SYSTEMATIC REVISION OF THE HELICOIDEA (GASTROPODA: STYLOMMATOPHORA)

by

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[Revision des Systems der Helicoidea
(Gastropoda: Stylommatophora)]

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SYSTEMATIC REVISION OF THE HELICOIDEA

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ABSTRACT

In this paper the systematics of the Recent Helicoidea is revised at the family level. This revision results from a critical examination of the work of Schileyko, who has changed the systematics radically.

In the first part of this paper, the importance of the characters of the Helicoidea for the definition of family taxa is discussed; the results are that at present almost none of the characters except those of the reproductive system are suitable. Reproductive characters, especially those of the stimulatory organ, and a few other characters that can be used (type of jaw, chromosome number) are analyzed, and the plesiomorphic and apomorphic character states are suggested.

In the second part of this paper the systematics of the families are revised in detail. The superfamily Helicoidea is redefined by elimination of some families which do not belong there (Camaenidae, Oreohelicidae, Ammonitellidae, Corillidae). The family taxa of Helicoidea are mainly characterized by their terminal genitalia, especially the stimulatory organ; additionally their distributions and the groups belonging to them are specified. The following family taxa are described as new: Xanthonychidae (Monadeniinae) n. subfam. (type genus *Monadenia* Pilsbry), Xanthonychidae (Trichodiscininae) n. subfam. (type genus *Trichodiscina* Martens), Xanthonychidae (Metostracinae) n. subfam. (type genus *Metostracon* Pilsbry), Lysinoinae (Leptariontini) n. trib. (type genus *Leptarionta* Fischer & Crosse), Humboldtianinae (Bunnyini) n. trib. (type genus *Bunnya* H. B. Baker), Trichiinae (Helicopsini) n. trib. (type genus *Helicopsis* Fitzinger), Ciliellinae (Trissexodontini) n. trib. (type genus *Trissexodon* Pilsbry), Ciliellinae (Oestophorini) n. trib. (type genus *Oestophora* Hesse), Ciliellinae (Caracollinini) n. trib. (type genus *Caracollina* Beck), and Geomitrinae (Trochoideini) n. trib. (type genus *Trochoidea* Brown). The most important results of the revision are the following: 1) It is unnecessary to separate the Sphincterochilidae as an independent superfamily Sphincterochiloidea *sensu* Forcart. 2) The Elonidae *sensu* Gittenberger can be ranked within the Xanthonychidae as a subfamily. 3) The majority of the Western Palaearctic Helicoidea should be separated into two families, Hygromiidae and Helicidae. 4) The Helicellinae and Helicodontinae *sensu* Hesse are polyphyletic groups and must therefore be divided among different subfamilies of the Hygromiidae. 5) The Macaronesian Leptaxinae and Geomitrinae *sensu* *auct*. are closely related to certain continental Hygromiidae and must therefore be ranked with their respective subfamilies. 6) The Ethiopian Helicoidea do not belong to the Bradybaenidae, but to the Hygromiidae.

In the third part of this paper an attempt is made to reconstruct the phylogeny of the Helicoidea. From the character comparison an earlier separation of the Sphincterochilidae and the Xanthonychidae and a later one of the Bradybaenidae, Hygromiidae and Helicidae result. The reconstruction of the phylogeny is compared with those of former authors, and the differences from that of Schileyko are emphasized.

INTRODUCTION

In Western cultures, systematics has played the role, during the last several decades, of a stepchild to the science of biology. This has been especially true in the field of malacology, which until recently has employed the classification, with slight variation, that was conceived in the first two decades of this century. The deficiencies of this revision induced a series of Soviet investigators in the 1960s and 1970s, namely Starobogotov, Golikov, Minichev, and Schileyko, to publish a classification of snails that is more or less radically different from the traditional one. They referred to these differences as significant improvements; they are, however, burdened with serious faults, because they were conceived rashly and without an extensive knowledge of groups occurring outside the Soviet Union. The radical nature of these changes from the traditional classification, as well as their publication in the Russian language, resulted in their being misunderstood or totally ignored in the West. In the interest of the development of malacology, this is surely not the proper method; their classification must be met with a direct argument by which a natural classification of the Mollusca can be reached.

An example of such a classification is Schileyko's (1978) proposed systematics of the Helicoidea, which he later (1979) modified somewhat in the framework of a classification of all the Stylommatophora. A critique against his classification[1], to which I was forced in the course of my systematic revision of the Stylommatophora (Nordsieck, 1985, 1986b), is the motivation for the present revision. This revision is confined to the family level; the generic and species levels must be left to specialists in the respective groups.

I. SYSTEMATIC CHARACTERS

The only characters that Schileyko (1978) really used for the systematic ordering of the Helicoidea are in the genitalia; also when, in the diagnoses of the families, additional data on the shell and distribution are given, the development of the genitalia is decisive. Against this there is little to say, because the shell and the other internal organs have so far offered hardly any character that can be used for definitions of family taxa. Shell characters can at best aid in the identification of subfamilies and tribes. Concerning the structure of the buccal region, the radula is insignificant for characterizing higher taxa in the Stylommatophora, whereas the jaw can be used for this purpose. Concerning the taxonomic importance of the other internal organs--for example the remaining organs of digestion, the excretory organs, the nervous system--very little is known; as yet no characters have been found among them for defining families. On the other hand, chromosome numbers are occasionally of use in establishing relationships among families.

The genital characters that Schileyko used were (following Nordsieck's, 1985, terminology) those of the terminal genitalia: position of the bursa with respect to the spermoviduct; presence or absence of a diverticulum; number, position, and structure of the stimulatory organ; presence or absence of a flagellum; and the development of the penis. For the systematics of the Helicoidea, however, the proximal part of the reproductive system may also be of significance, i.e. the hermaphroditic duct, the fertilization-pouch-seminal-receptacle-complex (FPSC) and the spermoviduct. The presence or absence of an accessory seminal vesicle on the hermaphroditic duct was previously used by Hesse (1931). The development of the FPSC was studied by Schileyko & Schileyko (1975) in a series of Palaearctic helicoids, but was not used later by Schileyko (1978) for the systematic classification. About the development of the spermoviduct, which can be significant for the definition of higher taxa as in other groups of Stylommatophora, little is known; the statements that Schileyko (1978) makes about this are unfortunately full of errors.[2]

As for the characters of the terminal genitalia, the greatest significance was attributed by Schileyko to the position of the bursa and the development of the stimulatory apparatus. The position of the bursa, as Hesse (1931) had already indicated, is a character[3] that is not sufficiently studied, especially in non-European groups; in several groups it appears to be developed differently than Schileyko stated.[4] It can be used therefore, provisionally, only with reservations; this can only change if there is more attention to it in dissection than previously. The development of the stimulatory apparatus is doubtless a very important character; its significance will at best be restricted by the tendencies of several groups toward its reduction. Schileyko attached particular importance to the stimulatory apparatus for phylogenetic reconstruction.[5] This is acceptable, but the interpretation of the evolution of the stimulatory apparatus, that Schileyko took from Ihering (1929), is false. Ihering and Schileyko thought that a multiple stimulatory apparatus is plesiomorphic. Schileyko assumed that a multiple stimulatory organ was derived twice in parallel from the vaginal wall, because there are two types: the Humboldtiana-type, quadruple and radially arranged, which ought to be plesiomorphic to most other stimulatory organs, and the Hygromiidae-type, quadruple in Schileyko's opinion[6], and serially arranged; he assumed it logical that the Helicoidea were of diphyletic origin, or even triphyletic if the Sphincterochilidae, with their divergently constructed stimulatory organ, be included. In the systematics of the Stylommatophora (1979) he therefore gave these three groups the status of superfamilies (Sphincterochiloidea, Helicoidea with all remaining families, and Hygromioidea). This concept is wrong. The stimulatory apparatus of the Helicoidea is not derived from the vaginal wall, but like the stimulatory apparatus of all higher (sigmurethran) Stylommatophora it is derived from the penial appendix of their orthurethran ancestors (compare H. Nordsieck, 1985). For the Helicoidea, the plesiomorphic condition is thus the single stimulatory organ and the apomorphic condition is the multiple organ. Therefore there is also no cause to assume a polyphyletic origin of the Helicoidea; the synapomorphies of the group, the development and position of the stimulatory organ and the development of the flagellum, indicate rather a monophyletic origin (see Section III), so that it should remain as the superfamily Helicoidea.

For the systematics of the Helicoidea it is of great significance to establish which characters of the reproductive system are plesiomorphic and which are apomorphic. As a comparison with the remaining Stylommatophora and Pulmonata generally showed (H. Nordsieck, 1985), the following characters are plesiomorphic for the group: the normal position of the bursa (on the spermoviduct), the presence of a diverticulum, the presence of a stimulatory organ that can be developed as a sarcobellum or a gypsobellum, and the presence of both epiphallus and flagellum. The development of the diverticulum, epiphallus, and flagellum are more or less correlated, because those structures are involved in making the spermatophore. Additional comments are necessary concerning the position of the bursa and the position and development of the stimulatory organ. In the Hygromiidae the bursa normally lies adjacent to the spermoviduct, whereas in the Helicidae and the Bradybaenidae it angles off and is attached away from the spermoviduct near the kidney and pericardium; in the remaining families this character has not been sufficiently studied (see above). The normal position of the bursa is plesiomorphic, because the bursa copulatrix originates by splitting off from the oviduct, and, as far as is understood, most Stylommatophora, especially the primitive ones, have this position of the bursa. The apomorphic free position of the bursa could have the advantage that the contents (degraded products of the spermatophore and sperm) could be better resorbed. This bursal position obviously arose numerous times within the Helicoidea, since the Bradybaenidae and the Helicidae do not form a monophyletic group (see Section III).

The stimulatory organ of the Helicoidea generally inserts on the vagina; its position on the atrium in the Sphincterochilidae can be regarded as plesiomorphic (see H. Nordsieck, 1985). This, however, is not true of the protrusion of the vagina inserting on the atrium that in many Xanthonychidae and Bradybaenidae carries the stimulatory organ (named the atrial sac, vestibulum, or neophore by American authors); thereby we are dealing with an apomorphic development, which enlarges the acting surface area of the stimulatory organ[7] (see Webb, 1952b).

