilla), and in *Rhabditoidea* and in nearly all "*Eurhabditis*" groups where the initial reduction is apparent (the progression of this reduction is particularly clearly traced within the subgenera *Rhabditis* and *Pellioiditis*). One could speak properly, therefore, of a "trend" to reduce the already somewhat smaller posterior-most papilla until its total disappearance in different evolutionary lineages. Vestiges of the 10th papilla, however, are still partially evident as "tail-knots" (Reiter, 1928) (subgenera *Rhabditis* and *Pellioiditis*) or "atavistically" as aberrations.²²⁸

²²³ Although Schneider probably considered this a natural law (i.e., something similar to a "developmental constraint"?), we might consider it a characteristic pattern shared by common descent.

²²⁴ This group included among others the leptoderan *Rhabditis* group (in the generic sense).

²²⁵ The original used the synonym *Rhabditella pseudoelongata* (see Sudhaus 1980 for the synonymization).

²²⁶ The original had the synonym *R. silvestris*.

²²⁷ The original had the synonym *Rhabditella pseudoelongata* (see Sudhaus 1980 for the synonymization).

²²⁸ As is demonstrated by developmental and other analyses, the 10th papilla

Now it must be emphasized that there are also groups that bear only nine bursal papillae (*Cruznema*/*Rhabpanus*, *Xylorhabditis*, *Caenorhabditis*) for which no clues exist concerning which pair of papillae could have been deleted. It need not in all cases be the 10th, since it has been demonstrated for another clade (*Mesorhabditis*) that nine bursal papillae could also originate by reduction of the sixth or the seventh papilla (p. 16). In this respect, the loss of the seventh papilla is particularly notable and will concern us later. Within the subgenus *Rhabditis* it can also be shown that, even in two cases (*R. reciproca* and the *Adenobia* group), nine papillae are obtained by the loss of the seventh papilla²²⁹ (p. 32), and presumably likewise in *Cephaloboides valida* (p. 29).

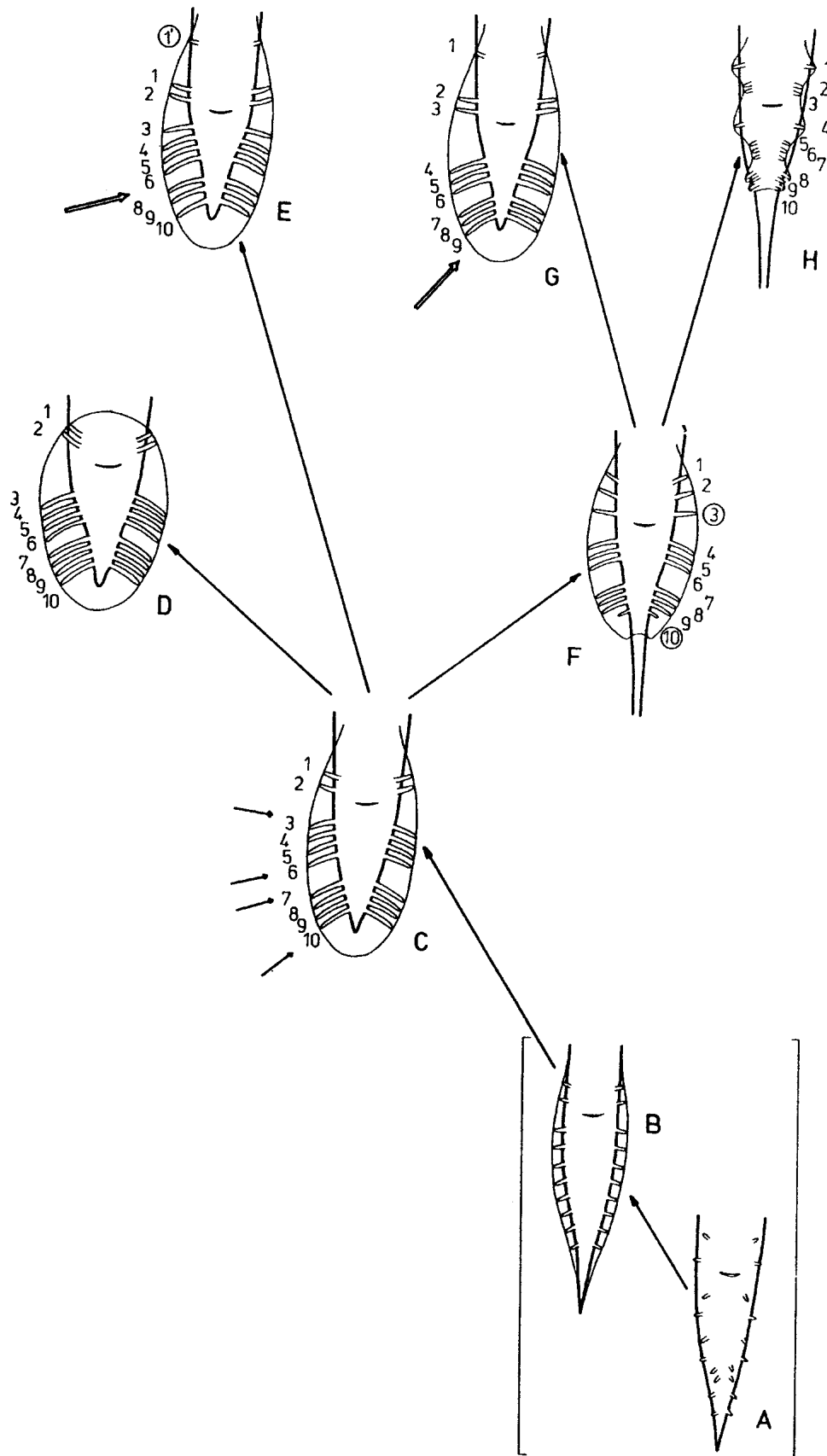
It is noteworthy for scientific history that Bütschli (1873:96, 109), in view of the still scant knowledge about species numbers at that time, assumed that in *Rhabditis* nine bursal papillae were plesiomorphic and a 10th papilla in *Rhabditis teres* "was placed between the second and third group," by which he must have meant (given the specification of this opinion [1876:365-366] with regard to *Rhabditis axei*) the fourth and not the seventh papilla in the currently typical order from anterior to posterior. Cobb (1898:449) also proposed that nine pairs of bursal rays were characteristic, as far as existing in the arrangement (3/3+3), but referred to illustrations of Strongylidae, without discussing the *R. cylindrica* pictured on the same page with its 10 pairs of papillae.

The reduction of the papilla number does not always stay at nine: there are individual species (though usually known but insufficiently), or entire species groups, that show only eight papillae. In the *Xylocola* group of *Protorhabditis* it can be shown that both the ninth and 10th papillae are missing (p. 11); in the species group containing *Caenorhabditis briggsae*, however, eight papillae arose by the loss or fusion of the papilla at the third position²³⁰ (p. 25). A further reduction to seven and even to six papillae has been described in *Mesorhabditis* species (the *Monhystera* group) and is furthermore as-

that is generally smaller than the other papillae in some groups (e.g., several species of "*Eurhabditis*" and at least one *Caenorhabditis* species) is not "vestigial," but is a fully structured phasmid. In the other species groups mentioned in which 10 fully developed bursal papillae are typical, the phasmid is generally not the 10th, but is anterior to at least the posterior three (Fitch and Emmons, 1995; Kiontke and Sudhaus, 2000; Fitch et al., unpubl.).

²²⁹ This inference correlates very well with developmental analyses, which show that the cell lineages that normally produce the "r8" (ray 8) homolog (see Appendix 3 for terminology for caudal, bursal, and ray papillae) do not occur in *R. blumi*, a member of the *Adenobia* group (shown in Fitch and Emmons, 1995; see also Fitch, 1997). (The r8 homolog often occurs in the seventh anteroposterior position in species of the *Rhabditis* subgenus.) Even though this ray has been lost in *R. blumi*, nine caudal papillae appear because the phasmid (which is the most posterior) is papilliform, though small.

²³⁰ In *Caenorhabditis briggsae*, this is indeed a fusion (not a loss) between rays 3 and 4 (see Fitch and Emmons, 1995), a variation that occurs quite frequently (~10-30% of sides). Fitch (1997) proposed that this apomorphy could have been effected by a gain-of-function change in the Hox gene *mab-5* or by a similar change in the anteroposterior patterning mechanism, a hypothesis currently being tested (D. Fitch et al., unpubl.).



74 FIG. 27. [Fig. 32 in the original.] Evolutionary trends in the formation of the bursa (the stages in brackets [A, B] are hypothetical). A) Male tail with sensory papillae. B) Caudal alae, supported by papillae, which are 10 in number by chance (arranged as 2/8). C) Peloderan bursa with ancestral number of papillae and clustering (the arrows point to relevant papillae involved in a change). D) Bursa closed. E) Three precloacal papillae through the novel origin of no. 1' and loss of no. 7. F) Secondarily derived leptoderan bursa and elongated tail. Three precloacal papillae [are formed] by displacement of the third; the 10th papilla is reduced to form a tail knot. G) Secondarily derived peloderan bursa, "tail knot" lost. H) Bursa reduced and radially arranged. (See text.)

serted for some *Rhabditis* species that are not well enough known.

b. Papilla order

Besides the decrease in the number of the papillae, a difference in their arrangement into groups occurs within Rhabditidae in different evolutionary lineages. Here also convergences must be dealt with, and a ground pattern²³¹ and different evolutionary trends are worked out only with difficulty. It was previously suggested that originally two papillae were precloacal, a situation that is dominant in nearly all groups of the Rhabditinae. Occasionally, there are alterations toward just one precloacal papilla by reduction (e.g., in the *Mesorhabditis Monhystera* group), about which too little is known in detail. However, the origin of three precloacal papillae is significant [for character evolution and] for the phylogenetic system as well. There are different evolutionary scenarios (that also apply to *Rhabditis*) to explain this pattern (cf. Fig. 27). Undoubtedly, the simplest one is where the third papilla first moves out of the first postcloacal papilla group, is then placed at the cloaca, and finally is shifted in front of the cloaca (heterotopy). This positional displacement does not appear problematic, but in *Rhabditis* (provided this is verifiable) has occurred only three times, namely in *Pelodera tretzeli* / *P. par*, *Caenorhabditis perrieri*, and probably in the ancestor of *Rhabditoides* / “*Eurhabditis*.” A model for a transitional form with regard to the positioning of papilla 3 is offered by some *Caenorhabditis* species (cf. Fig. 11).

Furthermore, three precloacal papillae are found in the *Pelodera Teres* group, a situation which may probably be explained by an 11th papilla arising far in front of the first, and a deletion of what was originally the seventh papilla (p. 21).²³² This uncommonly appearing mode of making novel papillae and reducing others to maintain a constant number of papillae finds further support in the fact that papilla seven in *Rhabditis* generally appears “labile” and (as already emphasized many times) was deleted in different groups (*Mesorhabditis*, the *Maupasi* group, the *Adenobia* group). According to an illustration by Wahab (1962), the loss of the

seventh bursal papilla on one side has also been observed in *Diploscapter lycostoma* Völk, 1950. Coming from an entirely different angle, Osche (1958) could show that in the closely related Strongylyna, the seventh papilla also plays a special role. He assumed that here the seventh and eighth papillae had fused to the “externodorsal ray.” Based on observations in *Rhabditis*, however, it appears worth verifying whether the seventh papilla could not simply have been deleted. In *Rhabditis*, there is almost no indication for a fusion of papillae in this region (7+8), if one ignores a corresponding aberration in *R. nidrosiensis* and the condition within the *Pelodera Coarctata* group, where papillae seven, eight, and nine have a common base (p. 23). The assumed addition of a 1' papilla far in front of the first papilla in *R. teres* is apparently easy to obtain; this is also observed in *R. axei*²³³ (Reiter, 1928), *R. curvicaudata* (my own observation), and *Diplogaster maupasi* (Potts, 1910:449).

A faulty interpretation held by Osche (1958:578) must be briefly corrected. He obviously starts out from the assumption that three precloacal papillae are plesiomorphic, and attempts to explain, using the example of *R. strongyloides* in comparison with *R. buetschlii* and *R. teres*, the development of two precloacal papillae through a loss of papilla one and a replacement with a new papilla in the region of papillae 4–7. In the last point he approaches the already cited interpretation of Bütschli. For his explanation—as well as for my exactly contrary argument (p. 21)—the aberration known in *R. strongyloides* with 11 papillae (three precloacal) becomes important. In the detail, the discussion is not correct (in *R. buetschlii* it is not papilla seven, but papilla 10 that is lost; the nine papillae in *R. tenuispicula* are not obtained by reduction of an alleged third precloacal papilla, but through loss of papilla seven) and is not tenable in presupposing three precloacal papillae as a symplesiomorphy.

The development of three precloacal papillae (discussed above [in the preceding paragraph]) that occurred convergently four times in *Rhabditis*, though in two different ways, was only sometimes modified further. Thus, there are some species that have secondarily and independently evolved again only two precloacal papillae (*R. aberrans*, *R. reciproca*, *R. seurati*). In the independent lineages of *R. guignardi* and *R. viguieri*, the second and third papillae were displaced behind the cloaca, so that only one precloacal papilla exists. Interestingly, in the subgenus *Diploscapteroides* and in *Cephaloboides nidrosiensis* / *C. valida*, all of the precloacal papillae have been shifted postcloacally, possibly by convergence (Fig. 14). In most cases, however, the species-rich “*Eurhabditis*” group also holds firmly to three precloacal papillae.

²³¹ Translated from “Grundtypus.” Although a “type” is implied by this term, an **ancestral** form is meant.

²³² This hypothetical scenario for the origin of three precloacal papillae by duplication and then deletion must be modified based on recent developmental analyses. Different patterns have generally evolved by changes in the relative positioning of the papillae, not by duplication and deletion (Fitch and Emmons, 1995; Fitch, 1997). The seventh papilla in *Pelodera teres* is actually the phasid (Fitch, unpubl.). In “*Eurhabditis*” and closely related groups, the phasid position is posterior, where it does not always adopt a papilliform morphology, resulting in what could be construed a “loss” of the seventh papilla. However, there are indeed variants in which new, ectopic papillae arise spontaneously. For example, in *R. blumi*, there is sometimes a new ray cell lineage that appears anterior of the ray 1 homolog, r1 (shown in Fitch and Emmons, 1995; discussed in Fitch, 1997; see Appendix 3 for ray homolog designations). A similar ectopic lineage may also explain the 11-rayed variant of *R. strongyloides* mentioned by Osche (1958:578). These ectopically expressed rays cannot yet be shown to have been fixed in any species.

²³³ The original has *R. pseudoelongata*, a synonym of *R. axei* (Sudhaus, 1980).

In this treatment of papilla pattern we have up to now restricted ourselves largely to the precloacal domain. For the postcloacal domain one may start from a "type" with eight bursal papillae placed at virtually equal intervals. These eight papillae could theoretically become grouped in any manner; the entire range of possible arrangements is, however, not generally observed.²³⁴ Only in *Parasitorhabditis* is a continuous change in the pattern of the papillae observed from species to species, such that no common type may be established. In other groups, the arrangement in the different species is more consistent, and the trend is clearly observed for the postcloacal papillae to cluster into two groups. Thus, the clusters may hold an equal number of papillae (4 + 4), or the scales may be tipped toward either side (3 + 5 or 5 + 3). The trend, then, is that the groups of papillae are steadily reduced, such that in the end, each group comprises only three (rarely two) papillae. Papilla displacement and reduction play a role in this trend. It is clear that the papillae in the third, sixth, seventh, and 10th positions must be particularly involved in this trend²³⁵ (cf. Fig. 27). These are, however, (except for the sixth) specifically those papillae to which the attention of the reader has been drawn repeatedly before: the third can be displaced precloacally, and the seventh and 10th can be reduced.

If one supposes that, as the "finalization" of this trend, all three groups resulted in an equal number of papillae (bursa type: 3 / 3 + 3), a situation often realized in "*Eurhabditis*" species, then from this bursa type further evolutionary trends may be followed, which once again involve the precloacal domain. The bursa type in which the three precloacal papillae lie very close together would be then plesiomorphic (e.g., *R. buetschlii*). Two possible evolutionary paths were then followed [with respect to the arrangement of the precloacal papillae]: either the spacings between the three papillae increased, but remained approximately equal (e.g., *R. pellio*, *R. longispina*), or the first papilla became displaced quite anteriorly and papillae two and three remained close together (*R. typica*, *R. gracilicauda*; Fig. 27). The latter represents a convergence to a situation that occurred in *Pelodera teres* and its relatives and which is reached by an entirely different morphogenetic process (cf. p. 51).

Thus are presented in the large picture the differences in papilla patterns, which individually play a large role in systematics. In conclusion, two more observations should be made about the evolutionary trends involving bursa construction and papilla arrangements in Rhabditinae: If the plesiomorphic situation of two

precloacal papillae is retained, then a trend exists toward a proximal closing of the bursa (apomorphic), which has been shown to occur convergently in *Proto-rhabditis*, *Pelodera*, and *Caenorhabditis* (p. 48). If, however, the bursa remains open (plesiomorphic), then its effectiveness (the suction-cup adherence to the female and the searching behavior for the vulval region) can apparently be increased by the anterior displacement (apomorphically) of a third precloacal papilla (*Rhabditoides* / "*Eurhabditis*," *Pelodera Teres* group). For both "rules" there are exceptions. Closed bursae are also known in two species with three precloacal papillae (*R. dubia*, *R. maxima*), for which a separate selection pressure would have derived from the considerable body size of these species. Conversely, there are species like *R. tretzeli* / *R. par* and *R. perrieri* / *R. craspedocerca*, which possess a third precloacal papilla despite having a closed bursa.

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VI. COMPARATIVE ECOLOGY AND BIOLOGY OF RHABDITINAE

9. Copulatory behavior

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a. Parallel form²³⁶ and spiral form

There are various copulatory positions in nematodes that can be distinguished (cf. Sudhaus, 1974b). The "spiral form" ("radial form" of Reiter, 1928) of copulation (in which the male winds particularly the posterior portion of its body spirally around and perpendicular to the body axis of the female and is thus stabilized) is the most broadly distributed and undoubtedly plesiomorphic form (cf. Fig. 28). In Adenophorea, the stabilization of the male can be supported by supplementary organs (usually glands) that are precloacal at the ventral midline. With the independent evolution of the bursa (cf. Chapter II, Section 7), a change in the copulatory position (to the "parallel form") was then possible, in which males could be stabilized on the surface of the female's body with the aid of a "suction-cup-like" bursa and supported by the secretion of cloacal glands. Because of this, the capacity for parallel mating could have been advantageous wherever the nematodes lay on their sides on a solid substrate, as is found particularly in terrestrial habitats. On the other hand, the position of the female vulva apparently does not influence the form of copulation. It appears that copulation by the spiral form is difficult in the case of species with a very posteriorly positioned vulva (e.g., *Diplogaster gracilis*); however, both must be interpreted as ancestral. The evolution of the bursa and the arrangement of the papillae are considerably influenced by copulatory behavior (cf. p. 46ff.). (The primary function of the papillae is sensory but they also allow the formation of a broad bursa velum, which is used secondarily in Stron-

²³⁴ Fitch (1997) suggests two possible causes underlying at least part of this constraint on the available palette of papilla patterns: (1) hierarchical genetic regulation results in correlated evolutionary changes and (2) the papillae are generally constrained by their affinities with and by the space occupied by neighboring hypodermal cells (see also Appendix 3).

²³⁵ Author's emphasis.

²³⁶ "Bursa type" in the original (term coined by Sachs, 1950).

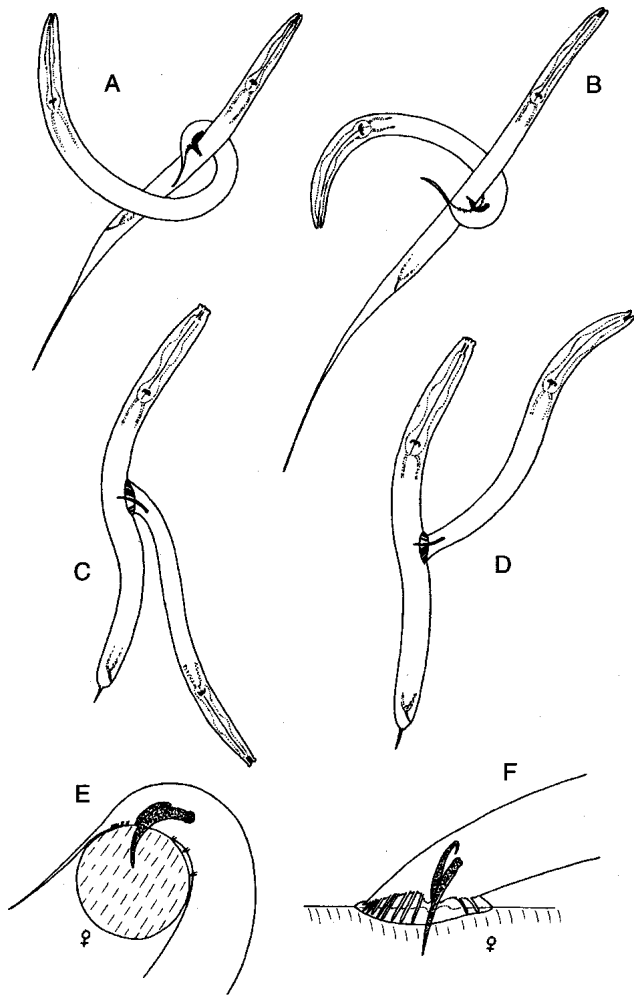


FIG. 28. [Fig. 51 in the original]. Copulatory forms. A) Right-handed spiral form. B) Left-handed spiral form. C) Parallel λ -form. D) Parallel Y-form. E) Cross section through the female in the region of the vulva during copulation in the spiral form (where bent spicules are more advantageous). F) Parallel form (where straight spicules are more advantageous).

gyloidea to grasp the female's body.)²³⁷ The secondary evolution of a reduced and radially arranged leptoderan bursa in *Rhabditis* must especially be viewed this way, such that a change in copulatory behavior from the parallel to the spiral form is preadaptive [for a reduced, radial, leptoderan bursa] (cf. p. 48).

Because a well-developed bursa is plesiomorphic in Rhabditidae, parallel copulation may be assumed as ancestral for this group. This form of copulation is the most frequent in this group and is found (as far as is known) as the exclusive or predominant form in all species groups with the exception of *Rhabditoides* and *Rhabditella*, which (corresponding to their reduced and radially arranged bursae) always copulate in the spiral

position (a secondarily evolved trait). *Cephaloboides oxyerca* also shows this form and behavior. Occasionally, the spiral form has been observed in *R. remanei* and *R. blumi*, particularly in liquid culture. It must be noted that many *Rhabditis* species (as well as those that copulate exclusively in the parallel form) first wind spirally around the female to search for the vulva. This is especially noticeable in liquid culture. When on solid substrate, however, the males slide along the surface of the female's body with their bursae when searching for the vulva. If a male is attached in the region of the vulva, then it will be dragged easily into an antiparallel position (λ -form) when the female moves, so that a small drag possibly exists because of the movement of the copulating pair ([on surfaces and] in mushy substrates). Therefore, copulation in the λ -form is the most frequent, particularly in agile species (e.g., all of the species of the *Pelodera-Coarctata* group inhabiting cow dung). It is not yet known if [the λ -form] is ever the only (genetically determined) form. In species for which large numbers of copulations could be observed, both the λ -form and the Y-form (bodies pointed in the same direction) were displayed, but the Y-form in a much smaller fraction. This is also the case for species such as *Mesorhabditis spiculigera* and *M. longespiculosa* that have a posteriorly positioned vulva and a vagina slanting anteriorly in the body, where because of anatomical reasons copulation in the Y-form is less stable.²³⁸ A predominance of Y-forms over λ -forms has so far been observed only for *R. mariannae*,²³⁹ also a species with a posterior vulva. In *R. strongyloides* and *R. marina*, both copulatory positions are almost equally frequent, and different selected lines [expressing exclusively one form or the other] could not be isolated.

b. Copulation plug

Copulation is especially tenacious in species with a [anteriorly] closed bursa (e.g., *Coarctata* group). With this bursa form, a suction effect is optimized.²⁴⁰ Of additional importance for good adherence is the "copulatory cement" secreted from the cloacal glands of the male and filling the entire space beneath the bursa. In this way, the copulatory plug is formed, which nearly always covers the vulva as a thick clump of secretion, remaining in place in some species until oviposition or until the juveniles are born (e.g., *Crustorhabditis*, *Cruznema*, *Pelodera*, *Teratorhabditis*, *Caenorhabditis*, *Pellioditis*). However, it can sometimes be torn off after copulation or removed later. In the species of *Rhabditoides*, *Rhabditella*, and *Cephaloboides oxyerca*, which copulate in the spiral form, such a copulatory plug is absent.

²³⁷ The assumption underlying this statement is that the rays (called "ribs" in some early literature) support the bursa velum. This notion may not be entirely correct, because some *C. elegans* males with some rays deleted genetically or by laser ablation of primordial cells can still develop rather broad bursae (D. Fitch, pers. obs.).

²³⁸ The original has "quite difficult," by which reduced stability was meant.

²³⁹ In the original the synonym *R. rovinjensis* was used.

²⁴⁰ Obviously not like suction cups in an octopus tentacle, as there are no muscles in these bursae; rather, the larger contact surface and flexibility allowed by an anterior extension of the bursa velum may promote adhesion through forces like surface tension.

In *R. spiculigera* it is also set inside the vagina as a plug (Sudhaus, 1974b).

One would like to assume that there is a secondary function of the plug, which appears like a "protective cap" over the vulva, especially when it has a particular form (as in *R. spiculigera*). One possibility could be that infection of the uterus by bacteria and fungal spores is hindered, especially if the secretion has a bactericidal effect. In contrast, exit of substances from the uterus also could be prevented. Finally, the copulatory plug could produce an additional (mechanical or chemical) signal to inhibit other males (who are ready for copulation) from mating with a female already supplied with sufficient sperm. This is not absolutely effective because in *R. strongyloides* (which has a voluminous copulatory plug) I was able to observe subsequent copulations several times. Additional experiments [allowing males to choose between plugged and unplugged females] would be necessary.

The formation of copulatory cement prior to sperm transfer is a preadaptation for the formation of spermatophores, as is found only as an exception in nematodes in a parasitic group (G. Osche, pers. comm.²⁴¹).

155 The possible functions of the copulatory plug could also be provided in nematodes by entirely different structures, especially by a cuticular flap over the vulva, as exists in the genus *Operculorhabditis*.

c. *Form of copulation and spicule shape*

The relation between the form of copulation and spicule shape is less obvious than that between form of copulation and shape of the bursa. A consequence of different copulatory positions is an important difference in the way that spicules are inserted into the nearly always slit-formed vulva of the female: During spiral copulation, both of the spicules push the vulval lips to either side with their lateral sides and can best penetrate by alternating the advance [of each spicule] into the vagina, whereas during parallel copulation, only one vulval lip must be pushed away with the dorsal side [of the spicules]. In the first case, it appears that separate spicules are advantageous such that the spicules can move against each other, whereas in the second case, a stable dorsal edge is preferable and fused spicules are at least not a disadvantage. The observation that all Rhabditidae with fused spicules copulate in the parallel position is consistent with this idea. However, not all species that copulate in the parallel position have distally fused spicules.

Another point to consider is that, when in a spiral position, the posterior end of the copulating male is considerably rounded in a manner corresponding with the cross-section of the female body, such that long and quite straight spicules would be a hindrance. On the

other hand, the curvature of the posterior end of the male barely changes from its normal position during parallel copulation and, corresponding to the straight vagina, nearly straight spicules are advantageous (cf. Fig. 28). But there are additional constraints on the degree of curvature of the spicules because strongly bent and even sickle-shaped spicules are also observed in species groups that copulate predominantly or exclusively in the parallel position. The required curving of the spicules need not be effected only by curvature of the main portion of the spicule itself, but can be synergistically effected by a dorsal thorn that slides against the gubernaculum (the structure that guides the extension of the spicules). In some *Parasitorhabditis* species with a posteriorly positioned vulva and an anteriorly slanted vagina, the very long spicules are dorsally concave, such that during parallel copulation in the λ -form, their shape is adapted exactly to the shape of the vagina.

APPENDIX 1

RECENT PHYLOGENETIC HYPOTHESES FOR SPECIES GROUPS WITHIN RHABDITINAE BASED ON MORPHOLOGICAL CHARACTERS

Walter Sudhaus

Because there have been several publications involving revisions and additions to the species groups discussed by Sudhaus (1976b), the relevant cladograms from these works have been reproduced here (Figs. 29–38) with translations of the legends (where necessary). Sources are noted in the figure legends.

APPENDIX 2

REINTERPRETATION OF THE PHYLOGENETIC RELATIONSHIPS WITHIN RHABDITINAE BASED ON MOLECULAR CHARACTERS

David Fitch

Using partial nucleotide sequences from small subunit ribosomal RNA genes (SSU rDNA, approx. 1,400 nucleotide characters), resolution is obtained with regard to several—but not all—relationships of the major species groups described by Sudhaus (1976b). There is not sufficient room in this appendix to present the data matrices or all of the results obtained from these phylogenetic analyses. Full analyses will be presented elsewhere (see also Fitch, 2000). However, we have become confident enough in some of the results to present a new phylogenetic hypothesis for the Rhabditinae that differs in some significant ways from that originally proposed by Sudhaus (1976b, emended). Presentation of this hypothesis is justified primarily because of these differences, but also because it provides interesting new predictions that can be tested with future molecular,

²⁴¹ i.e., in Rhigonematidae.