The dart-less gland-bearing stimulatory organ of the

Sphincterochilidae can likewise be construed as plesiomorphic, and those with a dart (= dart apparatus) of the remaining families as apomorphic. A single stimulatory apparatus, which consists of a dart sac with dart and a pair of simple glands, should be the plesiomorphic condition (see Fig. 1); such a stimulatory organ occurs in various groups of the Xanthonychidae and Helicidae. The glands are generally simple in the Xanthonychidae; in most Eurasian Helicoidea they are more or less divided, which should be considered apomorphic. The normal state of the glands (euadenous of Pilsbry, 1895) is probably plesiomorphic; the tubular = siphonal state (siphonadenous of Pilsbry), which occurs only in the Palaearctic and neighboring regions, is probably apomorphic. A dart apparatus in which the glands insert on the base of the dart sac is estimated to be plesiomorphic, because it is found in all families; a dart apparatus in which the glands insert more or less distant above the dart sac, which occurs in many Hygromiidae and in some Xanthonychidae, is construed to be apomorphic. The development of an accessory dart sac on the dart apparatus, which is found only in Eurasian Helicoidea, may be apomorphic. The accessory dart sac is not derived from a dart sac, but from the terminal portion of the dart glands, because it never contains a dart and probably serves for storing secretions; this is at least the case in the Bradybaenidae, in which it is more or less associated with the glands. This development of the accessory sac can be considered as plesiomorphic, while that of the Hygromiidae, in which the accessory sac and the dart glands are more or less broadly separated, as apomorphic. A single dart sac that inserts on the vagina should be plesiomorphic, while the development of additional accessory organs, i.e. the dart papilla and the dart papillae sac in many Xanthonychidae and the neophore in many Xanthonychidae and Bradybaenidae (see above), should be apomorphic. A single dart, that during copulation is merely thrust into the mate, must be considered plesiomorphic; a differentiated dart, as for example that of the Helicidae, that is discharged, would be apomorphic[8]. The development of one dart in the dart sac is surely plesiomorphic, the condition of two darts in the Humboldtianinae is apomorphic. Dart sacs without a dart, which have transformed into glandular organs, as in various groups of the Hygromiidae, are certainly apomorphic. That the single stimulatory apparatus is plesiomorphic to the multiple condition has already been stated; these assertions are true only for the Helicoidea, however. In the Hygromiidae the double dart apparatus ought to be plesiomorphic, since it appears in several subfamilies, and the glands that occur in taxa having a single dart apparatus usually insert on both sides of the vagina (see below). Likewise the dart apparatus of the Eloninae, which consists of a dart sac and at least two glands inserting on both sides, ought to be derived from a multiple dart apparatus (see below). It thus must be established for every group, what the proper interpretation is of the evolution of the dart apparatus in this respect. The regression leading to the loss of the dart apparatus, which occurs in all families of the Helicoidea, is without doubt apomorphic. The named evolutionary transformations of the dart apparatus either amount to optimization or revert to a change in function, which ought to correspond overall with a change in copulation: they are once more brought together in a clear arrangement in Fig. 2.

Yet another character must be discussed that has played a great role in the systematics of Palaearctic Helicoidea: the path of the right tentacular retractor muscle with respect to the paths of the terminal genitalia. The normal course (crossing the male terminal genitalia) must be evaluated as plesiomorphic, and the course next to (and not resting upon) them as apomorphic. The latter is found in the Sphincterochilidae and several groups of the Hygromiidae, in the Helicellinae *sensu* Hesse with the *Cochlicella*-group, and in the Geomitrinae *auct*. and the Thebinae *sensu* Hesse, thus in groups that differ so widely in other characters that this course of the right tentacular retractor muscle cannot be taken as a synapomorphy; furthermore, the groups it occurs in are all more or less xerophilic, so this character is interpreted as an adaptation acquired several times in parallel for this ecological niche (see Schileyko, 1972b, 1978). It therefore cannot be used for characterizing higher taxa of the Helicoidea; in particular, the traditional placement of the xerophilic Hygromiidae as a subfamily of the Helicellinae strictly on the basis of this character must be abandoned (see Schileyko).

An additional character that can be used for defining familial taxa of the Helicoidea is the development of the jaw. This is usually ribbed (odontognath), but can also be plicate (stegognath) or smooth (oxygnath). As is shown by a comparison with the related superfamilies of the "helicid" Sigmurethra (Camaenoidea, Mesodontoidea [Polygyroidea], Arionoidea), a ribbed jaw is plesiomorphic in the Helicoidea, while the plicate jaw of many Hygromiidae and the smooth jaw found in several families are apomorphic (compare Pilsbry, 1895). The apomorphic states of the jaw have obviously arisen many times through parallel evolution, so that the jaw has only a relatively slight taxonomic significance.

For the systematic classification of the Helicoidea the chromosome numbers should also be considered, insofar as they have been determined (see Rainer, 1967; Patterson, 1969); unfortunately these determinations are confined almost entirely to species of Eurasian Bradybaenidae, Hygromiidae, and Helicidae, while only one species of the Xanthonychidae and no species at all of the Sphincterochilidae and Halolimnohelicinae have been investigated. Significantly, the European Helicoidea have very different chromosome numbers; before these are used for systematics, it should be determined which number is plesiomorphic. The fact that many Bradybaenidae and Ariantinae and the one species of Xanthonychidae have 29 chromosomes suggests that this number corresponds approximately to the plesiomorphic condition; this hypothesis is supported by the fact that this number is the most frequent in the related Camaenoidea and Mesodontoidea (Polygyroidea). In the evolution of the European Helicoidea, therefore, a reduction in chromosome number (through combination or loss) has played a decisive role, that is to say that greater chromosome numbers can be evaluated as plesiomorphic, and smaller numbers as apomorphic; commonly shared small numbers, as in the Helicinae and several groups of the Hygromiidae, can be considered synapomorphies.

II. SYSTEMATICS

Only groups with a stimulatory organ belong to the superfamily Helicoidea, which was assembled by Pilsbry (1895) as belogonous helicids; they are, with the exception of several groups that have spread to southern continents (such as the Xanthonychidae to South America, the Hygromiidae to Africa), confined to the Northern Hemisphere. The other groups, that until now were placed in the Helicoidea - the Camaenidae, Oreohelicidae, Ammonitellidae = Megomphicidae, Corillidae = Plectopylididae - should be placed in independent superfamilies of the "helicid" Sigmurethra, or rather belong to the "achatinid" Sigmurethra (see Nordsieck, 1986b). The justification of this is as follows:

1) Camaenidae:

This group cannot be distinguished from the Helicoidea in shell form and it also agrees with them in the development of the jaw and flagellum; nevertheless it differs by the lack of a diverticulum and (usually) of a stimulatory apparatus. This would not be a decisive difference, if there were not found in some American Camaenidae and their probable relatives the Solaropsidae a stimulatory organ that inserts on the penis (see Pilsbry, 1894; Ihering, 1912). This supports the theory that the ancestor of the Camaenidae possessed a stimulatory organ on the penis, thus a plesiomorphic stimulatory organ, suggesting that the two clades divided before the stimulatory organ migrated from the penis to the vagina (H. Nordsieck, 1985). A further unique feature of the Camaenidae is the appearance of a phallic caecum, a plesiomorphic character that only seldom is found in the Helicoidea. It is therefore necessary to separate the Camaenidae (and probably the Solaropsidae) as a superfamily independent from the Helicoidea (H. Nordsieck, 1986b).

2) Oreohelicidae:

Pilsbry (1904, 1905a) separated Oreohelix from Patula, thus from the Discidae, only because of its holopod foot, although it resembles them remarkably in the structure of the shell, in the jaw, and in the terminalia of the reproductive system (see Pilsbry, 1939, 1948), and also fits them in distribution. Further indications of this relationship are found in the structure of the FPSC (see Schileyko & Schileyko, 1975) and in the chromosome number (see Patterson, 1969). It can be added that copulation in Oreohelix is one-sided (Webb, 1951), while in all groups of the Helicoidea it is reciprocal. Pilsbry's opinion that aulacopody was taxonomically an especially important taxonomic character has been refuted through several of his own studies (see Pilsbry, 1946); aulacopody developed in parallel in at least ten lineages of the Stylommatophora, so that this character cannot be used for the definition of higher taxa. The Oreohelicidae do not belong in proximity to the Camaenidae where Pilsbry (1939) placed them, but rather to, or close to, the Discidae, thus to the Punctoidea and thereby to the "achatinid" Sigmurethra (see H. Nordsieck, 1986b).

3) Ammonitellidae = Megomphicidae:

This group, whose holopodous members had first been adjoined to the Polygyridae = Mesodontidae and whose aulacopodous members had been first adjoined to the Zonitidae, was united by Pilsbry (1930, 1939, 1946) and attached to the Camaenidae. The development of the jaw and the reproductive system, especially the FPSC and the terminalia, indicate however that they are not closely related to this family; these characters, especially the presence of a characteristic vaginal appendicula which corresponds to the diverticulum (Webb, 1961), speaks for a relationship with the Caryodidae and the Strophocheilidae. The family therefore is classified in the Acavoidea and thus in the "achatinid" Sigmurethra (see H. Nordsieck, 1986b).

4) Corillidae = Plectopylididae:

This group was considered by Pilsbry (1894, 1905b) to belong to the Acavidae or the Camaenidae because of its anatomical characters. Solem (1978), however, following the standard of Thiele and Zilch, left it in the Polygyracea = Mesodontoidea; and

Schileyko (1979) placed it in the Helicoidea.[9] Until recently, three different groups were united under the name Corillidae: two Asiatic holopodous groups, the Corilla and Plectopylis groups, which exhibit considerable differences in shell structure and anatomy (see Pilsbry, 1894; Schileyko, 1973) and must be separated as subfamilies or full families; and the African aulacopodous Sculptaria group which in any case must be separated as a family (see Degner, 1923). All three groups belong to the "achatinid" Sigmurethra on the basis of anatomy and distribution and can be tentatively united as the superfamily Plectopylidoidea, which should be placed near the Acavoidea (see H. Nordsieck, 1986b).

Defined in this sense, the Helicoidea can be classified as follows:

Helicoidea Rafinesque 1815

Sphincterochilidae Zilch 1960 (Westerlund, 1886)[10]

Jaw smooth; hermaphroditic duct with an accessory seminal vesicle; diverticulum present; a single stimulatory organ present, consisting of a sheath (with or without a papilla), an appendage of the sheath = the appendicula,[11] and a dart gland; dart gland not siphonal, simple, inserting together with the appendicula on the sheath (Fig. 3).

S.W. Palaearctic.

The stimulatory organ inserts on the atrium; the tentacular retractor muscle runs next to the terminal genitalia. The statement of Schileyko (1978) that the bursa angles off from the spermoviduct needs reassessment.

The single recent genus of the family is Sphincterochila. The development of the hermaphroditic duct (Hesse, 1931) and the stimulatory apparatus (Frankenberger, 1919; Hesse, 1931; Forcart, 1972; Schileyko, 1972b) are unique within the Helicoidea, so that the Sphincterochilidae could be, as proposed by Forcart,[12] split off as a separate superfamily. In comparison to the Camaenidae, however, which were separated as a superfamily (see above), the reproductive system of the Sphincterochilidae corresponds more closely to that of the Helicoidea, so they should remain in this superfamily. The stimulatory apparatus can, by its position and development, be regarded as plesiomorphic to that of the remaining Helicoidea (see Section I), although it is not out of the question that it is derived from a dart apparatus (see Frankenberger, 1919), whereby the appendicula would correspond to the dart sac and the sheath to a neophore. In any case, a closer relationship of the Sphincterochilidae to one of the remaining families is not distinguishable, thus the systematic placement of the family within the superfamily must be regarded as isolated.

To the Sphincterochilidae probably belongs the Pseudoleptaxis group of the European Eocene and Oligocene, which can be separated as the subfamily Pseudoleptaxinae (H. Nordsieck, 1986a).

Xanthonychidae Strebel & Pfeffer 1880[10]

Jaw ribbed, but in some groups smooth; diverticulum present, but lacking in some groups; stimulatory organ present, single to quadruple, consisting of a dart sac, without an accessory dart sac, and one to several dart glands; dart glands not tubular, usually simple, inserting at the base of the dart sac, on the dart sac, or more or less above the dart sac.

W. Nearctic, N. and W. Neotropic, W. Palaearctic.

In some groups with a single stimulatory organ it inserts on a protrusion of the distal end of the female terminalia = the neophore.

The single species of the Xanthonychidae that has been examined for chromosomes (Monadenia fidelis Gray) had 29.