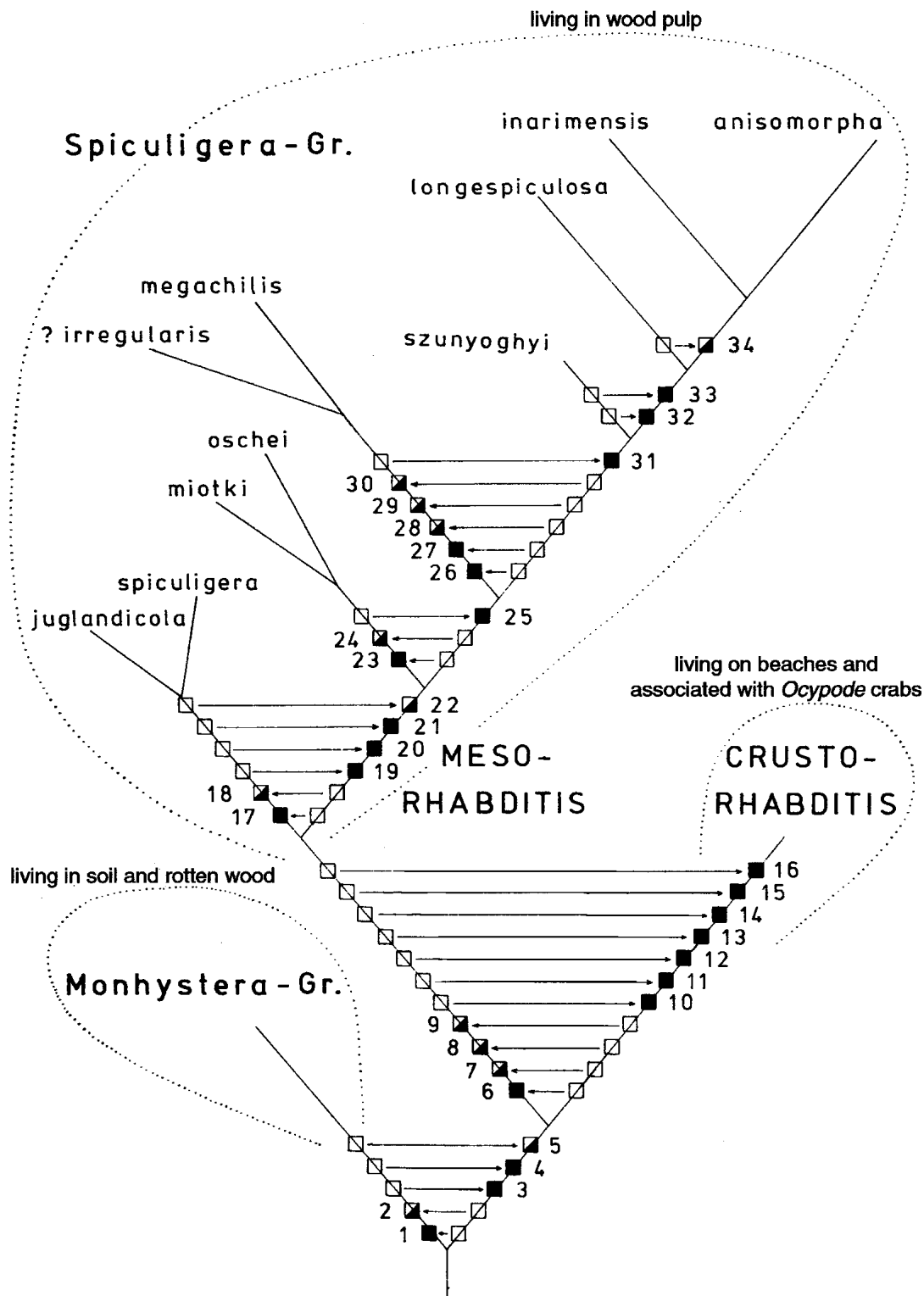


FIG. 29. Cladogram of *Mesorhabditis* and *Crustorhabditis* and the species of the *Spiculigera* group of *Mesorhabditis*. Because the value of the characters cannot be established easily, the relative degrees of confidence of the apomorphies are distinguished with two symbols: a filled square [indicating a well-supported apomorphy] and a half-filled square [indicating less confidence for the proposed apomorphy]. An open square denotes plesiomorphy. The numbers denote the following apomorphies: (1) bursa and papillae strongly reduced; (2) non-gonochoristic reproduction; (3) spicules distally fused; (4) length of spicules nearly doubled; (5) the third and perhaps the seventh bursal papillae [i.e., the phasmid; see Kiontke and Sudhaus, 2000] open on the dorsal surface of the velum; (6) the 10th papilla is bent dorsally and opens dorsally; (7) bursal papillae arranged (2/5+3); (8) spicules with a ventral velum distally; (9) living in wood pulp; (10) spicules fused for two-thirds of their length with a channel formed by their folded edges; (11) increase in body size; (12) edge of the bursa velum ruffled; (13) median bulb nearly as wide as terminal bulb [of pharynx]; (14) only remnants of transverse ridging of the inner lining of the pharynx; (15) ovoviviparous; (16) inhabitants of the beach area and the gill chamber of *Ocypode* crabs; (17) buccal tube narrowed; (18) seventh bursal papilla [i.e., the phasmid] labile; (19) third papilla opens ventrally and the fourth dorsally; (20) sixth bursal papilla is short, is placed sublaterally, and opens dorsally; (21) gubernaculum diverges proximally from the spicules (projection in lateral view); (22) eighth and ninth bursal papillae with a shared base; (23) gubernaculum proximally with a spoon-like process; (24) arrangement of bursal papillae (2/4+1+3); (25) phasmids in female anterior of anus level; (26) wall of vagina thickened; (27) teeth of metarhabdions enlarged and curved; (28) female tail conical to cupola shaped; (29) head of spicules hook shaped; (30) blind sacs at the vas deferens lost; (31) gubernaculum proximally pointed like a bow of a boat; (32) female (prodelphic) uterus with paired posterior blind sacs; (33) third and fourth bursal papillae shifted precloacally or adcloacally [i.e., to the same anteroposterior position as the cloaca]; (34) spicules distally with a U-shaped bend. [Modified from Fig. 14 of Sudhaus, 1978:452.]

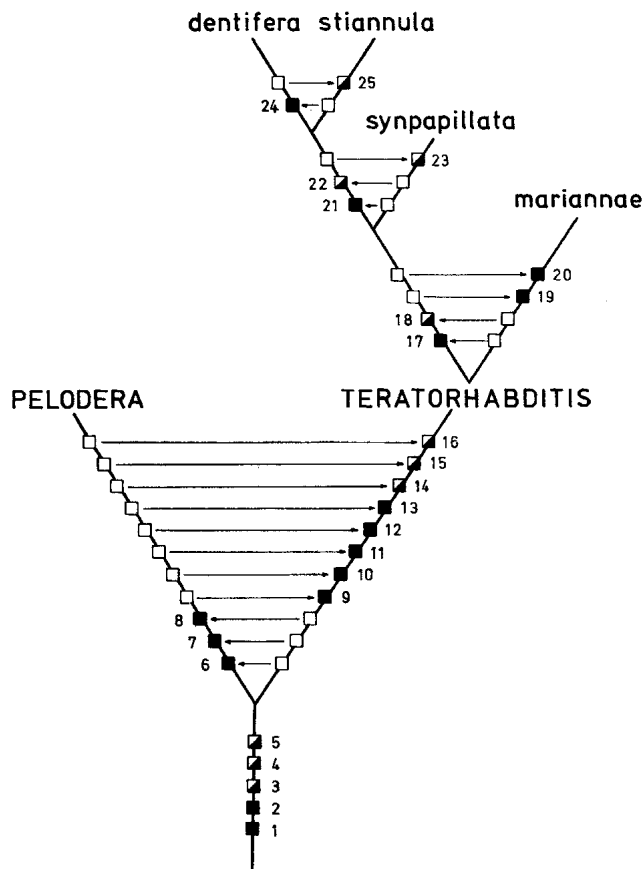


FIG. 30. Cladogram of *Pelodera* and *Teratorhabditis* and the species [of *Teratorhabditis*]. Open squares denote plesiomorphies. The apomorphies used in the argumentation are symbolized as filled squares and half-filled squares according to degree of confidence [see Fig. 29 legend]. The numbers denote the following apomorphies: (1) female tail cupola shaped with a spine; (2) spicules elongated and distally fused; (3) lips slightly offset; (4) body ungainly, cylindrical; (5) mating plug voluminous; (6) median vulva; (7) amphidelphic ovaries; (8) lips clearly offset; (9) lip margins cuticularized like *Teratocephalus*; (10) spicules fused by nearly 50% of their length; (11) a specific sphincter present in the uterus; (12) seventh bursal papilla [i.e., the phasmid; see Fitch and Emmons, 1995; Kiontke and Sudhaus, 2000] shortened; (13) cuticle with regular dots; (14) median bulb formed; (15) third and eighth bursal papillae point to the dorsal side; (16) $N=5$ chromosomes (six plesiomorphic); (17) structuring of the cuticle different within the body: at the anterior end with longitudinal ovals in regular rows and on most of the body with dots displaced in adjoining annules [cf. Fig. 1c in Sudhaus, 1985b:209]; (18) first and second bursal papillae fused basally, and seventh papilla isolated between the groups of papillae; (19) buccal tube anisomorphic; (20) viviparous; (21) female tail dagger shaped; (22) lips secondarily not offset; (23) bursal papillae 4-6 and 9+10 basally fused; (24) hermaphroditic; (25) metarhabdion warts (denticles plesiomorphic). [From Fig. 7 of Sudhaus, 1985b:222.]

morphological, and other data. A new classification, however, is not attempted at this time, even though Rhabditinae now appears to be paraphyletic with respect to major taxa that were explicitly excluded previously (e.g., Diploscapterinae, Diplogastridae, Strongylida). Such a phylogenetic view greatly expands the significance of studies of the Rhabditinae (e.g., with respect to the evolution of vertebrate and invertebrate parasitism and the evolution of morphology).

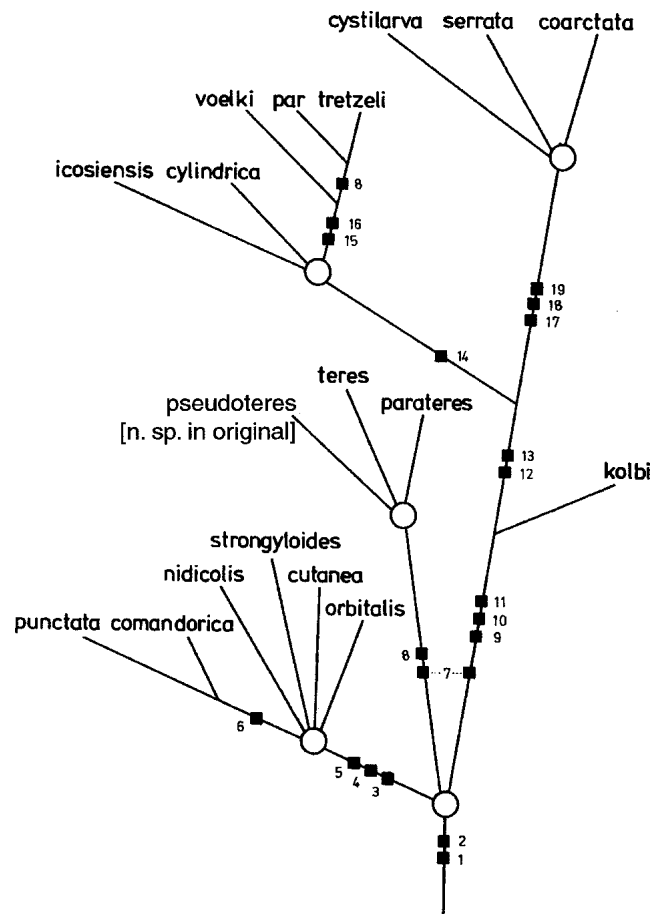


FIG. 31. Cladogram of the species of subgenus *Pelodera* of [genus] *Rhabditis* (without considering the dubious species *R. litoralis* and *R. operosa*). [*Rhabditis pseudoteres* replaces "*R. n. sp.*" of the original, since this species was subsequently described by Schulte (1989). Open circles indicate nodes of the cladogram that could not be resolved into dichotomies.] The cladogram is substantiated by the following apomorphies (filled squares): (1) female genital opening midbody and genital tracts paired; (2) lips conspicuously offset from the body; (3) spicules fused by more than 50% of their length; (4) a doubled blistery sphincter present between oviduct and uterus; (5) a special stage ("girdle-larva") in the development of the dauer juvenile with central intestine cells filled with excretory products that are moulted; (6) female tail conical; (7) pharyngeal sleeve formed (possibly synapomorphic for the *Teres* [*sensu stricto*] and *Coarctata* groups); (8) three preloocal papillae; (9) bursa anteriorly closed (arakoderan); (10) metastomal teeth stronger; (11) telorhabdions stronger; (12) bursal papillae 7-9 fused basally; (13) papillae 1, 4, and 10 open dorsally on the bursa velum; (14) bursa velum finely structured; (15) bursa narrower ["cinched in" at the middle]; (16) lips not set apart in the much smaller male; (17) third bursal papilla thickened; (18) cuticle of the dauer larva heavily sculptured; (19) dauer larvae stick to arthropods with their anterior ends and form cysts. [Modified from Fig. 2 of Sudhaus, 1987:151.]

Throughout the following discussion, however, the following caveats should be kept in mind. First and foremost, the new phylogenetic hypothesis is inferred from an incomplete representation of taxa. Although I have tried to represent the more significant groups (in terms of basal position of divergence in the tree and diversity), many interesting and possibly fundamentally important groups are entirely unrepresented. For ex-

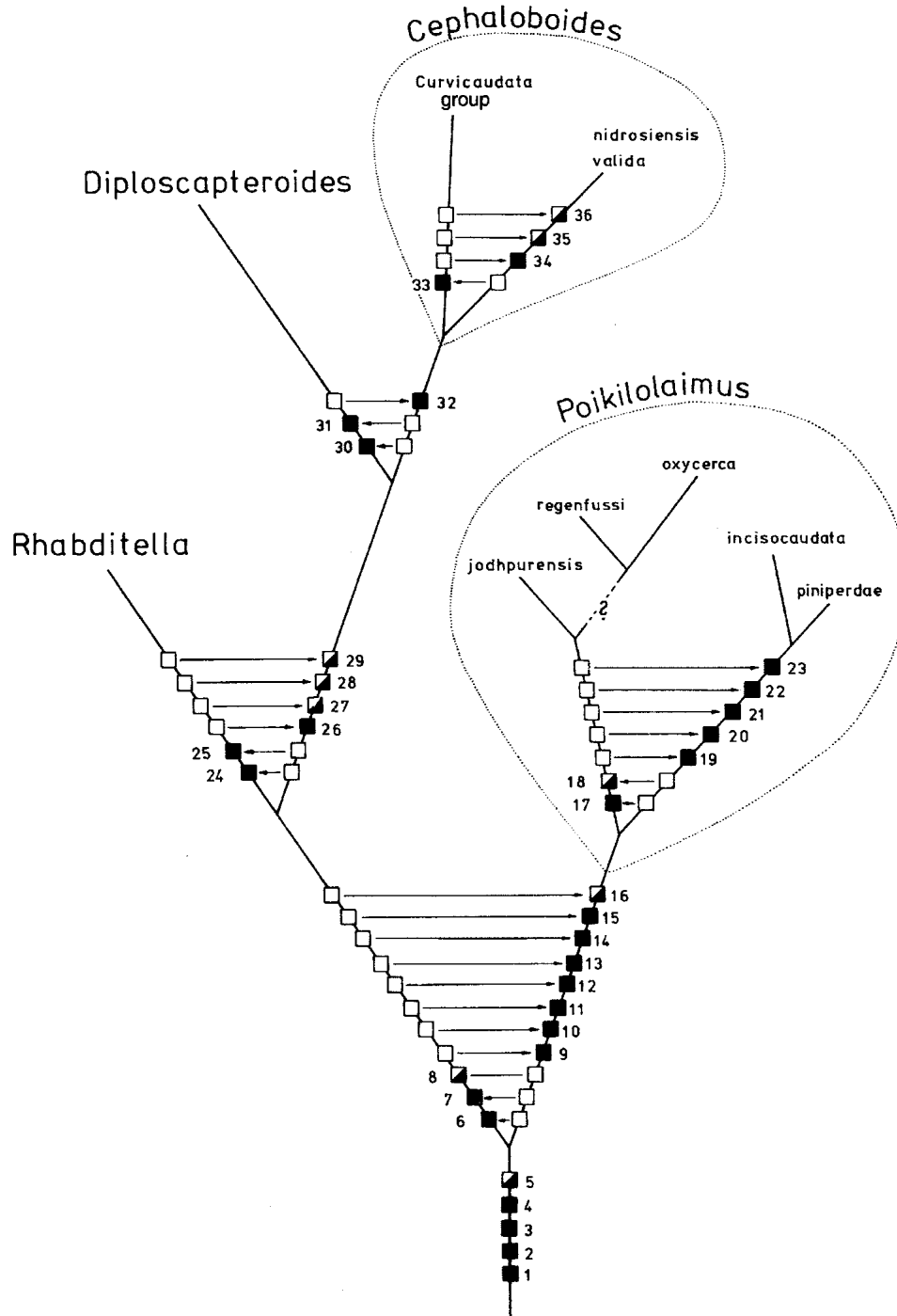


FIG. 32. Cladogram of four subgenera of *Rhabditis* and the species of subgenus *Poikilolaimus*. The apomorphies used in the reconstruction are represented as filled squares and half-filled squares according to degree of confidence [see Fig. 29 legend]. An open square denotes plesiomorphy. The numbers denote the following apomorphies: (1) bursa velum considerably reduced; (2) bursa with radially arranged papillae; (3) first, fourth, and eighth papillae lie sublaterally apart from the row of bursal papillae; (4) median bulb of pharynx weakly developed; (5) copulation according to the spiral form; (6) bursal papillae arranged (1+2/1+3+1+2) with the first, fourth, and eighth papillae in a sublateral position; (7) spicule with a ventral projection proximally and distally swollen; (8) spicule with a dorsal thorn; (9) metarhabdions with teeth; (10) cuticle able to wrinkle and inflate; (11) granules of lipids stored in the epidermis; (12) opening of excretory duct more strongly cuticularized; (13) apical lip sensilla setiform and protruding; (14) female gonad reflexed antidromously (i.e., flexure at the junction of ovary and oviduct); (15) ninth bursal papilla lost; (16) tail cupola shaped in both sexes; (17) first bursal papilla shifted prebursally; (18) head of spicule enlarged for insertion of the muscles; (19) female tail secondarily nearly conical; (20) bursal arrangement (2/1+1+2+1), with fourth and last papillae sublateral; (21) seventh bursal papilla lost; (22) reduction in body size; (23) spicule narrowed and lengthened; (24) tail thread strongly extended in both sexes; (25) waving in a tube (i.e., in the molted cuticle of the preceding second juvenile [stage]); (26) predisposition to form a double cuticle due to an incomplete last molt; (27) lips strongly offset from the body; (28) trend to shift anterior bursal papillae posterior of the cloaca; (29) copulation according to the parallel form ["bursa type" in the original] (i.e., in a parallel position); (30) lip edges cuticularized as in *Teratorhabditis*; (31) the first three bursal papillae shifted posterior to the cloaca; (32) tail cupola shaped in both sexes; (33) spicule with a distal cap of secretion; (34) transition to a peloderan bursa; (35) lips (secondarily) slightly offset; (36) spicules secondarily dagger shaped. [From Fig. 15 of Sudhaus, 1980:337.]