Within this family are united, despite their great diversity (see the Diagnosis), all American Helicoidea and the European Elona group, because splitting it into several families is not feasible for the following reasons. In the American Helicoidea all groups are so closely bound with one another that drawing boundaries would be arbitrary; this was also the reason why Pilsbry (1939) and Baker (1943, 1961, in Franc 1968) previously lumped all these American groups into one family. Also the separation of groups with multiple stimulatory organs as the independent family Humboldtianidae sensu Schileyko (1978)[13] is not possible, because these groups are allied in part to those having a single stimulatory organ (see below). What marks the Elona group, as previously detected by Ihering (1929), is that it is so similar in the construction of its stimulatory organ to those Xanthonychidae with multiple stimulatory organs, such as

Lysinoe and Humboldtiana, that a close relationship must be assumed; this was obviously overlooked by Gittenberger (1979), since he granted familial rank to the group. The resemblance of the Elona group to these groups of the Xanthonychidae is more extensive than Ihering acknowledged, so that its separation as a family would be based almost entirely on distribution.

The great diversity of the American Xanthonychidae, which is attained by no other family of the Helicoidea, makes a subclassification into numerous subfamilies necessary. Pilsbry (1939) arranged the family, which he named Helminthoglyptidae, into 8 subfamilies, of which he defined only the 4 occurring in North America: Helminthoglyptinae, Sonorellinae, Cepoliinae, and Humboldtianinae; in addition, he named the Epiphragmophorinae, and probably intended (judging from what appears in Pilsbry, 1900, 1927) to name the remaining three Central American groups the Lysinoinae, the Xanthonychinae, and the Metostracinae. Baker (1943, in Franc, 1968) accepted 6 subfamilies: Xanthonychinae, Epiphragmophorinae, Helminthoglyptinae, Cepoliinae, Humboldtianinae, and Sonorellinae. A comprehensive comparison of all groups, especially the reproductive systems, with additional consideration of the work of Webb (1952a and b, 1980), concluded that Pilsbry's arrangement, except for some changes in North American groups, can be accepted. Baker's system is faulty in that (1) normal shelled snails and semislugs should not be grouped in a single subfamily (Xanthonychinae sensu Baker), (2) Lysinoe and the Humboldtiana group must be placed in separate subfamilies because of their considerable differences, and (3) the groups with a missing stimulatory organ resulting from parallel evolution ought not to be united in a single subfamily (Sonorellinae *sensu* Baker).

The subfamilial classification of the American Xanthonychidae proposed in this work can only be provisional because of incomplete knowledge of several groups, especially the Central and South American ones, and is as follows: Monadeniinae n. subfam., Helminthoglyptinae, Cepoliinae, Epiphragmophorinae, Trichodiscininae n. subfam. Lysinoinae, Xanthonychinae, Metostracinae n. subfam., Humboldtianinae. Thus in the North American groups, *Monadenia* is split from the Helminthoglyptinae as a subfamily because of its important differences in the structure of the reproductive system, while the *Sonorella* group, which lacks a stimulatory organ, is transferred to the Helminthoglyptinae. The *Averellia* group is elevated to a separate subfamily, because it differs considerably from the other Central American groups, the Lysinoinae and those with reduced shells. That the Xanthonychidae also must include the European *Elona* group as a subfamily has already been discussed.

Monadeniinae n. subfam.

Type genus: *Monadenia* Pilsbry.

Diverticulum lacking; one dart sac; single dart gland inserting at the base of the dart sac (Fig. 4).

N.W. North America.

Hereto only _Monadenia_. This genus differs considerably from all other North American groups, especially in the structure of the stimulatory organ (see Pilsbry, 1939; Webb, 1952a). The stimulatory organ inserts not on the atrium of course, as Pilsbry reported, but on the vagina, which, along with the atrium, is more or less expanded, without forming a distinct neophore (see Webb). _Monadenia_ was placed by Pilsbry in the Helminthoglyptinae, and by Webb and Baker (1961) in close relation to the Central American groups; a closer connection exists however neither to the other North American groups nor to the Central American groups, which always have two dart glands that are of a different form, so that the erection of a separate subfamily is necessary.

Helminthoglyptinae Pilsbry 1939

Diverticulum present; one dart sac, two dart glands inserting at the base of the dart sac; dart glands lying along side the terminal genitalia (Figs. 5, 6); in some groups the stimulatory organ, and sometimes also the diverticulum, is lacking.

S.W. North America.

To the Helminthoglyptidae belong all North American groups except _Monadenia_. _Helminthogypta_ and the _Micrarionta_ group agree more with each other in the structure of the stimulatory organ than Pilsbry's (1939) information would lead one to suppose: the dart glands of _Helminthoglypta_ are not represented by the swelling of the gland duct, which is a muscular pump, but by the attached terminal portion that envelops the neophore in a sheath (see Webb, 1952b). This portion corresponds to the terminal part in Micrarionta, which is oppressed to the vagina or to the proximal penis.

The Sonorella group, which was separated as a subfamily by Pilsbry (1939) because of the lack of a stimulatory organ, is so closely allied through Sonorelix with the Micrarionta group (see Pilsbry, 1948) that it can only be evaluated as a tribe. Moreover there are still additional groups without a stimulatory organ, that are independent of the Sonorella group but evolved from other groups having a stimulatory organ (see Miller, 1970, 1972).

Helminthoglyptini

Diverticulum present; stimulatory organ present, lacking in one group.

Hereto Helminthoglypta, the Micrarionta group, and Greggelix.

Sonorellini Pilsbry 1939

Diverticulum usually lacking; stimulatory organ lacking.

Hereto the Sonorella group.

Cepoliinae (Ihering 1909) Pilsbry 1939.

Diverticulum lacking; one dart sac; dart glands unequal, one inserting apically on the dart sac and usually two inserting on the neophore (Fig. 7).

West Indies.

To this subfamily, which is also recognizable by the usually smooth jaw, belong all the West Indian Xanthonychidae. They possess a stimulatory organ (see Baker, 1943), which is provided with a neophore like that of Helminthoglypta, however in contrast to this genus it has a dart papilla sac and completely differently constructed glands. A union of the Cepoliinae and the Helminthoglyptinae, as proposed by Baker (1961), therefore is not acceptable. There is the question of whether the one gland on the the dart sac or whether the two on the neophore sheath is or are homologous with those of the other Xanthonychidae (see Pilsbry, 1939; Baker, 1943; Webb, 1952b); it seems to me, as it did to Baker, that the latter is more probable, because the sheath glands better correspond in position and number to the glands of the remaining members of the family than does the gland on the dart sac.

Epiphragmophorinae Hoffmann 1928

South America (greatest density in the middle Andes).

The few studied species of the Epiphragmophora group possess a reproductive system (Döring, 1875; Ihering, 1909; Hesse, 1930; Hylton Scott, 1962) that obviously resembles that of the Cepoliinae: diverticulum usually missing; one dart sac; dart glands unequal, one elongate, the other one or two compact, inserting on the dart sac or on its base (Fig. 8). The long dart gland seems sometimes to have been thought a part of the dart sac, causing it not to be mentioned (see Döring; Ihering, 1929). The short length of the bursal duct, which was viewed by Pilsbry (1939) as an important character of the subfamily, is not characteristic of all investigated species (see Hesse, Hylton Scott). An adequate definition of the subfamily will only be possible when the reproductive system is sufficiently studied; this is also a prerequisite for homologizing the glands of the Epiphragmophorinae with those of the remaining Xanthonychidae, which again could be of significance for interpreting those of the Cepoliinae _q.v._

Trichodiscininae n. subfam.

Type genus: _Trichodiscina_ Martens.

Diverticulum present; one or two dart sacs; two glands, inserting on the base of the dart sac, relatively long and strongly convoluted (Fig. 9).

Central America.

Hereto _Trichodiscina_ (see Baker, 1927), _Miraverellia_ (see Thompson, 1959) and probably _Averellia_, the reproductive system of which has not yet been studied. The _Averellia_ group, which is also well characterized conchologically, should be placed neither with the Lysinoinae, from which it differs especially in the structure of the stimulatory organ and of the posterior foot, nor with the Xanthonychinae, which are semislugs, so that the erection of a separate subfamily is necessary.

Lysinoinae Hoffmann 1928

Diverticulum lacking; one or two dart sacs; two or three glands, inserting on the base of the dart sac or on the vagina, relatively short (Figs. 10, 11); posterior foot keeled.

Central America.

Two Central American groups can be combined as the Lysinoinae; these groups exhibit considerable differences in the structures of the shell and the reproductive system, but may have the same origin because of their apomorphic formation of the posterior foot (see Pilsbry, 1927). These groups should be separated as tribes.

Leptariontini n. trib.

Type genus: Leptarionta Fischer & Crosse

One dart sac; two dart glands, inserting at the base of the dart sac; stimulatory organ missing in one group.

Hereto Leptarionta and Tryonigens (see Pilsbry, 1927).

Lysinoini

Two dart sacs; three dart glands, inserting on the vagina near the dart sacs.

Hereto only Lysinoe (see Fischer & Crosse, 1872). It is likely that Itzamna, which is conchologically similar but whose reproductive system is not yet studied, belongs in this tribe.

Leptarionta possesses, like the Trichodiscininae and Xanthonychinae, a single, therefore more plesiomorphic stimulatory organ, which may approximate that of the ancestor of the Xanthonychidae; Lysinoe on the other hand has two dart sacs and three glands, thus a stimulatory organ that is at least doubled. This group thereby resembles the Humboldtianinae, which differ significantly however by their differently constructed stimulatory organ and unkeeled posterior foot; it is probable therefore that the multiplication of the stimulatory organ in both groups can be traced to parallel evolution.

Xanthonychinae

Semislugs; kidney correspondingly shortened; diverticulum present or absent; one dart sac; two dart glands, inserting at the base of the dart sac (Fig. 12); posterior foot with a horn.

Mexico.

Hereto only Xanthonyx. The reproductive system of the group (see Strebel & Pfeffer, 1880; Pilsbry, 1900; Baker, 1942) resembles that of the Trichodiscininae and the Leptariontinae, and is therewith relatively plesiomorphic; the separation as an independent subfamily thus is based chiefly on characters produced by the reduction of the shell. The foot obviously shows a tendency toward aulacopody (see Strebel & Pfeffer).

Metostracinae n. subfam.

Type genus: Metostracon Pilsbry.

Slug; kidney correspondingly shortened, bilobed, surrounding the pericardium; diverticulum lacking; one dart sac (or neophore?); two dart glands, inserting on the apex of the dart sac (neophore?) (Fig. 13).

A new subfamily must be proposed for Metostracon, which has incompletely reached the slug stage by reduction of the shell and corresponding displacement of the visceral sac (see Pilsbry, 1900), because its differences from Xanthonyx are so great that parallel evolution between the two groups must be assumed. The kidney and reproductive system are very different from those of the other Xanthonychidae; it is impossible to determine to which of the other groups of the family it is most closely related. Indeed it must be stated that the reproductive system of Metostracon is insufficiently studied; it is possible that the dart sac, in which Pilsbry could find no dart, is in fact a neophore and that the true dart sac has degenerated, which would also be supported by the apical insertion of the glands. A renewed investigation of the reproductive system is necessary to remove the mentioned confusions and to clarify the systematic position of the group.

Humboldtianinae Pilsbry 1939

Diverticulum present; three or four dart sacs; a corresponding number of dart glands, inserting on the vagina near the dart sacs (Fig. 14).

Mexico, Texas.

To the Humboldtianinae belong two groups, _Humboldtiana_ and _Bunnya_, which differ so widely that they must be separated as tribes.

Humboldtianini.

Shelled snails; four dart sacs and dart glands; the bodies of the dart glands fused in a ring around the vagina; the number of stimulatory organs sometimes reduced.

Hereto _Humboldtiana_ (see Pilsbry, 1927, 1939, 1948; Solem, 1974). Webb (1980) established that in the species of _Humboldtiana_ he studied, as in _Bunnya_, two darts are formed in each dart sac.

Bunnyini n. trib.

Type genus: _Bunnya_ H.B. Baker.

Semislugs; three dart sacs with dart papilla sacs and dart glands; the bodies of the dart glands not fused; posterior foot bearing a horn.

Hereto _Bunnya_ (see Baker, 1942). The differences from _Xanthonyx_ show that both semislugs arose by parallel evolution.

The Humboldtianinae are to be seen as a relatively apomorphic group, owing to the multiplication of the stimulatory organ and its distinctive construction. Their similarity to the other American Xanthonychidae that have multiple stimulatory organs (_Miraverellia_, _Lysinoe_, _q.v._) is only slight; they therefore assume a relatively isolated systematic position within the family.

Eloninae Gittenberger 1979

Diverticulum present; one dart sac; two divided dart glands, inserting on the vagina above the dart sacs (Fig. 15).

W. Palearctic (Pyrenees).

Gittenberger (1979) erected the family Elonidae for the Elona group, to which Elona and Norelona belong (see H. Nordsieck, 1986a). The anatomy of the reproductive system (see Hesse, 1885; Ihering, 1929; Gittenberger) permits the following statements concerning the systematic position of the group. The presence of a diverticulum shows that it does not belong to the Hygromiidae or the Bradybaenidae. More important are the characters of the stimulatory organ: (1) the dart glands are not tubular, which means the group belongs neither to the Hygromiidae nor the Helicidae, (2) the dart glands insert above the dart sac onto the vagina, which means it does not belong to the Bradybaenidae. The group should not be evaluated as an independent family, but as a subfamily of the Xanthonychidae, because there is no substantial difference from the American groups, instead it has important similarities with them. These are the following: (1) the presence of a dart papilla in Elona and of a dart papilla sac (= cupula of Hesse, Ihering) in both genera of the group; (2) the number and position of the parts of the stimulatory apparatus: one dart sac and two divided dart glands that surround and insert into the vagina above the dart sac. The accessory organs named in (1) are otherwise only to be found in the Xanthonychidae (Cepoliinae and *Bunnya* - see Baker, 1942, 1943). The stimulatory organ mentioned in (2) was thus at least doubled in the *Elona* group; the dart sacs were reduced to one, while the dart glands stayed the same. These are conditions that occur only in the Xanthonychidae (with the exception of the Hygromiidae, which however have different dart glands), namely in *Lysinoe* (which however has two dart sacs and three undivided glands) and *Bunnya* (which has three dart sacs with two darts and a corresponding number of undivided glands). Both characters of the stimulatory organ thus speak for a relationship with the Central American Xanthonychidae; this conclusion is supported by the conchological resemblance of the fossil relatives of *Elona* with these groups (see H. Nordsieck, 1986a). The structure of the penis of *Elona* (with an internal penial tube, without a papilla) can be evaluated as further indication of a relationship with the American Xanthonychidae, since there is a resemblance to the phallic structure of *Helminthoglypta* (see Pilsbry, 1939; Gittenberger).

The *Elona* group is probably the remnant of a group of the Helicoidea that was richly represented in the European Tertiary from the Eocene to the Pliocene; these fossil Eloninae can be classified into two groups, which can be evaluated as tribes: the *Galactochilus* group = Elonini and the *Klikia* group = Klikiini. Of the Elonini only the *Elona* group survived the Pleistocene; of the Klikiini probably only *Soosia* remains (see H.

Nordsieck, 1986a).

Soosia, which was placed by Hesse (1918b) in his Helicodontinae, differs significantly from the remaining Helicodontinae *sensu* Hesse (which belong to the Hygromiidae, *q.v.*) in its shell, reproductive system, and geographic range. The reproductive system is, according to Soos (1917), much simplified (without diverticulum, stimulatory organ, or flagellum); for the remaining characters, however, it is insufficiently known, so that no conclusion as to the memberships of the species in one of the families of the Helicoidea is permitted. A precise investigation, especially of the male genitalia, is necessary therefore to be able to clarify the systematic position of the genus.

Bradybaenidae Pilsbry 1934 (Eulotidae Moellendorff 1898)[10]

Jaw ribbed, in some groups smooth; diverticulum lacking; a single stimulatory organ present, consisting of a dart sac, usually with an accessory dart sac, and one or two dart glands; dart glands not tubular, simple or divided, inserting on the accessory dart sac or on the base of the dart sac.

E. Palaearctic, one species W. Palaearctic, E. Oriental.

In the Bradybaenidae studied to date (Wiegmann, 1900; Schileyko, 1978), the bursa branches off from the spermoviduct. In several groups of the family the stimulatory organ inserts on a protrusion of the distal end of the female terminalia = the neophore.

All studied species of the Bradybaenidae have 28 or 29 chromosomes.

The Asiatic Bradybaenidae represent, in contrast to the American or the European Helicoidea, a strikingly consistent group, the greater part of which cannot be arranged into subfamilies; only the group distributed in the Philippines can be separated, because of the structure of its stimulatory organ, as the subfamily Helicostylinae.

Bradybaeninae

Stimulatory organ with two dart glands, that are usually divided (Figs. 16, 17).

Distributed as the family.

The different groups of the Bradybaeninae do not differ in the structure of the stimulatory organ and the male terminal ducts (see Pilsbry, 1895; Jacobi, 1898; Wiegmann, 1900; Schileyko, 1978; Azuma, 1982), sufficiently to permit their division into tribes, much less into subfamilies. The classification into Aegistinae and Bradybaeninae, which was proposed by Japanese malacologists (Habe, 1955; Azuma), was based only on a study of Japanese species; for the division the development of the flagellum is obviously decisive; that of the Aegistinae *sensu* Habe is more or less strongly developed, while in the Bradybaenidae *sensu* Habe it is either slightly developed or lacking. This distinction does not hold, however, for other

Asian species grouped in the same genera, because in these the flagellum is almost always lacking (see Wiegmann). This example shows that a subclassification of the Bradybaeninae is not possible before a complete revision is performed, especially of continental groups, at the generic level.

Helicostylinae Ihering 1909

Stimulatory organ with one simple dart gland (Fig. 18); in one group the stimulatory organ is lacking.

Philippines.

To the Helicostylinae belong Tricheulota, Chloraea, and the Helicostyla group (see Semper, 1873; Pilsbry, 1895). The development of the stimulatory organ suggests that this subfamily is relatively apomorphic compared to the Bradybaeninae; this may be connected with the fact that it arose as an isolate of the family in the Philippines.

Hygromiidae Tryon 1866

Jaw plicate, sometimes ribbed; diverticulum lacking; stimulatory organ single or double, consisting of a dart sac, sometimes with an accessory dart sac and usually several dart glands; dart glands tubular, usually divided, inserting in most groups more or less above the dart sac.

Palearctic to Cape Verde, especially W. Palearctic, E. Ethiopian.

In all studied members of the Hygromiidae the bursa copulatrix is adjacent to the spermoviduct.

To the Hygromiidae, which must be split from the Helicidae as a family (see Ihering, 1929; Hesse, 1931; Pilsbry, 1939; Schileyko, 1972b; 1978), belong, in addition to the Hygromiidae sensu Schileyko, the Helicodontinae sensu Hesse (without Soosia) and the Halolimnohelicinae, previously placed in the Bradybaenidae.

The Helicodontinae sensu Hesse have in common only the characters of a compressed shell and a tendency toward reduction of the stimulatory organ due to their secretive niche, but otherwise differ significantly in the development of the reproductive system, especially of the stimulatory apparatus. Schileyko (1978) recognized this heterogeneity, as he established four groups,[14] of which he considered two as possible relatives of the Hygromiidae; he held this group, however, as a family separate from the Hygromiidae, and later (1979) even raised it to a superfamily. This procedure is totally unsuitable and is obviously a faulty solution that can only be explained by the difficulty of classifying the groups concerned. In truth, most groups of the Helicodontinae sensu Hesse are revealed to be relatives of the Hygromiinae and can tentatively be left together in a subfamily, while the Helicodonta group sensu lato has an isolated systematic position (see below); Soosia, on the contrary may not belong to the Hygromiidae at all (see the Eloninae). On the other hand Ciliella, which Hesse ought to have placed in his Helicodontinae because of the development of the shell and reproductive system, can be attached to the group that stands near the Hygromiinae.

The relationship of the Halolimnohelicinae to the Hygromiidae has already been established (H. Nordsieck, 1986a).

The classification of the Hygromiidae into subfamilies is not easy. The division hitherto accepted, which goes back to Pilsbry's (1895) classification, into Fruticicolinae (= Hygromiinae), Helicellinae, and Helicodontinae (Kobelt, 1904; A.J. Wagner in Sturany & Wagner, 1914, 1915; Hesse, 1931), to which are to be added the Geomitrinae (see Zilch, 1960), cannot be supported, because the Helicellinae and the Helicodontinae are defined by adaptive characters of multiple origin and thus are polyphyletic (see above). This concerning the first group was already recognized by Schileyko (1972b, 1978), who arranged the Hygromiidae (except the Helicodontinae --see above) into numerous subfamilies. Of these, aside from the Hygromiinae, only the Trichiinae, Monachinae (= Euomphaliinae, 1978), and Geomitrinae can be accepted. The Cochlicellinae belong to the Monachinae, because they are connected to the *Monacha* group (Thebinae *sensu* Hesse) by the structure of the stimulatory organ. The Ciliellinae and Metafruticicolinae were established only on the absence of a stimulatory apparatus; they stand so close to other groups of the Hygromiidae that they can only be evaluated as tribes. The Archaicinae and Paedhoplitinae were split by Schileyko (1978) from the Hygromiinae and the Euomphaliinae respectively, because in his opinion they did not belong to these groups, but were derived directly from the Trichiinae. If this were to prove correct, they must differ somehow from the Hygromiinae or the Euomphaliinae; this is however obviously not the case, since Schileyko's diagnoses of these subfamilies extensively correspond with those of the groups named, which means that these subfamilies cannot be accepted.[15]

From what has been said, it appears that the subfamilial classification of the Hygromiidae must be completely revised. This is only possible in a limited way within the framework of this paper, because many groups of the family are not yet sufficiently known. The subfamilies must be distinguished by the development of the stimulatory organ even more than in the other Helicoidea, because the remaining parts of the reproductive system, insofar as they are sufficiently known, differ little; with the help of the stimulatory organ, it is also possible to draw elementary conclusions about the phylogeny of the groups (see Section I). The presence of two stimulatory organs must be viewed for the Hygromiidae all together as plesiomorphic, because it occurs in four different groups (Trichiinae, Geomitrinae, Monachinae, Halolimnohelicinae) either exclusively or frequently; further evidence for this is the presence of dart glands inserting on both sides of or around the vagina in most groups with a single stimulatory apparatus. Of the named groups with two stimulatory organs, the Trichiinae have a normal dart sac, thus they are in this respect the plesiomorphic subfamily, while the three others show a dart sac, each modified in another way, thus are more strongly apomorphic; they ought therefore to be considered as three subfamilies. Also more apomorphic are the groups with a single stimulatory organ, the Hygromiinae with a little modified, and the helicodontoid groups with greatly modified stimulatory organ, which, according to their structure, represent at least two independent evolutionary lineages and thus represent subfamilies, the Ciliellinae[16] and the Helicodontinae.