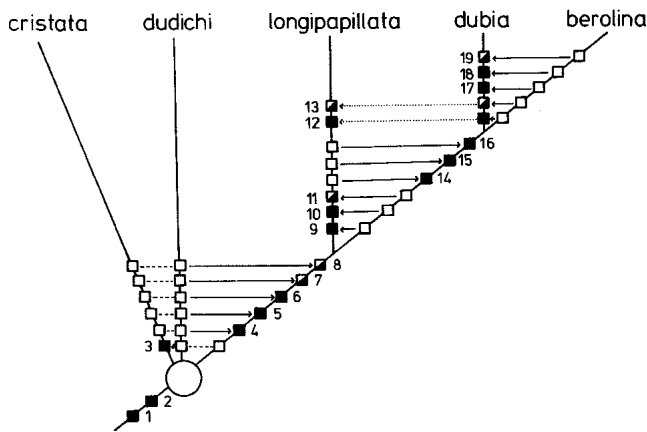


FIG. 33. Cladogram showing the phylogenetic relationship of *Rhabditis berolina* sp. n., *R. dubia*, *R. longipapillata*, *R. dudichi*, and *R. cristata*. Symbols used: filled square = apomorphy with a high degree of confidence, half-filled square = apomorphy with a lower degree of confidence, open square = plesiomorphy. The numbers denote the following apomorphies: (1) Second and third as well as fifth and sixth bursal papillae basally fused; (2) fusion of these papillae up to half their length; (3) hermaphroditism; (4) cheilorhabdions conspicuously sclerotized; (5) buccal walls diverging proximally; (6) metarhabdions each with three teeth; (7) spicules proximally without an offset knob; (8) reduction of the lip sensilla; (9) metarhabdions each with only one spoon-shaped tooth; (10) amphids shifted posteriorly; (11) cheilorhabdions specially arched; (12) bursa anteriorly closed; (13) buccal cavity particularly wide (more than 6 μ m); (14) adaptation of the life cycle to Psychodidae; (15) postcloacal papillae filiform; (16) first bursal papilla opens dorsally on the [bursa] velum; (17) female tail cupola shaped; (18) cuticular flaps beside the vulva; (19) spicules lengthened (more than 40 μ m). [From Fig. 3 of Sudhaus and Kühne, 1990:318.]

ample, no representatives of the *Monhystera* species group (of subgenus *Mesorhabditis*), *Rhabpanus*, or *Xylorhabditis* are represented. It is possible that future analyses including these taxa will necessitate a fundamental revision of the current phylogenetic view. Second, the characters used to infer the phylogeny come from a single genetic locus; thus, the assumption that the species phylogeny is identical to this gene phylogeny may not hold in some cases. Future analyses will include additional loci as well as morphological and developmental data that have any bearing on phylogenetic systematics. Third, although an attempt has been made to account for intraspecific variation, the populations sampled generally had been maintained in culture for some time with varying population sizes and could have had high inbreeding coefficients.

Phylogenetic analysis

The most conservative hypothesis: Most of the techniques for amplifying and sequencing SSU rDNA and for phylogenetic analysis have been presented elsewhere (Fitch et al., 1995). The strategy for the analysis presented here was to find only the most strongly supported clades. Because of this highly conservative strategy the “true tree” is unlikely to be rejected, but many “untrue” phylogenetic hypotheses will also not be re-

jected. Nevertheless, this method allows a good “first cut” such that the search for likely trees can be intelligently constrained without having to consider the set of all possible trees (which increases exponentially with increasing numbers of taxa). The cladogram depicted in Fig. 37 was obtained by performing a bootstrap analysis (evaluated with weighted parsimony²⁴²) using only unambiguously aligned nucleotide characters. Accordingly, branches for clades that fail to have high support (<68% bootstrap support) have been collapsed (indicating ambiguity, not polytomous branching of lineages). This very conservative estimate nevertheless shows very robust support for several relationships (Fig. 37):

1. The stronglyylid representative *Nematodirus battus* is closely related to the “*Eurhabditis*” species group.²⁴³
2. The insect-parasitic Heterorhabditidae is also closely related to the “*Eurhabditis*” species group, as suggested by Sudhaus (1993), and to the stronglyylids (see also Blaxter et al., 1998).
3. A monophyletic *Caenorhabditis* group has a branching order essentially identical to that recently proposed on the basis of morphology (Sudhaus and Kiontke, 1996).
4. *Diploscapter* species are derived from within a paraphyletic *Protorhabditis* group and are most closely related to a species of the *Xylocola* group.
5. A strongly supported clade contains the above groups and probably most other Rhabditinae that bear “posteriorly positioned” phasmids in male bursae, except for *Cruznema tripartitum* (Kiontke and Sudhaus, 2000). (See Appendix 3 for a complete discussion of this and other male tail characters.)²⁴⁴
6. A strongly supported clade includes *Parasitorhabditis* with *Crustorhabditis*, *Distolabrellus*, *Pelodera*, *Mesorhabditis*, *Rhabditoides regina*, *Rhabditoides stammeri*, and *Teratorhabditis*.
7. A close affinity of diplogastrids (*Pristionchus pacificus* and *Aduncospiculum halicti*) with *Rhabditoides inermis*.
8. A single branch leads to all the Rhabditida, at least with respect to the outgroup representatives chosen for the analysis (ascarids and plectids).

The best hypothesis we can make at the moment: Additional analyses such as neighbor-joining (Saito and Nei, 1987)

²⁴² PAUP* 4.0b4a (Swofford, 2000) was used for analyses. Only unambiguously aligned characters were used (1,477 characters of which 599 were parsimony-informative). Insertion/deletion events (“gaps” or “indels”) were ignored and were included only where unambiguously aligned. Transversions were weighted twice that of transitions; nucleotide characters were weighted equally, and 700 bootstrap replications were performed. Nearly identical results were obtained when taxa with long branches were excluded (i.e., *P. strongyloides* and *P. cystilarva*).

²⁴³ See also Fitch and Thomas (1997) with regard to this conclusion.

²⁴⁴ This hypothesis has recently been addressed at the morphological level in a taxonomically comprehensive study (Kiontke and Sudhaus, 2000).

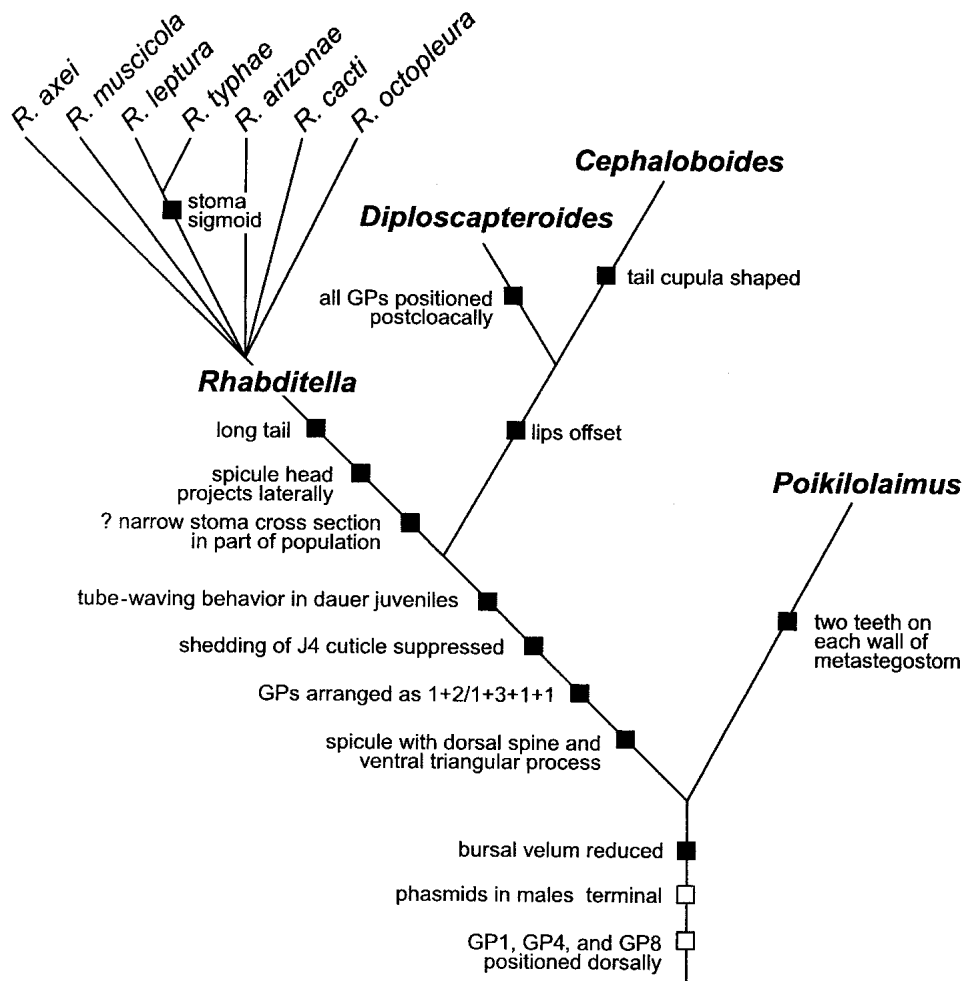


FIG. 34. Cladogram of four subgenera of *Rhabditis* including *Rhabditella*. Filled squares denote apomorphic characters; open squares denote plesiomorphies. [Modified slightly from Fig. 8 of Kiontke, 1999.]

bootstrap (2,000 replications), maximum likelihood puzzling (Strimmer and von Haeseler, 1996),²⁴⁵ and statistical tests of thousands of trees with the maximum likelihood ratio test (Kishino and Hasegawa, 1989) show additional low support²⁴⁶ for a clade that includes *Oscheius*, *Rhabditis*, *Rhabditella*, *Cephaloboides* (in the strict sense as shown in Fig. 32), *Pellioiditis*, *Cruzanema*, *Choriorhabditis*, *Heterorhabditis*, and the stronglylid representative. Low support is also provided for *Poikilolaimus* species and *Rhabditoides inermiformis* branching most basally from the other Rhabditidae. Finally, there is low support for a clade that includes all Rhabditidae but excludes the cephalobid representative (*Zeldia punctata*).

²⁴⁵ For both analyses, an HKY85 model was used that assumes that transitions are twice as likely as transversions, 40% of the characters are constant, and there is variation in evolution rate among the characters with a gamma shape parameter of 0.5 (analyses performed with PAUP* 4.0b4a; Swofford, 2000).

²⁴⁶ By "low support" is meant, for example, neighbor-joining bootstrap values <68% but >50%; in these analyses, maximum likelihood puzzling percentages were almost always lower than the neighbor-joining bootstrap values, consistent with the proposition by Strimmer and von Haeseler (1996) that the puzzling algorithm is extremely conservative.

The maximum likelihood tree: Reconstructing the branch lengths for the tree with the highest likelihood score that we could find (the "ML tree," not shown) shows that all of the ambiguities in branching order are apparently due to short branch lengths (i.e., where the accumulation of change at this locus was slow or speciation was rapid) and a resulting paucity of apomorphic changes. This result suggests that the best approach for resolving these relationships will be to obtain additional molecular data from loci that evolve slightly more quickly than 18S rRNA genes. Although it is too early to place any significance on the clades that are additionally "resolved" in this ML tree, it suggests at least one interesting possibility for a relationship that may never have been suggested before. Specifically, the *Protorhabditis*/*Diploscapter* clade may be a sister taxon to the *Caenorhabditis* clade. If this relationship is upheld in future analyses with better taxonomic and character representation, it will hold significance for comparative studies that employ the developmental genetic model *C. elegans*, especially given the remarkable degree of morphological diversity in these groups.

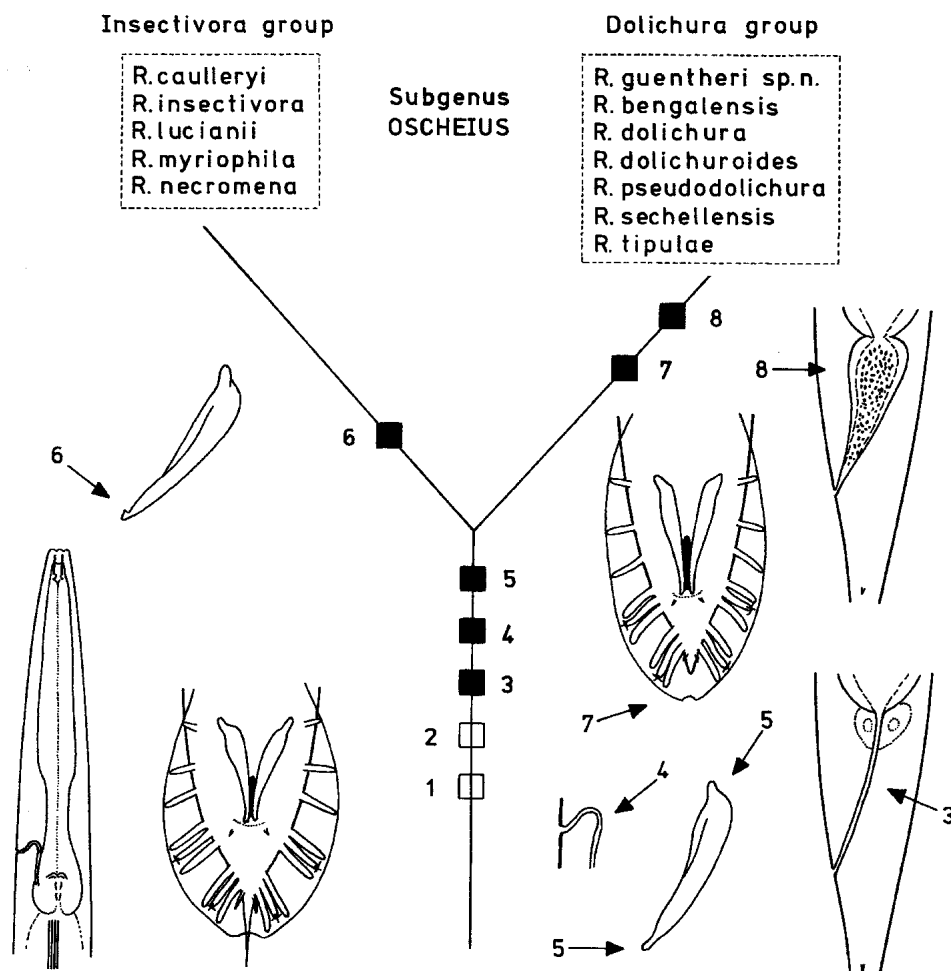


FIG. 35. Cladogram to demonstrate the monophyly of the subgenus *Oscheius* of *Rhabditis* and the sister group relationship of the *Insectivora* group and the *Dolichura* group. Filled squares = apomorphy; open squares = plesiomorphy. The numbers denote the following apomorphies: (1) vulva median; (2) female gonads amphidelphic; (3) female rectum elongated; (4) terminal duct of the cervical system coiled and its wall heavily sclerotized; (5) typical shape of spicules distally and proximally; (6) spicules distally shaped like a crochet needle; (7) bursa peloderan; (8) female rectum proximally expandable, filled with feces and undigested bacteria. [From Fig. 7 of Sudhaus and Hooper, 1994:523.]