The Macaronesian Hygromiidae, the Geomitra and Leptaxis groups, were previously, following Pilsbry's classification, evaluated as independent subfamilies (see C. Boettger, 1909; Thiele, 1931; Zilch, 1960); the membership of the Leptaxinae in the Hygromiidae was first recognized by Schileyko (1972a) and independently by myself.[17] The comparison of the stimulatory organ of both groups with those of the remaining Hygromiidae showed that they are closely related to certain mainland groups and therefore only have tribal rank; the Geomitra group forms with the Trochoidea group the subfamily Geomitrinae, while the Leptaxis group belongs to the Hygromiinae. The chromosome numbers of the studied species of the family differ and usually are more or less reduced. Several helicelloid species of two subfamilies (Hygromiinae, Geomitrinae) and Helicodonta have 27 or 26; most of the remaining species (of three subfamilies) have 24 or 23. The common higher number of helicelloid species is no evidence of their close relationship, because this condition is considered plesiomorphic (see Section I), while for example the corresponding number (23) of the studied species of *Euomphalia*, *Monacha* and *Cochlicella* is support for their combination in the subfamily Monachinae, since it is apomorphic.

Many groups of European Tertiary Helicoidea with hygromioid or helicodontoid shells, whose relations to Recent groups are not yet sufficiently investigated, may belong to the Hygromiidae (H. Nordsieck, 1986a).

Trichiinae Ložek 1956 (Kobelt 1904)[10]

Two dart sacs, normally developed, always with an accessory dart sac; dart relatively small, simple (Fig. 19).

W. Palearctic to middle Asia.

Hereto the Fruticicolinae and the Helicellinae *sensu* Hesse with two normal dart sacs (see Hesse, 1931, 1934; Schileyko, 1978), namely the Trichiinae *sensu* Schileyko, with the exception of *Helicella*, which belongs to the following subfamily (*q*.*v*.). This subfamily can be divided into two tribes based on the course of the tentacular retractor muscle.

Trichiini

Tentacular retractor muscle running between the terminal genitalia.

Hereto the majority of the genera.

Helicopsini n. trib.

Type genus: *Helicopsis* Fitzinger.

Tentacular retractor muscle running alongside the terminal genitalia.

Hereto the Helicopsis group.

Hygromiinae

One dart sac (two in one group), normally developed, sometimes with an accessory dart sac, dart relatively large more or less strongly differentiated (Fig. 20); in one group the stimulatory organ is missing.

Palearctic, plus Cape Verde.

Hereto the Fruticicolinae and Helicellinae sensu Hesse with a normal dart sac (see Hesse, 1931, 1934; Schileyko, 1972a, 1978), that is the Hygromiinae sensu Schileyko, as well as the Archaicinae Schileyko, Leptaxinae auct., Metafruticicolinae Schileyko, and Helicella.

The Archaica group belongs to the Hygromiinae (see above), as also originally proposed by Schileyko (1972a).

The Leptaxis group, which is considered an independent subfamily by most authors, and still was considered to be more closely related to the Helicidae by Mandahl-Barth (1950), doubtless belongs to the Hygromiinae according to the development of the jaw and reproductive system; in the development of the stimulatory organ it corresponds with the Hygromiinae (see Mandahl-Barth). Thus we are dealing with not a plesiomorphic, but rather a relatively apomorphic group, which owes its origin to isolation in the Macaronesian area; therefore it is quite unlikely that any Tertiary Helicoidea of the European mainland belong to the Leptaxis group (see H. Nordsieck, 1986a).

The Metafruticicola group, which was separated as a subfamily by Schileyko (1972b) because of the lack of a stimulatory organ, conforms to the Fruticocampylaea group in the structure of the male genitalia (see Hesse, 1931; Schileyko, 1972c) and in geographical range, so it can be classified as a tribe of the Hygromiinae. Helicella, which was placed in the Trichiinae by Schileyko (1978) because of the presence of two dart sacs, corresponds extensively to Cernuella and Candidula in the development of the dart sac and dart and in the innervation of the penis from the pedal ganglion; it must therefore be assumed that the double stimulatory organ resulted from a single one, thus is apomorphic (which is an exception for the Hygromiidae).

Therewith results the following tribal classification:

Hygromiini

Tentacular retractor muscle running between the terminal genitalia; always a dart sac.

Hereto the majority of genera, also the Archaica group.

Leptaxini C. Boettger 1909

As in the Hygromiini, dart with two distinct edges.

Hereto the Leptaxis group. The separation from the Hygromiini as a tribe is supported by the divergent shell and the geographic range.

Metafruticicolini Schileyko 1972

As in the Hygromiini, but lacking a stimulatory organ.

Hereto the *Metafruticicola* group.

Helicellini Ihering 1909 (Kobelt 1904)[10]

Tentacular retractor muscle running alongside the terminal genitalia; one or two dart sacs.

Hereto the *Cernuella* group, *Candidula*, and *Helicella*.

Ciliellinae Schileyko 1970[16]

As in the Hygromiinae, dart sac differently developed to lacking, when present bearing a dart that is distinctly large (Figs. 21, 22); several groups lacking a stimulatory organ.

S.W. to W. Palearctic.

Hereto most groups of the Helicodontinae *sensu* Hesse, and *Ciliella* (see Hesse, 1931; Odhner, 1931; Ortiz de Zárate, 1962; Gittenberger, 1968; Schileyko 1971b, 1972b). It is questionable whether these groups are truly closely related. The relationship of the *Trissexodon* and *Oestophora* groups is made probable by the development of a ligament of the dart sac (see Ortiz de Zárate, Gittenberger) and by the geographic range. *Caracollina*, despite the divergent development of its dart sac, agrees with the *Oestophora* group in the remaining characters of the reproductive system (see Hesse, Odhner). *Ciliella* resembles the *Oestophora* group in shell structure and in the development of the male genitalia (see Hesse, Schileyko). The subfamily can accordingly be arranged into four tribes:

Trissexodontini n. trib.

Type genus: Trissexodon Pilsbry

Dart sac with an accessory dart sac; dart small.

Hereto the Trissexodon group.

Oestophorini n. trib.

Type genus: Oestophora Hesse.

Dart sac without an accessory dart sac; dart distinctly large, or dart sac missing; in one genus the stimulatory organ is lacking.

Hereto the Oestophora group and Canariella.

Caracollinini n. trib.

Type genus: Caracollina Beck.

Dart sac without an accessory dart sac, but with an appendage; dart very small.

Hereto only Caracollina.

Ciliellini

Stimulatory organ lacking.

Hereto only Ciliella. The peculiarity of this genus and the remaining uncertainty of its systematic position make it advisable to maintain it as an independent tribe.

Geomitrinae C. Boettger 1909

One or two dart sacs, transformed to appendages without dart; without an accessory dart sac (Fig. 23).

S.W. Palearctic.

The _Trochoidea_ group of the Helicellinae _sensu_ Hesse as well as the _Geomitra_ group, which was previously evaluated by most authors as a subfamily, agree so closely in the development of the stimulatory organ that they must be united in a single subfamily (see Hesse, 1934; Mandahl-Barth, 1950). The dart sac is transformed to an appendage ("muscular gland" of Mandahl-Barth), which in comparison to the appendicula of the following subfamily is always of slight size and simply constructed. It is also possible that the dart sac was reduced and that the appendage arose from the accessory dart sac. In the _Geomitra_ group, the musculature of the appendage is supposed to contain no longitudinal muscles, in contrast to that of _Trochoidea,_ according to Mandahl-Barth, thus is more primitive in construction; its interpretation as the precursor of the dart sac which Mandahl-Barth proposed, stands contrary to the truth that the stimulatory organ of the Helicoidea did not originate in this group, but rather was carried over from their common ancestor (see Section I). This means that the _Geomitra_ group, just like the _Leptaxis_ group (see the Hygromiinae), is not a plesiomorphic but a relatively apomorphic group, which resulted from an isolate on Madeira; therefore the same is true for the classification of Tertiary Helicoidea with the Geomitra group as it is for their classification with the Leptaxis group. The subfamily can be arranged into two tribes:

Trochoideini n. trib.

Type genus: Trochoidea Brown.

Two dartless appendages; dart glands developed on both sides.

Hereto the Trochoidea group.

Geomitrini

One or two dartless appendages; dart glands correspondingly developed on one or both sides; stimulatory organ lacking in one group.

Hereto the Geomitra group. The separation as a tribe is supported, as in the Leptaxini, by the shell structure and the geographic range; the Geomitrini are an ideal example of the adaptive radiation of a group in a relatively small, isolated region (Madeira).

Monachinae Wenz 1930 (Kobelt 1904)[18]

One or two dart sacs, transformed into appendages lacking darts = appendiculae[11]; without an accessory dart sac (Figs. 24, 25).

W. Palearctic to Abyssinia and middle Asia.

To this subfamily, which had originally been erected only for the *Monacha* group (Thebinae *sensu* Hesse), also belong the *Euomphalia* group of the Fruticicolinae *sensu* Hesse, in addition the Paedhoplitinae Schileyko (see above), and the *Cochlicella* group of the Helicellinae *sensu* Hesse (see Hesse, 1931, 1934; Schileyko, 1972b, 1978). These groups are characterized by the possession of a specific stimulatory organ, the appendicula,[11] which may be homologous with the dart sac (see Frankenberger, 1919); it consists of a sheath and a terminal appendage, which is more or less clearly set apart. The relationship of the *Euomphalia* and *Monacha* groups had been recognized previously by Schileyko (1978); he considered (1972b) the *Cochlicella* group, on the other hand, as an independent subfamily, because he wrongly homologized their divided appendage of the appendicula with the dart glands. The unification of these three groups into a subfamily is supported by the identical chromosome number (23) of their species that have been studied, since this number is considered apomorphic (see above). The three groups can be considered tribes:

Euomphaliini Schileyko 1978

Two appendiculae; dart glands present; tentacular retractor muscle running between the terminal genitalia.

Hereto the *Euomphalia* group, to which the *Paedhoplita* group should be attached (see above). The Ethiopian *Lejeania* group, which has a stimulatory organ like the *Euomphalia* group, should also belong to this tribe, although in it a different course of the tentacular retractor muscle possibly occurs (see Pfeffer, 1931; Verdcourt, 1969). The Euomphaliini make up the plesiomorphic group of the subfamily, while both of the following tribes are considered to be strongly apomorphic.

Monachini[18]

One appendicula, with a simple appendage; dart glands present; tentacular retractor muscle running alongside the terminal genitalia; stimulatory organ more or less reduced in several groups.

Hereto the _Monacha_ group.

Cochlicellini Schileyko 1972

One appendicula, with a divided appendage; dart glands lacking; tentacular retractor muscle running alongside the terminal genitalia.

Hereto _Cochlicella_ and _Monilearia_.

Helicodontinae Kobelt 1904

A dart sac, transformed to an appendage without a dart, without an accessory dart sac, or lacking a dart sac; one dart gland, inserting together with the dartless appendage when present (Fig. 26).

W. Palearctic, especially S. Europe.

To this subfamily belong two groups of the Helicodontinae *sensu* Hesse, which extensively correspond in the structure of the reproductive system, especially of the FPSC and the male genitalia. They can be evaluated as tribes on the basis of the following named differences; this classification is supported by the differences in shell structure.

Helicodontini

Dartless appendage present; penial retractor muscle branching from the columellar muscle.

Hereto *Helicodonta* and *Drepanostoma* (see Hesse, 1931, 1934; Schileyko, 1971b, 1978). The appendage of the stimulatory organ may, as A. Schmidt (1855) previously supposed, derive from the dart sac, as is to be concluded from its position and from its development being different from the dart gland;[19] that it inserts together with this and likewise is glandular, is not evidence (contrary to Schileyko's opinion) that it represents a dart gland.

Lindholmiolini Schileyko 1978

Dartless appendage lacking; penial retractor muscle inserting on the diaphragm.

Hereto *Lindholmiola* (see Hesse, Schileyko). Whether *Atenia*, whose reproductive system resembles that of *Lindholmiola* (see Gittenberger, 1968), indeed belongs to this tribe, remains to be investigated.

Halolimnohelicinae H. Nordsieck 1986

Two dart sacs, transformed into appendages without a dart; without an accessory dart sac; dart glands inserting together with the dartless appendages (Fig. 27); stimulatory organ lacking in one group.

Ethiopian (middle and E. Africa).

The Ethiopian Halolimnohelix group corresponds in the structure of the reproductive system, apart from the insertion of the dart glands, to the Hygromiidae, while it differs from the Bradybaenidae, in which it had been placed since Pilsbry's (1919) treatment, by its bursa lying adjacent to the spermoviduct, the presence of two stimulatory organs, and the tubular structure of the dart glands (see Pilsbry, Pfeffer, 1931; Verdcourt, 1973, 1974). Thus while an association with the Bradybaenidae cannot be considered, it remains to be clarified whether the group is to be considered as a subfamily of the Hygromiidae or as an independent family, since the differences from the Palearctic Hygromiidae are somewhat greater than those among hygromiid subfamilies; in comparison to the other families of the Helicoidea, it would by all means be better classified as a subfamily. The development of two stimulatory organs, which is plesiomorphic for the Hygromiidae, and the plesiomorphic insertion of the glands together with the dart sacs support the theory that the Halolimnohelicinae arose from an isolate of the Hygromiidae that immigrated relatively early into Ethiopia.

Helicidae Rafinesque 1815

Jaw ribbed, in some groups smooth; diverticulum usually present; stimulatory organ single, consisting of a dart sac, without an accessory dart sac, and two dart glands; dart glands tubular, usually divided, inserting on the base of the dart sac.

W. Palearctic plus Cape Verde, also one species in the N.E. Nearctic.

In all Helicidae studied to date, the bursa angles off from the spermoviduct.

After the separation of the Hygromiidae (q.v.), the Helicidae present a comparatively consistent group, which can be arranged into two subfamilies, Ariantinae and Helicinae, based on the structure of the reproductive system, especially the stimulatory organ, and which also differ in chromosome number and in geographic range. The separation of a third subfamily, as proposed by Hesse (1918a: Murellinae), Germain (1929: Tacheocampylaeinae), or Schileyko (1972b: Thebinae), does not seem supportable, because these groups are not sufficiently different from the Helicinae (q.v.).

To the Helicidae belong several groups of European Helicoidea of the Tertiary. While the Ariantinae have been indicated by only a few species from the Miocene on, the Helicinae are richly represented since the Eocene, especially in the Neogene with the Cepaea group (see H. Nordsieck 1986a).

Ariantinae Mörch 1864

Dart glands single to forked; dart less differentiated, with two edges (Fig. 28).

Europe (except the Caucasus), one species in N. Africa. The Ariantinae represent a consistent group that cannot be arranged into tribes despite the aberrant shell structure of several genera; it can be viewed as relatively plesiomorphic according to the structure of the stimulatory apparatus and of the male genitalia (see Hesse, 1931, 1934; Schileyko, 1971a, 1978). The concept of a consistent, plesiomorphic group is confirmed by chromosome counts, which in all studied species amounts to 29 or 30; a reduction has evidently not occurred in the Ariantinae as it has in the Helicinae.

Helicinae

Dart glands usually more or less divided; dart usually more differentiated, with four edges (Fig. 29).

Distributed as the family.

The Helicinae are a less uniform group than the Ariantinae, so that some groups can be separated as tribes (see above); in comparison to the Ariantinae, they are relatively apomorphic, based on the structure of the stimulatory organ and of the male genitalia (see Hesse, 1907-1920, 1931; Schileyko, 1978). This holds also for the chromosome numbers, which are usually reduced compared to those of the Ariantinae; in most studied species these amount to 28, 27, 26, or 25, and in a few species 30 or 22.

In spite of their great diversity, a subdivision of the Helicinae is not easy, because all divergent groups are connected with the remaining groups through less divergent ones. Two groups, which have previously been separated as subfamilies, can be evaluated as tribes:

Murellini Hesse 1918

Dart glands simple to slightly divided; dart with or without a crown.

Hereto Marmorana (Murella), as well as Macularia and Tacheocampylaea, which lead over to the Helicini in the structure of the dart. This separation of the Murellini as a tribe is supported by the development of the shell, especially of the bands, and by the geographic range; they are to be considered as relatively plesiomorphic with respect to the shell and reproductive system. A restriction of this tribe to Murella, as proposed by Hesse (1918a) because of the lack of the crown in this group, is not well founded, because still other groups of the Helicinae have a dart without a crown. Also, the separation of Tacheocampylaea, which Germain (1929) advocated because of the development of its dart cannot be accepted, because it does not differ significantly in this character from the other Helicinae.

Helicini

Dart glands more or less divided; dart usually with a crown.

Hereto the remaining groups, except for the following.

Euparyphini Perrot 1939[20]

Dart glands simple, wide; dart with a crown.

Hereto only Theba. The separation of this group as a subfamily, which was proposed by Schileyko (1972b), cannot be accepted, since it extensively corresponds to the Helicini except for the development of the dart glands.[21] The dart glands have an aberrant internal structure in contrast to that of the Ariantinae and the Murellini (see Schileyko); the Euparyphini are thus relatively apomorphic in this respect.

III. Phylogenetics.

The Helicoidea belong to the "helicid" Sigmurethra and are related to the Camaenoidea and the Mesodontoidea (Polygyroidea), with which they are also geographically more or less vicariant (see H. Nordsieck, 1986b). In contrast to these, the Helicoidea usually possess a stimulatory apparatus that inserts on the atrium or the vagina; this is the essential synapomorphy of the superfamily. The ancestor of the Helicoidea thus possessed, in addition to the plesiomorphic characters of the Stylommatophora and the apomorphic characters of the "helicid" Sigmurethra (see H. Nordsieck, 1985), a stimulatory organ that probably inserted on the atrium; this could have been a stimulatory organ resembling that of the Sphincterochilidae (see Section I). The remaining families of the Helicoidea may represent a monophyletic group, since they possess a common stimulatory organ (the dart apparatus) and (except for the Hygromiidae and Helicidae of the W. Palearctic) are geographically more or less vicariant. This group may have originated in the W. Palearctic, since it has the greatest diversity there, and may have spread from there to America and Asia; in this respect it corresponds to the Clausiliidae, which have the same region of origin and the same distributional pattern (see H. Nordsieck, 1986b). The stimulatory organ of this group was the plesiomorphic dart apparatus (Fig. 1), which consists of a dart sac with two simple glands inserting at its base (see Section I).

From this group, the Xanthonychidae may have split off first, because they have a broad range and a very high diversity at the family level; indeed they have only plesiomorphic characters in common, e.g. the simple dart glands. Concerning the remaining families, there is the question of whether the Bradybaenidae and the Hygromiidae, or the Hygromiidae and the Helicidae, constitute a monophyletic group. The decision depends on how one evaluates the possible synapomorphies of the first group (lack of a diverticulum, development of an accessory dart sac on the stimulatory organ) versus those of the second group (tubular dart glands, tendency toward reduction of the number of chromosomes), that is to say whether they are true synapomorphies or whether they arose through parallel evolution. The problem is not to be solved with the help of the geographic relationships of the three families or of their diversities. It is true that the

Bradybaenidae and the Hygromiidae are geographically more or less vicariant, while the Hygromiidae and Helicidae, both of whose distributional center is in the western Palearctic, are ecologically more or less vicariant there. There is no transition among all three families, neither in Europe, where the Hygromiidae and the Helicidae occur together, nor in Asia, where the range of the Bradybaenidae intersects that of the Hygromiidae. Concerning diversity, it is established that the Hygromiidae have a relatively high diversity at the family level, and the Bradybaenidae and Helicidae, in comparison, do not. Overall, it appears more likely that the tubular dart glands, whose development is unique within the "helicid" Sigmurethra, only arose once, thus represent the true synapomorphy, that is to say that the Hygromiidae and the Helicidae constitute a monophyletic group. The result of these reflections on the phylogeny of the Helicoidea is presented in summary in the cladogram of Fig. 30.

Comparing this described phylogeny with those previously proposed by Pilsbry (1895), Ihering (1929), Pilsbry (1939), and Schileyko (1978) (Fig. 31), indicates a general correspondence with Pilsbry's second proposal (with the exception of the Sphincterochilidae, which he did not consider). While both older proposals, in which only one character had been considered essential (Pilsbry: structure of the dart glands; Ihering: presence or absence of the diverticulum), need not to be discussed, the essential differences from the proposal of

Schileyko are once more set forth (see Section I, Sphincterochilidae not considered): (1) the Helicoidea are not diphyletic, but are monophyletic; (2) not a multiple stimulatory organ, but a single stimulatory organ, is plesiomorphic; (3) neither the remaining Helicoidea (without the Hygromiidae) nor their subgroups *sensu* Schileyko, *i.e.* the Humboldtianidae + Helicidae and the Helminthoglyptidae + Bradybaenidae, are monophyletic groups. The phylogenetic reconstruction by Schileyko must thus be regarded as false in its basic features.

Systematics of the Helicoidea.

Helicoidea Rafinesque
  Sphincterochilidae Zilch
      Sphincterochila
  Xanthonychidae Strebel & Pfeffer
    Monadeniinae n. subfam.
      Monadenia
    Helminthoglyptinae Pilsbry
      Helminthoglyptini
        Helminthoglypta, *Micrarionta*-Group, *Greggelix*
      Sonorellini Pilsbry
        Sonorella-Group
    Cepoliinae (Ihering) Pilsbry
      Setipellis, *Cepolis*, *Polymita*, *Dialeuca*
    Epiphragmophorinae Hoffmann
      Epiphragmophora-Group

  - Trichodiscininae n. subfam.
      - *Averellia*-Group
  - Lysinoinae Hoffmann
    - Leptariontini n. trib.
      - *Leptarionta*, *Tryonigens*
    - Lysinoini
      - *Lysinoe*
  - Xanthonychinae
      - *Xanthonyx*
  - Metostracinae n. subfam.
      - *Metostracon*
  - Humboldtianinae Pilsbry
    - Humboldtianini
      - *Humboldtiana*
    - Bunnyini n. trib.
      - *Bunnya*
  - Eloninae Gittenberger
    - Elonini
      - *Elona*-Group
    - Klikiini H. Nordsieck
      - *Soosia*
- Bradybaenidae Pilsbry
  - Bradybaeninae
      - *Aegista*-Group, *Pseudobuliminus*, *Stilpnodiscus*, *Bradybaena*-Group, *Euhadra*, *Dolicheulota*, *Nesiohelix*
  - Helicostylinae Ihering

Tricheulota, *Chloraea*, *Helicostyla*-Group

Hygromiidae Tryon

Trichiinae Ložek

Trichiini

Trichia-Group, *Ponentina*, *Xerocampylaea*, *Caucasigena*-Group, *Leucozonella*-Group

Helicopsini n. trib.