There are as yet no data on the placement of *Operculorhabditis*,²⁴⁷ the *Monhystera* species group, *Xylorhabditis*, and *Rhabpanus*.

Reinterpretation

It is not possible in this appendix to present an adequate reinterpretation of the morphological evolution of every species group treated by Sudhaus (1976b). A full treatment will have to wait for the next monograph on this group. Instead, only some general comments can be made about the overall relationships within Rhabditinae in light of the phylogenetic hypothesis presented above (see Fig. 37).

²⁴⁷ Although a live strain (DWF1604) has been deposited at the Caenorhabditis Genetics Center (CGC) under the name of "*Operculorhabditis* sp.," this strain does not conform to the description of this subgenus; especially, females do not have an "operculum," although males do leave very large mating plugs that might have been mistaken for such a structure. Rather, this species is morphologically identical to and produces fertile progeny in reciprocal crosses with the DF5024 strain of *Distolabrellus veechi*. The SSU rDNA sequences of these two strains are also identical (D. Fitch, personal observations).

The most significant differences between the evolutionary interpretations presented here and that of Sudhaus (1976b) result from the derived position of taxa (*Parasitorhabditis*, *Protorhabditis*, and probably *Prodontorhabditis*) that were previously assumed to have primitive features and to be ancestrally diverged. Especially significant in this regard was the assumption that a glottoid apparatus, once formed, was not lost (except once in the lineage to *R. stammeri*). According to the gene phylogeny presented here, the glottoid apparatus has changed its basic structure as well as its embellishments (i.e., denticles, ridges, and warts) multiple times in the phylogenesis of the Rhabditinae.²⁴⁸ Specifically, it has been lost at least three times: once in the lineage to *Protorhabditis* and once in the lineage to *Parasitorhabditis*, as well as in the lineage to *R. stammeri*.

Because of the basal (and apparently paraphyletic)

²⁴⁸ In retrospect, perhaps this should not be surprising, given the strong selection under which feeding structures are likely to evolve and thus are likely to show convergences, reversals, or parallel changes.

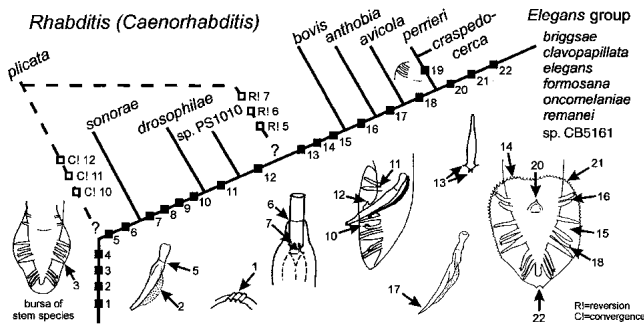


FIG. 36. Cladogram showing the phylogenetic relationships of eight of *Caenorhabditis* species and the *Elegans* group, and the two possible positions of *R. plicata* with their consequences (convergences or reversions). [Exclamation marks denote character transformations that could be alternatively interpreted as either convergences or reversals, depending on the position of *R. plicata* in the cladogram.] *Rhabditis fruticicolae* and *R. genitalis* are not included. Apomorphies are symbolized as filled squares (or open squares for *R. plicata*). The numbers denote the following apomorphies: (1) adults with 3 lateral cuticular ridges; (2) spicules with dorsal velum; (3) sixth ray papilla thickened at its base; (4) dauer juveniles unsheathed; (5) spicules with transverse seam; (6) pharyngeal sleeve present; (7) triangular tooth on the metarhabdion (R! 7: reversion to three ridges); (8) sexually dimorphic cephalic sensilla; (9) precloacal lip of type B [i.e., with a small dome of cuticularization]; (10) anterior dorsal ray in the fourth position [i.e., the fourth bursal papilla opens dorsally on the bursa velum; the "anterior dorsal ray" is the first postcloacal ray that opens dorsally]; (11) no space between the first and second ray papillae; (12) precloacal lip of type C [i.e., proximal edge of the cuticular dome flares out anteriorly]; (13) distal end of gubernaculum with lateral "ears" and forked terminal part; (14) bursa closed; (15) arrangement of rays as (2/1+3+3); (16) second ray papilla does not extend to the bursa margin; (17) spicules pointed; (18) anterior dorsal ray in fifth position; (19) hermaphroditism and the third ray papilla shifted anterior of the cloaca; (20) precloacal lip of type D (hook); (21) bursa margin serrated; (22) bursa velum terminally notched. [*Rhabditis* (*Caenorhabditis*) *sonoroae* Kiontke, 1997 replaces "sp. 1" of the original; *R. (Caenorhabditis) drosophilae* Kiontke, 1997 replaces "sp. 2" of the original; undescribed species with strain designations PS1010 and CB5161 replace "sp. 3" and "sp. 4" of the original, respectively.] [Modified from Fig. 7 of Sudhaus and Kiontke, 1996.]

divergence of *Rhabditoides* in the gene tree (as well as preliminary molecular evidence suggesting perhaps an even more ancient divergence of *Poikilolaimus* species), some of the symplesiomorphic features listed for Rhabditinae cannot be correct. In particular, the stem species of Rhabditinae apparently possessed a well-formed glottoid apparatus, since this feature is found in *Rhabditoides* (and *Poikilolaimus*). This does not reject the possibility expressed by Sudhaus (1976b) that a glottoid apparatus evolved after a precursor of such structures as denticles, ridges, and warts. Additionally, a median vulva and a pharyngeal sleeve were likely to have already been present in the Rhabditinae stem species. The number of embellishments per metarhabdion may or may not have been three.

Assuming that features shared between *Parasitorhabditis* and *Protorhabditis* were primitive resulted in the previous suggestion that the most recent ancestral form of the Rhabditinae male tail was peloderan. In view of the gene phylogeny, however, a more parsimonious in-

terpretation of male tail evolution is that the stem species of Rhabditinae had a leptoderan bursa with a radial arrangement of papillae (perhaps three situated precloacally), a rudimentary velum, and separate spicules. This form also "fits better" with the pointy tail tips and bursa-deficient forms of taxa that are closely related to Rhabditidae (i.e., Panagrolaimidae and Cephalobidae), as well as Sudhaus' proposed model of the earliest rhabditine ancestor (see Fig. 27).

These evolutionary inferences suggest that, in general, many male tail characters are likely to be phylogenetically informative (i.e., these morphological characters appear to be very consistent with the molecular data).²⁴⁹ For example, phasmid position in the male tail relative to the posterior papillae is a highly informative character; in Rhabditinae, phasmid position shifted very few times from anterior to posterior. Such a shift occurred once in the lineage leading to a group including "*Eurhabditis*," *Caenorhabditis*, *Protorhabditis*, and Strongylida (Kiontke and Sudhaus, 2000; see also Appendix 3), although a reversal could have occurred in the lineage to *Cruzanema*, and once in the stem lineage to *Poikilolaimus*. However, one of the more homoplasious of the male tail characters is the tail tip. In this respect it should also be noted that a peloderan tail tip could be plesiomorphic for "*Eurhabditis*" and that a leptoderan tail tip could be due to a reversal²⁵⁰ (as originally proposed by Sudhaus for Rhabditinae).

One of the more astonishing conclusions from the gene phylogeny is that Rhabditinae (as it currently stands) is paraphyletic with regard to taxa that have even been placed in different groups: e.g., order Strongylida and family Diplogastridae.²⁵¹ Strongylids apparently were derived from a clade containing "*Eurhabditis*"²⁵² and diplogastrids were probably derived from a *Rhabditoides* lineage. In this context, the observation seems very foresighted that *Rhabditoides* species "attain a high degree of similarity to Diplogastridae with regard to the arrangement of papillae, the extensive reduction of the bursa velum, and the threadlike tail" (Sudhaus, 1976b:29).

This phylogenetic hypothesis is significant not only because it suggests Rhabditinae is paraphyletic (and therefore suggests comparisons that may not otherwise have been appreciated) but also because it places important developmental models into an appropriate

²⁴⁹ Using a smaller set of taxa, Fitch (1997) also suggested that male tail characters were not only consistent with data from 18S rRNA gene sequences, but were complementary in some cases (i.e., male tail characters were sometimes phylogenetically informative where 18S data failed to be informative and vice versa).

²⁵⁰ In this case, "reversal" refers only to the gross morphological level and is not meant to connote a direct reversal of the underlying mechanism. In fact, leptoderan tail tips in different groups (as well as different peloderan tail tips) appear to be constructed in fundamentally different ways at the cellular level (Fitch, 2000; Nguyen et al., 1999).

²⁵¹ This paraphyly has been previously noted by Fitch and Thomas (1997) and Blaxter et al. (1998).

²⁵² Note that the composition of this taxon must be altered if *Poikilolaimus* species are to be excluded from "*Eurhabditis*."

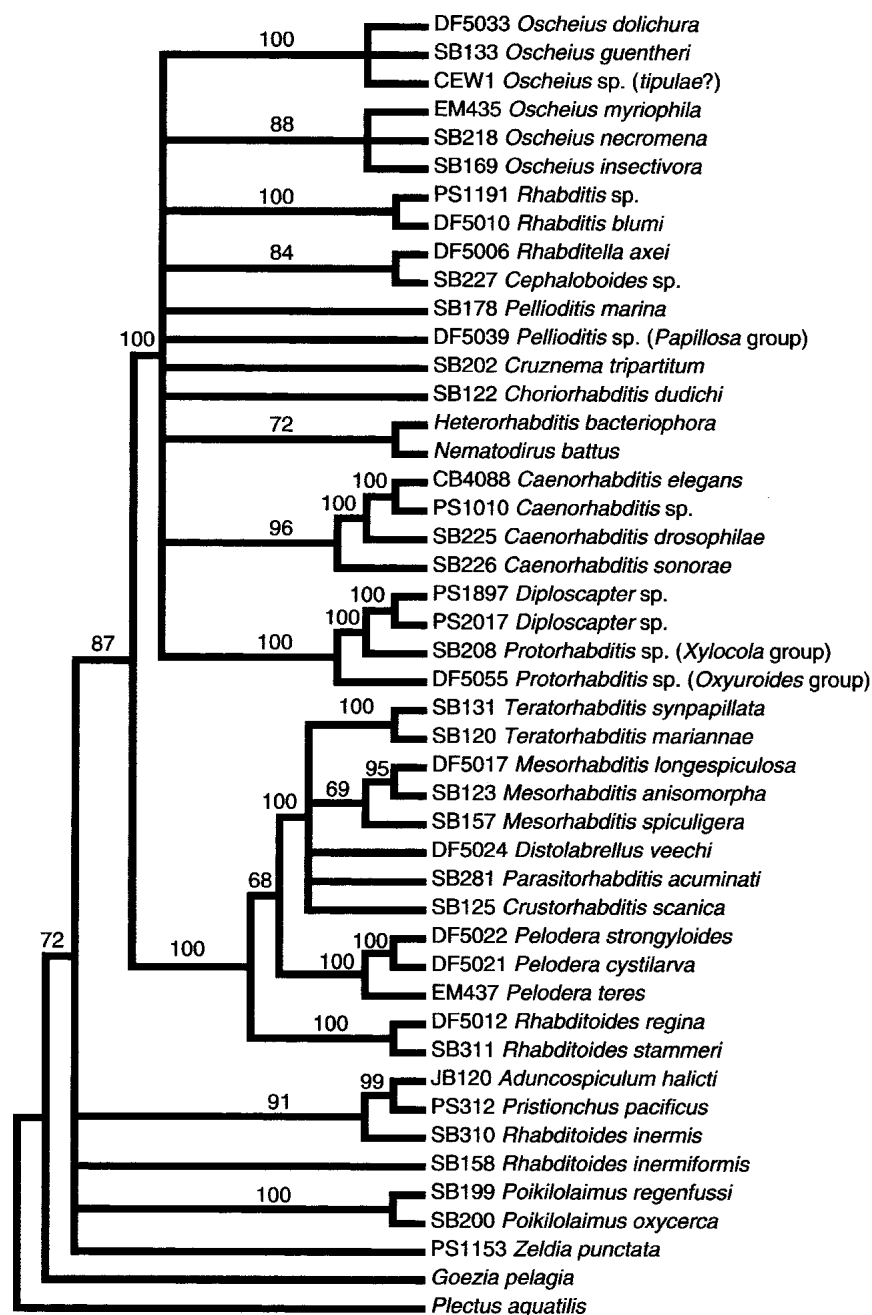


FIG. 37. Results of a preliminary phylogenetic analysis of SSU rDNA by weighted parsimony bootstrap. Sequences deposited in GenBank have accession numbers U13932-U13936 (from Fitch et al., 1995; U13936 corrected by J. Vanfleteren and A. Vierstaete, Univ. of Gent) and AF082996-AF083028 (Fitch et al., unpubl.). Sequences obtained from GenBank include *N. battus* (U01230), *H. bacteriophora* (AF036593), *C. elegans* (identical to X03680), *Diploscapter* sp. PS2017 (U81586), *A. halicti* (U61759), *Z. punctata* (U61760), and *Plectus aquatilis* (AF036602). Alignments were constructed using secondary structure predictions for some key taxa kindly provided by R. De Wachter (Univ. of Antwerp). Strain designations are listed before species names. Polytomies represent uncertainty in the branching order (i.e., <68% bootstrap support), not simultaneous branching. A full analysis will be presented elsewhere (Fitch et al., unpubl.).

phylogenetic context.²⁵³ For example, *C. elegans* and *Pristionchus pacificus* (Sommer et al., 1996), both of

which are becoming important genetic as well as developmental models, are more closely related to each other than previously thought and are less closely related to *Panagrellus redivivus*, for which the entire post-embryonic cell lineage has been obtained (Sternberg and Horvitz, 1981, 1982).

²⁵³ See Fitch and Thomas (1997) for a review of studies that use these model systems in comparative and evolutionary studies of especially developmental mechanisms.

APPENDIX 3

REINTERPRETATION OF MALE TAIL CHARACTER
HOMOLOGIES AND EVOLUTION

David Fitch

One of the most important features used to infer phylogenetic relationships in Rhabditinae (and presumably in some other nematode groups) is the suite of characters known collectively as the male copulatory bursa (i.e., the bursa velum with bursal papillae, including the phasmids, and the tail tip). Only recently have tools become available that allow the cellular and developmental analysis required to understand the ontogenetic origins of these characters, especially important for proposing indicators for homology for the caudal papillae. Here, a comparison is presented between the results of recent studies using these tools and the results of the older but more phylogenetically representative analyses that were based primarily on adult states. First, a brief overview is presented of how the developmental tools have allowed new indicators of homology for tail tip and caudal papilla characters. Second, a brief reinterpretation of male tail evolution is presented, so far as this is feasible with the limited phylogenetic representation of taxa for which these tools have been used (see also Fitch, 2000).