Helicopsis-Group

Hygromiinae

Hygromiini

Hygromia-Group, *Pyrenaearia*, *Portugala*, *Perforatella*-Group, *Chilanodon*-Group, *Fruticocampylaea*-Group, *Archaica*-Group

Leptaxini C. Boettger

Leptaxis-Group

Metafruticicolini Schileyko

Metafruticicola-Group

Helicellini Ihering

Xerosecta, *Cernuella*, *Candidula*, *Helicella*

Ciliellinae Schileyko

Trissexodontini n. trib.

Trissexodon-Group

Oestophorini n. trib.

Oestophora-Group, *Canariella*

Caracollinini n. trib.

Caracollina

        - Ciliellini
            - *Ciliella*
    - Geomitrinae C. Boettger
        - Trochoideini n. trib.
            - *Trochoidea*-Group
        - Geomitrini
            - *Geomitra*-Group, *Pseudocampylaea*
    - Monachinae Wenz
        - Euomphaliini Schileyko
            - *Euomphalia*-Group, *Hesseola*, *Paedhoplita*-Group, *Lejeania*
        - Monachini
            - *Monacha*-Group
        - Cochlicellini Schileyko
            - *Cochlicella*, *Monilearia*
    - Helicodontinae Kobelt
        - Helicodontini
            - *Helicodonta*-Group
        - Lindholmiolini Schileyko
            - *Lindholmiola*
    - Halolimnohelicinae H. Nordsieck
            - *Halolimnohelix*-Group
- Helicidae
    - Ariantinae Mörch
            - *Helicigona*-Group, *Cylindrus*, *Isognomostoma*-Group
    - Helicinae
        - Murellini Hesse

Marmorana, Macularia, Tacheocampylaea

Helicini

Levantina-Group, Hemicycla, Lampadia, Iberus-Group,

Cepaea-Group, Helix-Group, Otala-Group, Eremina

Euparyphini Perrot

Theba

FOOTNOTES

[1] Shileyko's classification is generally remarkable, because he is a pronounced splitter not only at the generic level but also at the family level. The latter mainly has to do with the fact that he does not use the category of tribe; as a result, his classification erects too many subfamilies that are not real. This holds true for the Helicoidea, for example, several of his subfamilies of the Hygromiidae (q.v.) which are only tribes in my opinion.

[2] There are two serious errors underlying Schileyko's interpretation of his illustrated sections through the reproductive system (1978; Fig. 20, I-III): the part with gland cells that he labels (in I) as the sperm groove is not the sperm duct (= autosperm duct), but rather the allosperm duct. The prostate does not have, as he shows (in II), a central cavity, but consists instead of follicles that discharge into the autosperm duct, which is missing in his illustration.

[3] This character has taxonomic significance not only in the Helicoidea, but also in the Clausiliidae and probably also in other groups of the Stylommatophora. In the Clausiliidae, however, it characterizes subfamilies (see H. Nordsieck 1978); this is one of several indications that subfamilies of the Clausiliidae have approximately the same rank as families of the Helicoidea (also see H. Nordsieck 1986a).

[4] In the cladogram with which Schileyko (1978: Fig. 29) elucidates his concept of the phylogeny of the Helicoidea, the statement concerning the position of the bursa in the various groups must be called into doubt. While, for example, it has been demonstrated for the Helicidae and the Bradybaenidae through Schileyko's own investigations that their bursa angles off from the spermoviduct, this statement concerning, for example, the Xanthonychidae (Humboldtianidae and Helminthoglyptidae *sensu* Schileyko) and the groups not belonging to the Helicoidea (see Section II), is based only on a hypothesis of Schileyko; this hypothesis is refuted by appropriate illustrations of the reproductive systems of these groups (by Pilsbry, for example), in which the bursa lies adjacent to the spermoviduct. An investigation of this character therefore would be highly desirable, especially in the Xanthonychidae.

[5] The presentation of the stimulatory apparatus by Schileyko (1978: Fig. 29) leaves something to be desired, especially in the non-European groups. Thus for example the presentation of that of the Helminthoglyptidae and of the the Bradybaenidae is misleading, because the dart sac and the neophore are not distinguished from each other. This creates the illusion of a greater resemblance than exists in reality; a close relationship between these two families, which Schileyko deduced from this character, does not exist.

[6] The stimulatory apparatus of the Hygromiidae is not quadrupled, but doubled. Schileyko's incorrect evaluation was a consequence of the fact that he mistook the accessory dart sac of the Hygromiidae for a dart sac and illustrated it accordingly (1978: Fig. 29), whereas he neglected the accessory dart sac of the Bradybaenidae in the same illustration. It must be emphasized nevertheless that neither the accessory dart sac of the Hygromiidae nor that of the Bradybaenidae is homologous with a dart sac (see Section I).

[7] The insertion of the stimulatory organ in some Xanthonychidae on the atrium is thus not to be viewed as plesiomorphic, as I earlier proposed (H. Nordsieck, 1985:17).

[8] Unfortunately, little is known of the mating behavior of the various groups of the Helicoidea. The former mentioned behavior was observed in groups of the Xanthonychidae (see Webb, 1942, 1952b); it may represent that of all Helicoidea with small, simple darts (Xanthonychidae, Bradybaenidae, Hygromiidae), whereas the latter mentioned behavior may occur in groups with large, differentiated darts (many Hygromiidae, Helicidae).

[9] The assumption I made earlier (H. Nordsieck, 1985:5) that the Corillidae were related to Asian Helicoidea, originated in Schileyko's (1979) placement of this group.

[10] Sphincterochilidae Zilch, 1960, is the replacement name for Leucochroidae Westerlund 1886, due to homonymy of the type genus; it retains the date of the replaced name (ICZN Article 39, 40A). The same holds for Trichiinae Ložek, 1956 (= Fruticicolinae Kobelt, 1904) and Helicellinae Ihering, 1909 (= Xerophilinae Kobelt, 1904). Bradybaenidae Pilsbry, 1934, is the replacement name for Eulotidae Moellendorff, 1898, because of synonymy of the type genus; it likewise retains the date of the replaced name (ICZN, Article 40, 40A). For the nomenclature of family-level taxa of non-European Helicoidea, see H.B. Baker (1959).

[11] The terms appendicula and appendix were used in the Helicoidea (and universally in the Stylommatophora), for different, non-homologous parts of the reproductive system. The term "appendicula" was used to denote (1) the appendage of the stimulatory apparatus of the Sphincterochilidae, (2) the transformed dart sac of the Monachinae, and (3) a basal appendage of the vagina of <u>Trochoidea</u> (Geomitrinae), which are not homologous with each other; nor are they homologous with the appendicula of the Acavoidea and the Plectopylididae, which corresponds to the diverticulum. The term "appendix" was used to denote basal appendages of the penis, which occur in the Sphincterochilidae and in the two helicelloid groups of the Trichiinae and Geomitrinae and are not homologous with each other; they also are homologous with neither the penial appendix

nor the terminal penial caecum of other Stylommatophora.

[12] Indeed, the reasons that Forcart (1972) gives for splitting the Sphincterochilidae as an independent superfamily are certainly partially invalid. That the appendicula on the sheath of the stimulatory organ is not homologous with the dart sac can surely not be based on the fact that the stimulatory apparatus inserts on the atrium. The structure of the penis (_sensu_ Forcart = penis plus epiphallus) is likewise not a suitable basis for this division, because not all Helicoidea have the complex penial structure of the Helicinae.

[13] Unfortunately Schileyko (1978) gave no details as to which groups ought to belong to his family Humboldtianidae: _Humboldtiana_ alone, the Humboldtianinae, or all Xanthonychidae with multiple stimulatory apparatus. Also, the close relationship to the Helicidae that he claimed was not substantiated.

[14] It is to be noted that Schileyko (1978), in addition to these four groups, named _Canariella_ and _Soosia_, which he obviously could not classify. One of his four groups moreover is heterogeneous again, because it contains the _Helicodonta_ group and _Caracollina_; a stimulatory apparatus, as he illustrated for this group (Fig. 31), does not exist. Also, Schileyko likewise ascribed to _Atenia_, which was classified in this group too, an

appendicula, which is, however, a dart gland, according to Gittenberger (1968).

[15] It is not acceptable, as Schileyko (1978) proposed, to present the Hygromiinae and the Euomphaliinae as monophyletic groups based on the structure of the stimulatory organ, and at the same time to derive those middle-Asian groups with the same stimulatory organ (the Archaica and Paedhoplita groups) independently of them from the Trichiinae, which have a different stimulatory organ, only because species of these two groups bear a close resemblance to certain neighboring species of the Trichiinae. In any case, it is entirely unrealistic to believe these groups could have derived from the Trichiinae since the Pleistocene (Schileyko, 1978: Fig. 33).

[16] This subfamily must unfortunately bear the name of a group that has no stimulatory apparatus, thus is not representative of the subfamily; the reason for this is Schileyko's early and premature erection of a tribe Ciliellini for those Hygromiidae without a stimulatory apparatus.

[17] After I had discovered, with the help of the literature on the anatomy (jaw, reproductive system) of Leptaxis, that it belonged to the Hygromiidae, I ascertained that Schileyko had already (1972a) placed Leptaxis undata Lowe, based on the structure of its reproductive system, next to Monachoides and hence to the

Hygromiidae. This association of the group with *Monachoides* goes too far, however, because its peculiarities have not been sufficiently considered. The membership of *Leptaxis* in the Hygromiidae and Hygromiinae has in the meantime been confirmed through the anatomical investigation of several species that I obtained from K. Groh of Darmstadt.

[18] Monachinae Wenz, 1930 (as Monachea) is the replacement name for Thebea Wenz, 1923, because of homonymy, whereas Thebea was the replacement name for Carthusianea Kobelt, 1904, because of synonymy of the type genus. Monachinae Wenz is certainly preoccupied by the pinniped mammalian group Monachinae (type genus Monachus), so that the case must be brought before the Commission under Article 55 (a) of the ICZN.

[19] This difference is apparently more strongly expressed in *Drepanostoma* than in *Helicodonta*, which caused Hesse (1918b, 1931, 1934) to compare the appendage of the former with a dart sac, and the appendage of the latter with a dart gland. This is, however, not permissible, because the appendages of both are doubtless homologous.

[20] Thebinae Schileyko 1972 non Wenz 1923 = Euparyphini Perrot 1939.

[21] The penial papilla, the lack of which Schileyko (1972b) stated

as an additional characteristic of his Thebinae, occurs in _Theba_ the same as in all Helicinae, as Noyce (1973) has shown through detailed studies.