*Tail tip*²⁵⁴

The rhabditid tail tip is formed primarily from three or four hypodermal cells that originate during embryogenesis. The generally tapered form of these cells remains unchanged in both sexes throughout development until near the end of the last juvenile stage. At this point in males (and sometimes to a lesser extent in females, as in *R. strongyloides* during the formation of a cupola-shaped tail tip), tail morphogenesis occurs such that cells in the male tail change shape, reduce their volume, and “retract” inwardly and anteriorly. The adult cuticle flattens in the wake of these retractions, forming the bursa velum. In most **peloderan** species,²⁵⁵ male tail morphogenesis originates at the tail tip, where the tip cells retract away from the juvenile cuticle, resulting in a rounded (blunt) shape. In **leptoderan** species, morphogenesis does not generally affect the tail tip cells or at least does not greatly affect the most

posterior cell, resulting in a retention of the pointed shape of the juvenile tail tip to greater or lesser extents.²⁵⁶ Because rhabditid female tail tip cells usually do not undergo this morphogenetic change, their tail tips are usually pointed or cupola shaped.²⁵⁷

Although leptoderan tail tips may be generally distinguished from peloderan ones by retaining much of the juvenile cellular form, not all leptoderan states are equivalent. In many leptoderan tail tips (e.g., in the *Rhabditella* subgenus), the four cells that form the male tail tip remain unfused, just as they are in the juvenile stages. Other leptoderan tail tips (e.g., at least one unidentified species in the *Rhabditis* subgenus) may not strictly retain the juvenile state for all of the cells, such that the anterior tail tip cells fuse while the most posterior cell (homologous to hyp10 in *C. elegans*) remains unfused.

Similarly, not all peloderan tail tips are equivalent. All four male tail tip cells fuse before they retract in *C. elegans*, but do not fuse at all in *R. typica*. Even the tail tip cells themselves may not be entirely equivalent, since there are four cells that make the tail tip in some clades (e.g., “*Eurhabditis*”), but only three cells in other clades (e.g., *Pelodera-Teratorhabditis*). Because morphologically similar tail tips may have very different cellular bases, such similarities could be mistaken as evidence for common ancestry on the basis of adult morphology alone. For example, the reversals that are proposed in some lineages may actually represent new, derived states. A clearer picture of the evolution of this feature can come only from continued exploration at the cellular and developmental levels.

Caudal papillae

Terminologies: Sudhaus and Kiontke (1996) and Kiontke and Sudhaus (2000) have proposed precise definitions for terms that have been used to describe the papillae in the caudal region of rhabditid males. Accordingly, the term **caudal papillae** is used in a broad sense to refer to the series of subventral papillae that lie anterior and posterior of the cloaca on the male tail, regardless of whether or not they occur in a bursa. Although this definition excludes the circumcloacal papillae, phasmids may be included (e.g., where they may not be distinguishable from the other papillae by light microscopy). **Bursal papillae** are only those caudal pa-

²⁵⁴ Most of the work described here on the development of tail tips is shown, but not thoroughly discussed, by Fitch and Emmons (1995) and Fitch (1997). Complete serial sections of developing *C. elegans* male tail tips at several different stages have been analyzed by transmission electron microscopy; development in several additional representative species has been analyzed by immunofluorescent staining with an antibody that recognizes adherens junctions (Nguyen et al., 1999).

²⁵⁵ There may be cases in which the tail tip cells are essentially “leptoderan” and pointy in terms of the retention of the juvenile state, but in which the cuticle of the velum still encompasses the tail tip cells (and thus technically “peloderan”). This dichotomous terminology thus does not encompass the diversity of tail tip forms.

²⁵⁶ Retention of the juvenile form does not necessarily imply that an evolutionary paedomorphic change has occurred (for this inference, of course, we need to know the ancestral form). Rather, this terminology refers only to the progression of the morphogenetic process in these cells.

²⁵⁷ The cupola-shaped tail tips of *R. strongyloides* females are due to retraction of cells anterior to the tail tip (which thus form the convex base of the cupola), not the tail tip cells themselves (which thus retain the point). Other cupola-shaped tails (e.g., *R. palmarum*) may be formed earlier than the last juvenile stage.

pillae that are associated with the bursa velum, regardless of whether or not the bursa is well developed or rudimentary. Again, this term may include phasmids that are not easily distinguishable from the other bursal papillae. **Rays** are only those bursal papillae that are not phasmids. These rays are considered to be serially homologous (homonomous), and are presumably homologous to the muscular rays of Strongyloidea, from which the term was borrowed. Sudhaus and Kiontke (1996) also referred to the relative, ordinal positions of the caudal papillae as P1-Pn (from anterior to posterior). The Pn designation was not intended to suggest homologous comparisons (e.g., the dorsally opening P5 of *C. elegans* is probably homologous with the dorsally opening P4 of *R. anthobia*).²⁵⁸ **Genital papillae** are homologous to rays, but may not necessarily be associated with a bursa velum. Phasmid organs will be called **phasmids**, regardless of their particular morphology (e.g., ray-like or barely discernible apertures). Genital papillae arising during development of the male tail in the J4 stage of rhabditids not yet associated with a bursa velum will sometimes be referred to as **ray papillae**.

Ray homologies: Criteria for proposing homologies for particular ray papillae in different species are crucial for using these characters to infer phylogenetic relationships or for reconstructing evolutionary change. However, the specific patterns of papillae in adults result from morphogenetic movements that vary among different species (Fitch and Emmons, 1995), suggesting that ordinal positions of caudal papillae in adults alone are insufficient criteria for proposing interspecific homologies between particular papillae. Fitch and Emmons (1995) and Fitch (1997) showed that, at least within Rhabditidae, homologies for the ray papillae could be proposed based on the patterns of their developmental origins in the lateral hypodermis, since these patterns were identical (symplesiomorphic) in all of the rhabditids studied (see Fig. 38A).

This pattern of ray cell origins in the lateral hypodermis is a result of cell lineages that produce both ray cells and hypodermal "tail seam" cells in the same relative positions in different species (Fitch and Emmons, 1995). In all the rhabditid species studied so far, each ray is produced from three cells of an initial four-cell cluster (see Fig. 38A). In *C. elegans* and *Panagrellus redivivus* (for which the cell lineages have been completely determined, but presumably also in other rhabditid species), each cluster of four cells descends from a precursor cell called *Rn.a* (where $n = \{1, 2, \dots, 9\}$ for the left and right sides; Fig. 38D).²⁵⁹ One cell in each cluster undergoes apoptotic cell death, and each ray papilla

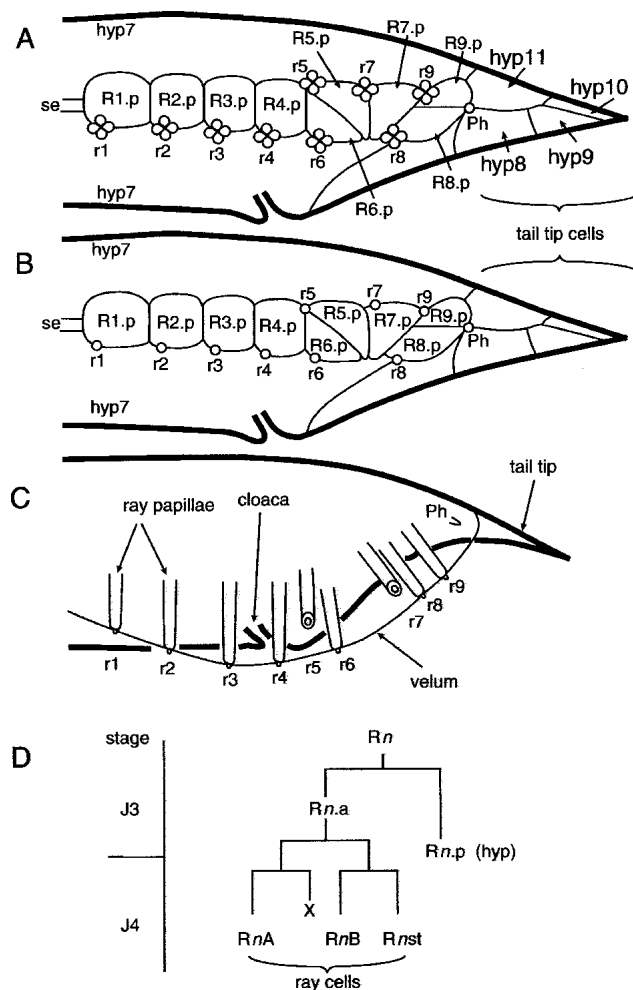


FIG. 38. Archetype of rhabditid male tail development. A-C) View is of the left lateral hypodermal surface, anterior to the left. Thick lines represent body outline; thin lines represent cell boundaries (A, B) or external morphological structures (C). Ph = phasmid; se = body seam (i.e., the lateral field that often produces lateral alae in adults and some juvenile stages); hyp7 = main body hypodermal syncytium. A) Early J4 (L4) after ray cell lineages are completed, showing the **symplesiomorphic** pattern of ray cell clusters of four cells each (r1-r9) and tail hypodermal cells (Rn.p). B) Archetypal late J4 stage. For each cluster of four ray cells shown in (A), one cell undergoes apoptotic cell death (X in D) and the two neuronal cells (RnA and RnB) sink below the hypodermal surface, leaving only the structural cell (Rnst) at the hypodermal surface (the single circular cells labeled r1-r9). C) Archetypal adult bursa with ray papillae (r1-r9). In this archetype, r5 and r7 open on the dorsal surface of the bursa velum while the other ray papillae open at the velum margin. If the ray structural cells remain at the same positions at which the ray cells originate, this hypothetical "default" pattern of ray papillae would result from male tail morphogenesis. D) Canonical ray cell lineage in *C. elegans* (from Sulston et al., 1980, amended 1988).

is formed from the three remaining cells: a structural cell (Rnst) that anchors the distal tip of the ray to the fan (velum) cuticle, and the dendritic endings of two neuronal cells (RnA and RnB; see Fig. 38). The sister of *Rn.a*, called *Rn.p*, is a "tail seam" hypodermal cell. Although the ray cell lineages of other rhabditid species are currently unknown, rays in these species are derived from cells that originate during development

²⁵⁸ This ordinal labeling scheme also should not be confused with the ventral Pn cells (as defined in *C. elegans*), some of which are precursors to the female vulva (Sulston and Horvitz, 1977).

²⁵⁹ Cell nomenclature is that used for *C. elegans* (Sulston et al., 1980; White, 1988:119).

of the last juvenile (J4 or L4) stage in the same relative positions as in *C. elegans*.

Because this specific and complex pattern of relative positions and cellular connections is the same (symplesiomorphic) in all the rhabditids studied so far, homologous ray papillae can be postulated to be those whose cells originate at the same relative position (Fitch and Emmons, 1995; Fitch, 1997). To facilitate explicit homologous comparisons, these rays are hereby designated r1 to r9, as shown in Fig. 38A-C. In an outgroup representative, *P. redivivus*, the pattern of genital papilla origins (Sternberg and Horvitz, 1982) is nearly identical to that of the rhabditids, except that the homologs of what would be the anterior two papillae in most rhabditids are absent in *P. redivivus*, further supporting this pattern as a plesiomorphy for Rhabditidae (see Appendices 1 and 3 of Fitch [1997] for a more detailed argument using this outgroup representative).

Although the pattern of ray cell origins is the same in different species, subsequent morphogenetic movements of ray and hypodermal cells differ substantially. During this morphogenetic process, the dendritic endings of the two ray neurons sink slightly into the hypodermis, leaving only the structural cells of each ray at the surface (the small circles labeled r1-r9 in Fig. 38B). These cells become anchored in the cuticle in a taxon-specific pattern. This planar array of structural cells in the J4 cuticle prefigures the species-specific pattern of rays in the adult male tail (Fig. 38C). During the next period of morphogenesis, the cells in the male tail retract inwardly and anteriorly, causing the lateral cuticle to collapse, fold, and flatten into the bursa velum.²⁶⁰ Because the apical tips of the rays are anchored in the epidermis, the rays are formed as tubes of cytoplasm in the wake of the retraction. In the archetypal adult bursa shown in Fig. 38C, which represents the hypothetical (developmental default) state in which ray cell migrations would not occur, the rays would arise at the same positions at which the ray cells originate. So far, there is no species characterized in which no ray cell migrations occur and the archetype thus does **not** represent an ancestor (see Fitch, 1997; Fitch, 2000). Because of these migrations, which may result in very different anteroposterior orders of the ray papillae (for specific examples, see Fitch and Emmons, 1995; Fitch, 2000), it is not always possible to infer which rays are homologous by comparing only adult male tails. There are, however, some highly conserved features; for example, the r5 and r7 cells remain dorsal relative to the other ray cells throughout morphogenesis, and thus open on the dorsal surface of the bursa velum in all species characterized. Prior to male tail morphogenesis, the other ray cells shift along the anteroposterior axis ventral to r5

and r7. Because of this, r5 can often be found anterior of r3 (e.g., in *R. (Pelodera) stronglyloides*, the order of the bursal papillae from anterior to posterior is: r1 r2 / r5 r3 r4 r6 Ph r8 r9 r7, where Ph represents the phasmid and the slash represents the relative position of the cloaca).

Phasmids: Phasmids are formed very early during juvenile development and differ from ray sensilla in cellular structure and function (Sulston et al., 1980). For example, phasmids can be distinguished by having a little hole instead of a seta at the papilla terminus (Sudhaus and Kiontke, 1996) and by staining with lipophilic dye such as DiO, carmine indigo, or with FITC (see Fitch and Emmons, 1995; Kiontke and Sudhaus, 2000). Immunofluorescent staining with an antibody that recognizes an epitope in *zonulae adherens* (ZA) junctions displays a unique structure of the phasmid cells that is maintained throughout juvenile development in both females and males (Fitch and Emmons, 1995).

In Rhabditidae, phasmid position can be generally described as either posterior or anterior of ray papillae r7–r9. In the species examined with the ZA immunofluorescent staining, phasmid position in the male bursa corresponds closely with phasmid position in the female. When male phasmids lie posterior of all the ray papillae, female phasmids lie posterior to the cells that form the lateral seam, and phasmids in both sexes lie adjacent to the tail tip cells. When male phasmids are anterior of r7–r9, female phasmids lie within the lateral seam, and phasmids in both sexes are spaced away from and anterior to the tail tip cells. According to the rhabditid phylogeny presented in Appendix 2, phasmid position has changed rarely in Rhabditinae, and clearly delineates a clade containing “*Eurhabditis*,” *Protorhabditis*, and *Caenorhabditis* (among other species groups) and excluding such groups as *Pelodera*, *Teratorhabditis*, *Crustorhabditis*, *Parasitorhabditis*, and *Rhabditoides* (among others) (see Kiontke and Sudhaus, 2000).²⁶¹

This apparently “saltational” evolutionary change could have resulted from a rather simple developmental change (Fitch, 1997; see also Kiontke and Sudhaus, 2000). In *C. elegans*, the phasmid and r7–r9 papillae on each side are derived from the same blast cell, called the T cell (TL on the left and TR on the right), which divides asymmetrically to produce the phasmid lineages from the posterior daughter and the r7–r9 lineages from the anterior daughter (Sulston and Horvitz, 1977). A simple reversal of this one asymmetric cell division would place the phasmid lineages anterior to those producing r7–9 (see Fitch, 1997:165).²⁶²

²⁶⁰ This retraction occurs to various extents in different species, corresponding with the size of the velum.

²⁶¹ Posterior-most phasmid position in Rhabditinae is homoplasious with posterior-most phasmid position in Panagrolaimidae (Kiontke and Sudhaus, 2000).

²⁶² In *C. elegans*, the polarity of the T cell division is governed by the LIN-44 signaling pathway (Herman and Horvitz, 1994). In reduced-function mutants

Reinterpretations

Form of the tail tip and the bursa: Although a peloderan bursa was originally proposed for the most recent common ancestor of the Rhabditinae, the SSU rRNA gene cladogram (see Appendix 2) suggests that a conical, leptoderan bursa was ancestral. Because of the probably basal position of *Poikilolaimus* and *Rhabditoides* in Rhabditinae, the leptoderan form (and rudimentary bursa velum) of these species is not derived from a peloderan form as previously suggested (Sudhaus, 1976b). This arrangement has additional implications with regard to the polarity of changes in other taxa. For example, the broad, planar, peloderan bursa apparently evolved early in the Rhabditinae, after the divergence of these species from *Rhabditoides* and Diplogastridae, such that most changes are actually predicted to be peloderan-to-leptoderan. However, because the cellular anatomies and developmental profiles of different leptoderan and peloderan tail tips can be so different, these peloderan-to-leptoderan changes cannot be regarded with any certainty as reversals, but may be novel, derived states (Nguyen et al., 1999).

The developmental analyses provide additional insight with regard to the conditions that might allow the transformation from peloderan to leptoderan tail tips. As stated above, leptoderan tail tips result from the retention of the juvenile state. Thus, it is not that an extension of the adult female tail is a prerequisite to the evolution of a leptoderan tail tip, but that a pointed tail tip exists in juveniles, a symplesiomorphic condition. The conclusion that reduction and (or) radial arrangement of the bursa is neither sufficient nor required for forming a leptoderan tail tip is supported not only by the species comparisons of Sudhaus (1976b) but also by mutations in *C. elegans* that affect tail tip development without affecting the development of the bursa velum (Y. Yang, T. Del Rio, and D. Fitch, unpubl.).

Papilla number and arrangement: The inference that the ancestral condition for Rhabditinae was 10 bursal papillae remains unchanged, although the spaces between the papillae may not have been equal and one of these bursal papillae is the phasmid.²⁶³ After the changes in phasmid position to the posterior-most (10th) position, the phasmids became smaller. This size reduction may have been due at least partially to the phasmid position itself: The breadth of the bursa velum is often much less extensive in the posterior as opposed to the mid-bursa region. Phasmid position and velum

size cannot be the only explanation, because phasmids can be different sizes in species of the same clade that have similar velum sizes (e.g., *Caenorhabditis*; see Sudhaus and Kiontke, 1996). It is possible, for example, that the degree of adherence of the distal terminus of the phasmid to the cuticle may influence whether phasmids are elongated during male tail morphogenesis like the rays (D. Hall, pers. comm.). This reduction in the size of the phasmid papilla does not indicate any trend toward loss, however, since the phasmids are present in all Rhabditidae species investigated so far (Kiontke and Sudhaus, 2000). Because phasmids are not posterior-most in *Rhabditoides*, any inferred "reduction" of the 10th papilla in these species cannot be due to the same changes as reduction of phasmid size in "*Eurhabditis*," for example.

Changes in the number of ray papillae can be correlated with the loss of particular ray cell lineages in developmental analyses. For example, in *R. blumi* (of the *Adenobia* species group), the r8 cell lineage fails to occur (although the R8 blast cell does appear), resulting in only eight rays (Fitch and Emmons, 1995; Fitch, 1997). (The small ninth papilla is the phasmid.) Aberrations with 10 papillae result from an ectopic ray lineage expressed anterior of r1 (Fitch and Emmons, 1995). Because r8 often appears in the seventh antero-posterior position (P7), this loss correlates well with previous observations of "reduction" of the seventh papilla (Sudhaus, 1976b) in species in which phasmid position is posterior-most. However, the correlation cannot be carried to the species in which phasmid position is mid-bursal, since the phasmid is generally the seventh papilla (P7) in these species. That is, the difference between species with mid-bursa phasmid position (e.g., *Mesorhabditis*, *Pelodera*) and species with posterior-most phasmid position (e.g., *Caenorhabditis*, "*Eurhabditis*") results from a shift in phasmid position along the antero-posterior axis (and a corresponding reduction in phasmid size when in the posterior position). Thus, the two different kinds of "seventh papilla labilities" discussed by Sudhaus (1976b) involve nonhomologous papillae and should not be confused (e.g., the phasmid as the labile seventh papilla on pp. 16 and 22; r8 as the labile seventh papilla on pp. 32 and 35).

Because of the basal positions of *Rhabditoides* and *Poikilolaimus* in the gene cladogram (Appendix 2), the best hypothesis for the number of precloacal papillae in the most recent common ancestor of Rhabditinae is three. Depending on how the deeper branches within Rhabditinae will be resolved, the three precloacal papillae of "*Eurhabditis*" species would thus be either conserved (plesiomorphic) or due to reversal.

Other hypotheses for the evolution of papilla arrangements may also be modified (or supported) based on the recent developmental analyses. For example, the hypothesis for the origin of three precloacal papillae in the *Teres* species group by addition of a new 11th papilla

of the *lin-44* gene, the polarity of this division is reversed. In the simplest model for the evolution of posterior phasmid position, a new pattern of activity of the LIN-44 signaling pathway could have occurred (see Fitch, 1997; Kiontke and Sudhaus, 2000).

²⁶³ The hypothetical default development (i.e., the archetypal pattern without ray cell migrations) from the symplesiomorphic pattern of cell origins in the lateral hypodermis does not yield equal ray spacings (Fig. 38A). Of course, this archetypal pattern is also not likely to have been expressed in the most recent common ancestor to Rhabditinae (Fitch, 1997).

and concomitant deletion of the seventh papilla is not supportable. Instead, r3 in *R. teres* does not migrate posterior to reside close to r4 and r6 (as it does in *R. strongyloides*, for example), but remains closer to the position in which the r3 cell lineages originated during juvenile development. Indeed, most (if not all) of the ray papilla patterns in Rhabditinae can be explained by ray cell migration rather than by addition-deletion models. As predicted by the archetypal model (Fig. 38), the dorsal positions of the r5 and r7 cell clusters in the J4 lateral hypodermis are likely to be highly conserved (resulting in papillae r5 and r7 terminating on the dorsal surface of the bursa velum), with the other ray cell clusters migrating along the anteroposterior axis below r5 and r7 (resulting in different arrangements of papillae r1, r2, r3, r4, r6, r8, and r9 with regard to the dorsal r5 and r7 while maintaining the relative order among the seven lateral papillae). The ray arrangements are superimposed over the phasmid (which is patterned early during development, is positioned mid-bursa, and is ray-like in some species lineages, but is posterior-most and sometimes inconspicuous in other lineages). Thus, the peculiar morphology of the phasmid, the landmark dorsal rays (r5 anterior, r7 posterior), and the conserved order of the other (lateral) rays relative to each other now allow homologies to be predicted accurately for other species in which detailed developmental analyses have not yet been performed (except perhaps for cases in which certain papillae have been lost or gained).

With these new interpretations of character homologies, a new phylogenetic reconstruction using these morphological characters (in progress) should provide not only an important confirmation or test of the molecular results but may also help resolve relationships that have been difficult to resolve in the past. An understanding of the ontogeny (and thus perhaps the developmental constraints) of these characters additionally provides tools for building models of character evolution that could additionally aid resolution (see Fitch, 1997). For example, there is probably a good deal of flexibility allowed for changing the positions of the lateral ray papillae relative to the two dorsal ray papillae (r5 and r7) along the anteroposterior axis in the male tail. However, the anteroposterior order of the lateral papillae relative to each other (i.e., r1-r2-r3-r4-r6-r8-r9) is probably difficult or impossible to change because it is unlikely that a lateral ray cell can jump over an adjacent ray cell (at least, this has never been observed, even in mutants in which the identities of the ray cells are altered and certain rays move together and sometimes fuse [Baird et al., 1991]). In combination with classical morphological studies, these new molecular and developmental tools provide an outstanding opportunity for tackling the difficult questions of how Rhabditidae are related and how such a diversity of forms has evolved.

LITERATURE CITED

- Ambros, V., and Fixsen, W. 1987. Cell lineage variation among nematodes. Pp. 139-159 in (R. A. Raff, and E. C. Raff, eds.) *Development as an evolutionary process*. MBL lectures in biology, vol. 8. New York: Alan R. Liss.
- Andrássy, I. 1958. Erd- und Süßwassernematoden aus Bulgarien. *Acta Zoologica Academiae Scientiarum Hungarica* 4:1-88.
- Andrássy, I. 1962. Neue Nematoden-Arten aus Ungarn. I. Zehn neue Arten der Unterklasse Secernentea (Phasmidia). *Acta Zoologica Academiae Scientiarum Hungarica* 8:1-23.
- Andrássy, I. 1966. Erd- und Süßwasser-Nematoden aus Ghana Klasse Secernentea (Phasmidia). *Annales Universitatis Scientiarum Budapestinensis de Rolando Eötvös Nominatae, Sectio Biologica* 8:5-24.
- Andrássy, I. 1970. Freilebende Nematoden aus Vietnam. *Opuscula Zoologica Budapest* 10:5-31.
- Andrássy, I. 1976. *Evolution as a basis for the systematization of nematodes*. London: Pitman, London.
- Artigas, P. 1927. Nematodeos de invertebrados. V. *Cruzinema cruzinema* novo genero e nova especie. *Boletim Biológico Laboratório de Parasitologia Faculdade de Medicina de São Paulo* 10:209-211.
- Baird, S. E., D. H. A. Fitch, and S. W. Emmons. 1994. *Caenorhabditis vulgaris* sp. n. (Nematoda:Rhabditidae): A necromenic associate of pill bugs and snails. *Nematologica* 40:1-11.
- Baird, S. E., D. H. A. Fitch, I. Kassem, and S. W. Emmons. 1991. Pattern formation in the nematode epidermis: Determination of the arrangement of peripheral sense organs in the *C. elegans* male tail. *Development* 113:515-526.
- Baldwin, J. G., L. M. Frishe, J. T. Vida, C. D. Eddleman, and W. K. Thomas. 1997. An evolutionary framework for the study of developmental evolution in a set of nematodes related to *Caenorhabditis elegans*. *Molecular Phylogenetics and Evolution* 8:249-259.
- Bastian, H. C.. 1865. Monograph on the Anguillulidae, or free nomatoids, marine, land, and fresh-water; with descriptions of 100 new species. *Transactions of the Linnean Society of London* 25:73-184.
- Blaxter, M. L., P. De Ley, J. R. Garey, L. X. Liu, P. Scheldeman, A. Vierstraete, J. R. Vanfleteren, L. Y. Mackey, M. Dorris, L. M. Frishe, J. T. Vida, and W. K. Thomas. 1998. A molecular evolutionary framework for the phylum Nematoda. *Nature* 392:71-75.
- Bovien, P. 1937. Some types of association between nematodes and insects. *Videnskabelige Meddelelser fra Dansk Naturhistorik Forening (København)* 101:1-114.
- Buckley, J. J. C. 1931. On a new species of *Rhabditis* found in an ice-chest. *Journal of Helminthology* 9:197-204.
- Bütschli, O. 1873. Beiträge zur Kenntnis der freilebenden Nematoden. *Nova Acta der Kaiserlich-Leopoldinisch-Carolinischen Deutschen Akademie der Naturforscher (Dresden)* 36:1-144.
- Bütschli, O. 1876. Untersuchungen über freilebende Nematoden und die Gattung *Chaetonotus*. *Zeitschrift für wissenschaftliche Zoologie* 26:363-413.
- Chitwood, B. G., and M. B. Chitwood. 1950. *Introduction to nematology*. Section 1. Anatomy. Baltimore, MD: Monumental Printing Co.
- Cobb, N. A. 1893. Nematodes, mostly Australian and Fijian. Department of Agriculture, New South Wales, Miscellaneous Publications (Sydney) 13:1-59.
- Cobb, N. A. 1898. Extract from MS report on the parasites of stock. *Agricultural Gazette of New South Wales* 9:296-321, 419-454.
- Cobb, N. A. 1929. Observations on the morphology and physiology of nemas; including notes on new species. *Journal of the Washington Academy of Sciences* 19:283-286.
- De Ley, P., M. C. Van de Velde, D. Mounport, P. Baujard, and A. Coomans. 1995. Ultrastructure of the stoma in Cephalobidae, Panagrolaimidae and Rhabditidae, with a proposal for a revised stoma terminology in Rhabditida (Nematoda). *Nematologica* 41:153-182.
- De Man, J. G. 1876. Onderzoekingen over vrij in de aarde levende Nematoden. *Tijdschrift der Nederlandsche Dierkundige Vereeniging* 2:78-196.

- De Man, J. G. 1927. Das Männchen der *Rhabditis monhystera* Bütschli. Zoologischer Anzeiger 70:51-57.
- Dougherty, E. C. 1953. The genera of the subfamily Rhabditinae Micoletzky, 1922 (Nematoda). Thapar Commemoration Volume, pp. 69-76.
- Dougherty, E. C. 1955. The genera and species of the subfamily Rhabditinae Micoletzky, 1922 (Nematoda): A nomenclatorial analysis, including an addendum on the composition of the family Rhabditidae Orley, 1880. Journal of Helminthology 29:105-152.
- Dujardin, F. 1845. Histoire naturelle des helminthes ou vers intestinaux. Paris.
- Farkas, K. 1973. *Teratorhabditis mariannae* n. sp., eine neue Nematodenart aus Chapignonkulturen. Opuscula Zoologica Budapest 11: 61-64.
- Fitch, D. H. A. 1997. Evolution of male tail development in rhabditid nematodes related to *Caenorhabditis elegans*. Systematic Biology 46:145-179.
- Fitch, D. H. A. 2000. Evolution of "Rhabditidae" and the male tail. Journal of Nematology 32(3):235-244.
- Fitch, D. H. A., B. Bugaj-Gaweda, and S. W. Emmons. 1995. 18S ribosomal RNA gene phylogeny for some Rhabditidae related to *Caenorhabditis*. Molecular Biology and Evolution 12:346-358.
- Fitch, D. H. A., and S. W. Emmons. 1995. Variable cell positions and cell contacts underlie morphological evolution of the rays in the male tails of nematodes related to *Caenorhabditis elegans*. Developmental Biology 170:564-582.
- Fitch, D. H. A., and W. K. Thomas. 1997. Evolution. Pp. 815-850 in D. Riddle, T. Blumenthal, B. J. Meyer, and J. Priess, eds. *C. elegans* II. Plainview, NY: Cold Spring Harbor Laboratory Press.
- Fuchs, G. 1915. Die Naturgeschichte der Nematoden und einiger anderer Parasiten. 1. Des *Ips typographus* L. 2. Des *Hylobius abietis* L. Zoologische Jahrbücher (Systematik) 38:109-222.
- Fuchs, G. 1931. Einige neue *Rhabditis*-Arten. Zoologische Jahrbücher (Systematik) 62:119-148.
- Fuchs, G. 1937. Neue parasitische und halbparasitische Nematoden bei Borkenkäfern und einige andere Nematoden. 1. Teil. Zoologische Jahrbücher (Systematik) 70:291-380.
- Goodey, T. 1963. Soil and freshwater nematodes. 2nd ed. (rev. J. B. Goodey). London: Methuen.
- Hennig, W. 1966. Phylogenetic systematics. Urbana, IL: University of Illinois Press.
- Hennig, W. 1969. Die Stammesgeschichte der Insekten. Frankfurt am Main, West Germany: Kramer.
- Herman, M. A., and H. R. Horvitz. 1994. The *Caenorhabditis elegans* gene *lin-44* controls the polarity of asymmetric cell divisions. Development 120:1035-1047.
- Hirschmann, H. 1952. Die Nematoden der Wassergrenze mittelfränkischer Gewässer. Zoologische Jahrbücher (Systematik) 81:313-407.
- Khera, S. 1968. Nematodes from the banks of still and running waters. 4. Description of a new subgenus of *Rhabditis* and a new species from India (Subfamily Rhabditinae). Journal of the Zoological Society of India 20:38-41.
- Khera, S. 1969. Nematodes from the banks of still and running waters. VI. Rhabditida from sewer. Journal of Helminthology 43:347-363.
- Kiontke, K. 1999. The *Rhabditis* (*Rhabditella*) *octopleura* species complex and descriptions of three new species. Russian Journal of Nematology 7:71-94.
- Kiontke, K., and W. Sudhaus. 2000. Phasmids in male Rhabditida and other secernentean nematodes. Journal of Nematode Morphology and Systematics 3:1-37.
- Kishino, H., and M. Hasegawa. 1989. Evaluation of the maximum likelihood estimate of the evolutionary tree topologies from DNA sequence data, and the branching order in Hominoidea. Journal of Molecular Evolution 29:170-179.
- Körner, H. 1954. Die Nematodenfauna des vergehenden Holzes und ihre Beziehungen zu den Insekten. Zoologische Jahrbücher (Systematik) 82:245-353.
- Kreis, H. A. 1967. Beiträge zur Kenntnis parasitischer Nematoden. XXVI. Ein neuer Nematode aus der Schnecke *Fruticicola* (*Acusta*) *sieboldiana* Pfeifer, *Rhabditis fruticicolae* n. sp. (Rhabditoidae; Rhabditidae). Pp. 171-181 in Jahrbuch 1963-1965, Naturhistorisches Museum der Stadt Bern.
- Lazarevskaya, S. L. 1965. Nematodes of insects harmful to forests. 1. Biological characteristics of nematodes belonging to the genus *Parasitorhabditis* Fuchs, 1937 (Rhabditidae: Parasitorhabditinae). Trudy Gel'minthologicheskoy Laboratorii (Akademija Nauk, SSSR) 15:93-100. (In Russian.)
- Leuckart, R. 1876. Die menschlichen Parasiten und die von ihnen herrührenden Krankheiten. Leipzig: Winter.
- Loof, P. A. A. 1964. Free-living and plant-parasitic nematodes from Venezuela. Nematologica 10:201-300.
- Marinari, A. 1957. *Pelodera melisi* n. sp. (Nematoda, Rhabditida, Rhabditidae). Redia 42:273-276.
- Massey, C. L. 1971. Two new genera of nematodes parasitic in the eastern subterranean termite, *Reticulitermes flavipes*. Journal of Invertebrate Pathology 17:238-242.
- Maupas, E. 1900. Modes et formes de reproduction des nématodes. Archives de Zoologie Expérimentale et Générale 8:463-624.
- Maupas, E. 1916. Nouveaux *Rhabditis* d'Algérie. Comptes Rendus des Séances de la Société de Biologie et de ses Filiales (Paris) 79:607-613.
- Maupas, E. 1919. Essais d'hybridation chez des nématodes. Bulletin Biologique de France et Belgique 52:466-498.
- Mayr, E. 1963. Animal species and evolution. Cambridge, MA: Belknap Press, Harvard University Press.
- Mayr, E. 1974. Cladistic analysis or cladistic classification? Zeitschrift für Zoologische Systematik und Evolutionsforschung 82: 94-128.
- Mengert, H. 1953. Nematoden und Schnecken. Zeitschrift für Morphologie und Ökologie der Tiere 41:311-349.
- Meyl, A. H. 1960. Die Freilebenden Erd- und Süßwassernematoden (Fadenwürmer). Die Tierwelt Mitteleuropas 1:1-164.
- Meyl, A. H. 1961. Fadenwürmer (Nematoden). Stuttgart: Franckh.
- Micoletzky, H. 1922. Die freilebenden Erd-Nematoden mit besonderer Berücksichtigung der Steiermark und der Bukowina, zugleich mit einer Revision sämtlicher nicht mariner, freilebender Nematoden in Form von Genus-beschreibungen und Bestimmungsschlüsseln. Archiv für Naturgeschichte (1921) 87A(8-9):1-650.
- Nigon, V. 1949. Modalités de la reproduction et déterminisme du sexe chez quelques nématodes libres. Annales des Sciences Naturelles / Zoologie 11:1-132.
- Nigon, V., and E. C. Dougherty. 1949. Reproductive patterns and attempts at reciprocal crossing of *Rhabditis elegans* Maupas, 1900, and *Rhabditis briggsae* Dougherty and Nigon, 1949 (Nematoda: Rhabditidae). Journal of Experimental Zoology 112:485-503.
- Nguyen, C. Q., D. H. Hall, Y. Yang, and D. H. A. Fitch. 1999. Morphogenesis of the *Caenorhabditis elegans* male tail tip. Developmental Biology 207:86-106.
- Örley, L. 1880. Az anguillulidák magánrajza (Monographie der Anguilluliden). Természettudományi Füzetek (Budapest) 4:16-150. (In Hungarian.)
- Örley, L. 1886. Die Rhabditiden und ihre medicinische Bedeutung. Berlin: R. Friedländer and Son.
- Osche, G. 1952a. Die Bedeutung der Osmoregulation und des Winkverhaltens für freilebende Nematoden. Zeitschrift für Morphologie und Ökologie der Tiere 41:54-77.
- Osche, G. 1952b. Systematik und Phylogenie der Gattung *Rhabditis* (Nematoda). Zoologische Jahrbücher (Systematik) 81:190-280.
- Osche, G. 1954. Über die gegenwärtig ablaufende Entstehung von Zwilling- und Komplementärarten bei Rhabditiden (Nematodes). Zoologische Jahrbücher (Systematik) 82:618-654.
- Osche, G. 1955a. Der dreihöckerige Schwanz, ein ursprüngliches Merkmal im Bauplan der Nematoden. Zoologischer Anzeiger 154: 136-148.

- Osche, G. 1955b. Über die Vergesellschaftung von Nematoden und Crustaceen, mit einer Beschreibung von *Matthesonema tylosa* n. g. n. sp. (Nematoda) aus dem Kiemenraum einer Assel. Zoologischer Anzeiger 155:253-262.
- Osche, G. 1958. Die Bursa- und Schwanzstrukturen und ihre Aberrationen bei den Strongylina (Nematoda). Zeitschrift für Morphologie und ökologie der Tiere 46:571-635.
- Paetzold, D. 1955. Untersuchungen an freilebenden Nematoden der Salzwiese bei Aseleben. Wissenschaftliche Zeitschrift der Universität Halle, Mathematisch-Naturwissenschaftliche Reihe 4:1057-1090.
- Potts, F. A. 1910. Notes on the free-living nematodes. Quarterly Journal of Microscopical Science 55:433-485.
- Reiter, M. 1928. Zur Systematik und Ökologie der zweigeschlechtlichen Rhabditiden. Arbeiten aus dem Zoologischen Institut der Universität Innsbruck 3:3-94.
- Riemann, F. 1969. Nematoden aus dem Kiemenraum karibischer Landkrabben: *Monhystrium inquilinus* nov. spec. (Monhysteridae). Veröffentlichungen des Instituts für Meeresforschung in Bremerhaven 11:239-244.
- Rühm, W. 1956. Die Nematoden der Ipiden. Parasitologischer Schriftenreihe 6:1-437.
- Rühm, W. 1960. Ein Beitrag zur Nomenklatur und Systematik einiger mit Scolytiden vergesellschafteter Nematodenarten. Zoologischer Anzeiger 164:201-213.
- Rühm, W. 1964. Ein Beitrag zur Vergesellschaftung zwischen Nematoden und Insekten [*Pelodera bakeri* n. sp. (Nematoda, Rhabditoidea, Rhabditidae) eine mit *Calvertius tuberosus* Perm. et Germ. (Coleoptera, Curculionidae, Hylobiinae) vergesellschaftete Nematodenart an *Araucaria araucana* (Mol.) Koch.]. Zoologischer Anzeiger 173:212-220.
- Rühm, W., and C. Chararas. 1957. Description, biologie et histologie de quatre espèces nouvelles de nématodes parasites de *Dryocoetes hectographus* Reit. (Col. Scolytidae). Entomophaga 2:253-269.
- Sachs, H. 1950. Die Nematodenfauna der Rinderexkremente. Eine ökologisch-systematische Studie. Zoologische Jahrbücher (Systematik) 79:209-272.
- Saito, N., and M. Nei. 1987. The neighbor-joining method: A new method for reconstructing phylogenetic trees. Molecular Biology and Evolution 4:406-425.
- Sanwal, K. C. 1959. *Cuticonema vivipara* n. g., n. sp., a new saprophagous nematode of the subfamily Panagrolaiminae Thorne, 1937, from Canada, with a note on the genus *Brevibucca* Goodey, 1935. Canadian Journal of Zoology 37:223-229.
- Schneider, A. 1866. Monographie der Nematoden. Berlin: G. Reimer.
- Schulte, F. 1989. Description of *Rhabditis (Pelodera) pseudoterres* n. sp. (Rhabditidae:Nematoda) with a redescription of its sibling *R. (P.) teres* (Schneider, 1866). Revue de Nématologie 12:387-394.
- Schuermans Stekhoven, J. H., and R. J. H. Teunissen. 1938. Nématodes libres terrestres. Exploration du Parc National Albert Mission G. F. de Witte (1933-1935) (Bruxelles) Fasc. 22:1-229.
- Skwarra, E. 1921. Diagnosen neuer freilebender Nematoden Ostpreußens. Zoologischer Anzeiger 53:66-74.
- Slobodianiuc, O. V. 1973. *Parasitorhabditis subelongati* (Parasitorhabditinae, Rhabditida), a new species of nematodes from *Ips subelongatus*. Zoologicheskij Zhurnal 52:1070-1073. (In Russian.)
- Sommer, R. J., L. K. Carta, S.-Y. Kim, and P. W. Sternberg. 1996. Morphological, genetic, and molecular description of *Pristionchus pacificus* sp. n. (Nematoda: Neodiplogastridae). Fundamental and Applied Nematology 19:511-521.
- Steiner, G. 1933. The nematode *Cylindrogaster longistoma* (Stefanski) Goodey, and its relationship. Journal of Parasitology 20:66-68.
- Steiner, H. 1955. Die Bedeutung der Zufallszahlen in der stammesgeschichtlichen Entwicklung der Tiere. Natur und Volk 85:133-143.
- Sternberg, P. W., and H. R. Horvitz. 1981. Gonadal cell lineages of the nematode *Panagrellus redivivus* and implications for evolution by the modification of cell lineage. Developmental Biology 88:147-166.
- Sternberg, P. W., and H. R. Horvitz. 1982. Postembryonic nongonadal cell lineages of the nematode *Panagrellus redivivus*: Description and comparison with those of *Caenorhabditis elegans*. Developmental Biology 93:181-205.
- Strimmer, K., and A. von Haeseler. 1996. Quartet puzzling: A quartet maximum-likelihood method for reconstructing tree topologies. Molecular Biology and Evolution 13:964-969.
- Sudhaus, W. 1974a. Nematoden (insbesondere Rhabditiden) des Strandanwurfs und ihre Beziehungen zu Krebsen. Faunistisch-Ökologische Mitteilungen 4:365-400.
- Sudhaus, W. 1974b. Zur Systematik, Verbreitung, Ökologie und Biologie neuer und wenig bekannter Rhabditiden (Nematoda). 1. Teil. Zoologische Jahrbücher (Systematik) 101:173-212.
- Sudhaus, W. 1974c. Zur Systematik, Verbreitung, Ökologie und Biologie neuer und wenig bekannter Rhabditiden (Nematoda). 2. Teil. Zoologische Jahrbücher (Systematik) 101:417-465.
- Sudhaus, W. 1976a. Nomenklatorische Bemerkungen Über Arten und Gattungen der Unterfamilie Rhabditinae sensu lato (Rhabditidae, Nematoda). Nematologica 22:49-61.
- Sudhaus, W. 1976b. Vergleichende Untersuchungen zur Phylogenie, Systematik, Ökologie, Biologie und Ethologie der Rhabditidae (Nematoda). Zoologica (Stuttgart) 43:1-229.
- Sudhaus, W. 1978. Systematik, Phylogenie und Ökologie der holzbewohnenden Nematoden-Gruppe *Rhabditis (Mesorhabditis)* und das Problem "geschlechtsbezogener" Artdifferenzierung. Zoologische Jahrbücher (Systematik) 105:399-461.
- Sudhaus, W. 1980. Systematisch-phylogenetische und biologisch-ökologische Untersuchungen an *Rhabditis (Poikilolaimus)*-Arten als Beitrag zu Rassenbildung und Parallelevolution bei Nematoden. Zoologische Jahrbücher (Systematik) 107:287-343.
- Sudhaus, W. 1985a. Conspecificity of *Rhabditis parateres* Cobb, 1924 and *R. conica* Reiter, 1928 (Nematoda, Rhabditidae). Nematologica 31:8-12.
- Sudhaus, W. 1985b. Revision der Untergattung *Teratorhabditis* von *Rhabditis* (Nematoda) und Beschreibung einer neuen Art. Zoologische Jahrbücher (Systematik) 112:207-224.
- Sudhaus, W. 1987. Fragestellungen und Ergebnisse evolutionsbiologischer Untersuchungen an saprobionten Fadenwürmern (Nematoda). Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin (N. F.) 27:145-163.
- Sudhaus, W. 1991. Check list of species of *Rhabditis sensu lato* (Nematoda: Rhabditidae) discovered between 1976 and 1986. Nematologica 37:229-236.
- Sudhaus, W. 1993. Die mittels symbiontischer Bakterien entomopathogenen Nematoden-Gattungen *Heterorhabditis* und *Steinernema* sind keine Schwestertaxa. Verhandlungen der Deutschen Zoologen Gesellschaft 86:146.
- Sudhaus, W., and D. J. Hooper. 1994. *Rhabditis (Oscheius) guentheri* sp. n., an unusual species with reduced posterior ovary, with observations on the *Dolichura* and *Insectivora* groups (Nematoda: Rhabditidae). Nematologica 40:508-533.
- Sudhaus, W., and K. Kiontke. 1996. Phylogeny of *Rhabditis* subgenus *Caenorhabditis* (Rhabditidae, Nematoda). Journal of Zoological Systematics and Evolutionary Research 34:217-233.
- Sudhaus, W., and R. Kühne. 1989 (published 1990). Nematodes associated with Psychodidae: Description of *Rhabditis berolina* sp. n. and redescription of *R. dubia* Boven, 1937 (Nematoda: Rhabditidae), with biological and ecological notes, and a phylogenetic discussion. Nematologica 35:305-320.
- Sudhaus, W., and K. Rehfeld. 1992. Einführung in die Phylogenetik und Systematik. Gustav Fischer Verlag, Stuttgart.
- Sulston, J. E., D. G. Albertson, and J. N. Thomson. 1980. The *Caenorhabditis elegans* male: Postembryonic development of nongonadal structures. Developmental Biology 78:542-576.
- Sulston, J. E., and H. R. Horvitz. 1977. Post-embryonic cell lineages of the nematode *Caenorhabditis elegans*. Developmental Biology 56:111-156.
- Sulston, J., H. R. Horvitz, and J. Kimble. 1988. Appendix 3: Cell lineage. Pp. 457-489 in W. B. Wood, ed. The nematode *Caenorhabditis elegans*. Plainview, NY: Cold Spring Harbor Laboratory Press.
- Swofford, D. L. 2000. PAUP*. Phylogenetic analysis using parsimony (*and other methods). Version 4.0 beta 4a. Sinauer Associates, Sunderland, Massachusetts.
- Timm, R. W. 1959. *Cheilorhabditis* and *Odontorhabditis*, two new genera of soil nematodes allied to *Rhabditis*. Nematologica 4:198-204.

Timm, R. W. 1961. *Prodontorhabditis*, n. gen. (Rhabditidae, Prodontorhabditinae n. subf.), a new soil nematode from East Pakistan. *Proceedings of the Helminthological Society of Washington* 28:115-117.

Völk, J. 1950. Die Nematoden der Regenwürmer und aasbesuchenden Käfer. *Zoologische Jahrbücher (Systematik)* 79:1-70.

Volz, P. 1951. Untersuchungen über die Mikrofauna des Waldbodens. *Zoologische Jahrbücher (Systematik)* 79:514-566.

Wahab, A. 1962. Untersuchungen über Nematoden in den Drüsen des Kopfes der Ameisen (Formicidae). *Zeitschrift für Morphologie und ökologie der Tiere* 52:33-92.

Weingärtner, I. 1952/53. Die Nematoden des Kompostes. *Sitzungsberichte der Physikalisch-Medizinischen Sozietät Erlangen* 76:86-107.

White, J. 1988. The anatomy. Pp. 81-122 in W. B. Wood, ed. *The nematode Caenorhabditis elegans*. Plainview, NY: Cold Spring Harbor Laboratory Press.

Yarwood, E. A., and E. L. Hansen. 1969. Dauerlarvae of *Caenorhabditis briggsae* in axenic culture. *Journal of Nematology* 1:184-189.

Zhao, C., and S. W. Emmons. 1995. A transcription factor controlling development of peripheral sense organs in *C. elegans*. *Nature* 373:74-78.