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SUPPLEMENT BY HARTMUT NORDSIECK, 1989

The dates of some names must be corrected. The names Leucochroidea Westerlund 1886, Fruticicolinae Kobelt 1904, and Theba Wenz 1923 have not been founded on homonyms, but on wrongly typified genera resp. wrongly used generic names. Sphincterochilidae Zilch 1960 is the replacement name for Albeidae Pallary 1909, due to synonymy of the type genus (see Forcart 1972). According to the revised ICZN (International Commission on Zoological Nomenclature 1985) the respective names of familial taxa should be written as follows:

Sphincterochilidae Zilch 1960 (1909);
Bradybaenidae Pilsbry 1934 (1898);
Trichiinae resp. Trichiini Ložek 1956 (see section 3);
Helicellini Ihering 1909;
Monachinae Wenz 1930 (1904).

In the Sphincterochilidae, Forcart (1974) stated that in the species group of Sphincterochila the right tentacular retractor muscle crosses the terminal genitalia, i.e. has a normal course. If this is confirmed it is further evidence for the slight taxonomic value of this character.

For the Hygromiidae, the results of recent investigations and of a further comprehensive comparison are that the groups with two stimulatory organs with normal dart sac and those with a single one should not be separated as the subfamilies Trichiinae and Hygromiinae but united in a subfamily Hygromiinae, because the evolution from a double dart apparatus to a single one obviously occurred several times in a parallel way. This has been shown in helicelloid groups of Europe (see Hausdorf 1988), but also in groups of middle Asia with normal course of tentacular retractor muscle (Nanaja-Archaica, see Schileyko 1987). The groups with normal stimulatory organs are thus treated correspondingly as those with modified ones (Geomitrinae, Monachinae), in which groups with a double stimulatory organ and those with a single one are united, too. In this connection the hypothesis that the stimulatory organ of the Helicella group is secondarily doubled must be abandoned; its double dart apparatus may be plesiomorphic as in all other Hygromiidae with two stimulatory organ, because it can be derived from that of the Helicopsis group through intermediate form (e.g. Xeromicra Monterosato).

Accordingly, the Hygromiinae can be characterized as follows:

One or two dart sacs, normally developed, in most groups with accessory dart sacs; in some groups stimulatory organ missing.

Hereto the Trichiini, Helicopsini, Helicellini, Hygromiini, Leptaxini, and Metafruticicolini. It must be emphasized once more that the tribal classification of the Hygromiidae can only be provisional, since many groups belonging to it are not yet sufficiently investigated.

Concerning the chromosomes of the Monachinae, it can be added that those of Monacha and Cochlicella do correspond not only in the number but also in other characters (see Rainer 1967); this is an additional support for their belonging to the same subfamily. The cytological examination of further European Hygromiidae (see

Ramos & Aparicio 1985) has shown that higher chromosome numbers can be found also in the non-helicelloid groups of the Hygromiinae and in the Monachinae; the single examined species of the Ciliellinae has a high chromosome number. These results speak in favor of the hypothesis that the reduction in chromosome number occurred in several lineages through parallel evolution.

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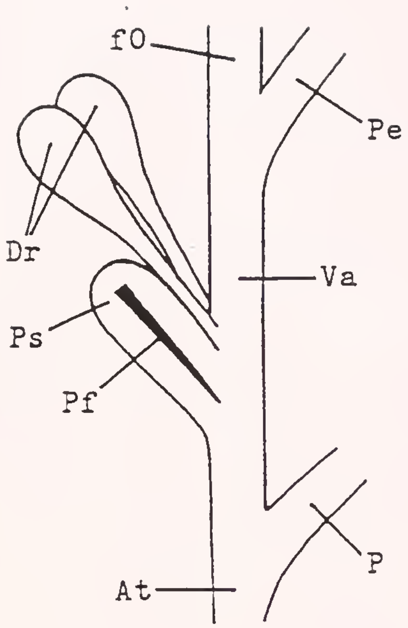


Fig. 1. Dart apparatus (plesiomorphoric condition). At = atrium; Dr = dart glands (mucous glands); fO = free oviduct; P = penis; Pe = stalk of bursa copulatrix; Pf = dart; Ps = dart sac; Va = vagina

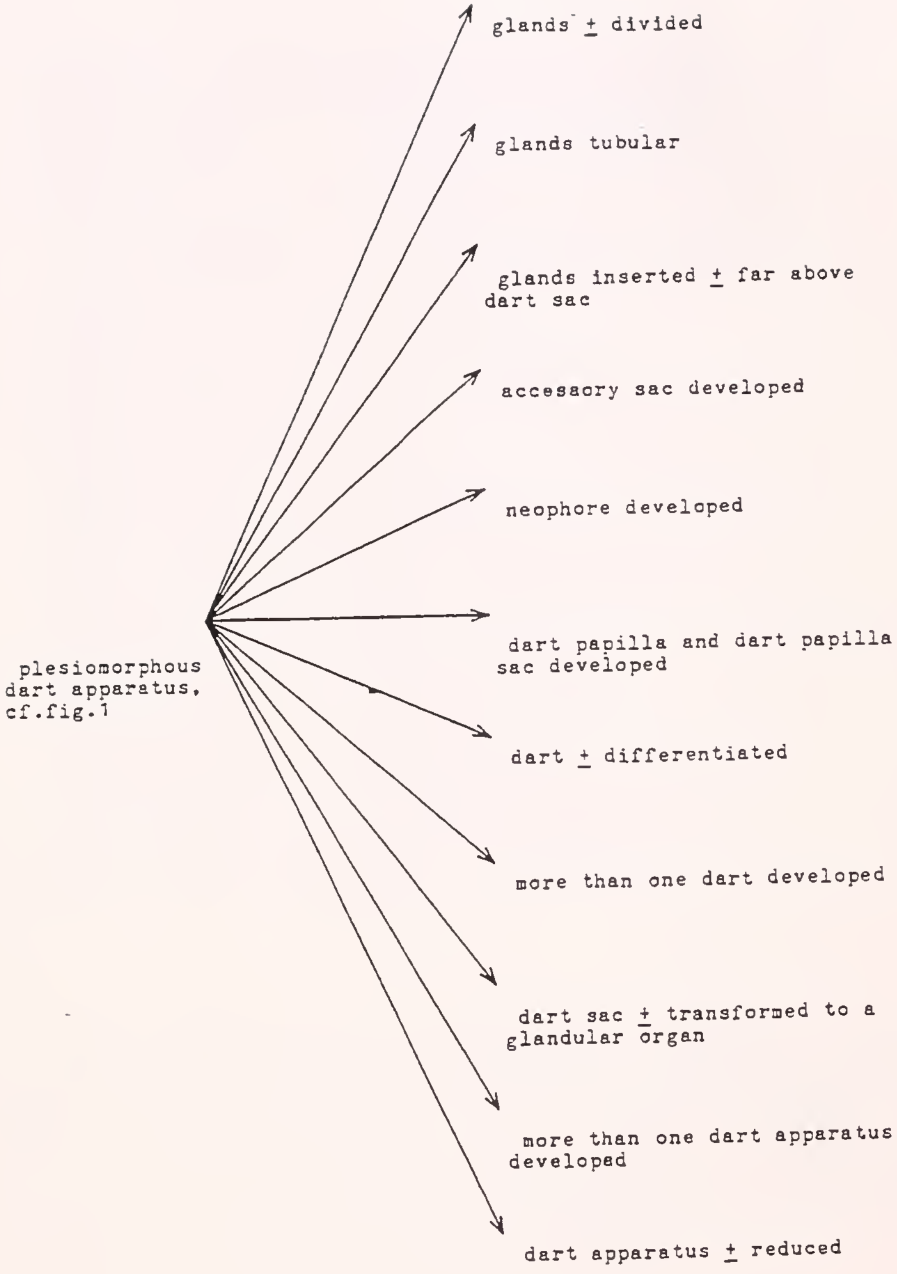
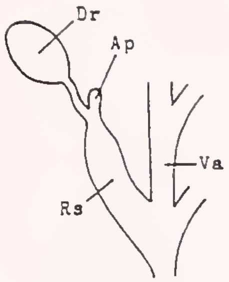


Fig. 2. Evolutionary transformations in the dart apparatus.

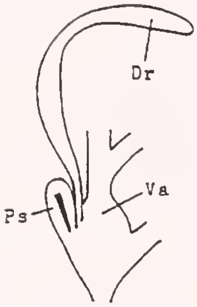
Figs. 3-29. Stimulatory organs of Helicoidea
(schematic, from various authors).

3. *Sphincterochila* (Sphincterochilidae)
4. *Monadenia* (Xanthonychidae, Monadeniinae)
5. *Micrarionta* (X., Helminthoglyptinae)
6. *Helminthoglypta* (X., Helminthoglyptinae)
7. *Cepolis* (X., Cepoliinae)
8. *Epiphragmophora* (X., Epiphragmophorinae)
9. *Trichodiscina* (X., Trichodiscininae)
10. *Leptarionta* (X., Lysinoinae)
11. *Lysinoe* (X., Lysinoinae)
12. *Xanthonyx* (X., Xanthonychinae)
13. *Metostracon* (X., Metostracinae)
14. *Humboldtiana* (X., Humboldtianinae)
15. *Elona* (X., Eloninae)
16. *Fruticicola* (Bradybaenidae, Bradybaeninae)
17. *Aegista* (B., Bradybaeninae)
18. *Helicostyla* (B., Helicostylinae)
19. *Trichia* (Hygromiidae, Trichiinae)
20. *Hygromia* (H., Hygromiinae)
21. *Oestophora* (H., Ciliellinae)
22. *Caracollina* (H., Ciliellinae)
23. *Trochoidea* (H., Geomitrinae)
24. *Euomphalia* (H., Monachinae)
25. *Cochicella* (H., Monachinae)
26. *Helicodonta* (H., Helicodontinae)
27. *Vicariihelix* (H., Halolimnohelicinae)
28. *Helicigona* (Helicidae, Ariantinae)
29. *Helix* (H., Helicinae)

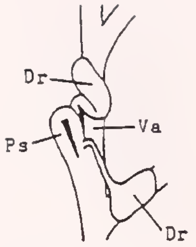
Ap = appendicula (of Sphincterochilidae) or appendage without a dart (of Hygromiidae); At = atrium; Dr = dart glands (mucous glands); fO = free oviduct; Ne = neophore; Ns = accessory dart sac; P = penis; Pe = stalk of bursa copulatrix; Pf = dart; Pp = dart papilla sac; Ps = dart sac; Rs = sheath of stimulatory organ (of Sphincterochilidae); Va = vagina



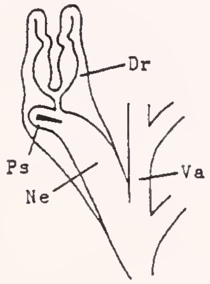
Sphincterochila



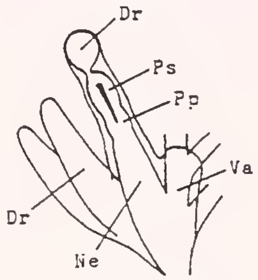
Monadenia



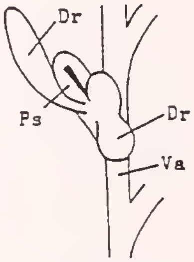
Micrarionta



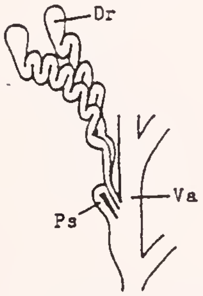
Helminthoglypta



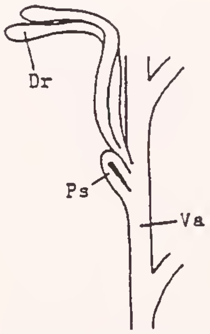
Cepolis



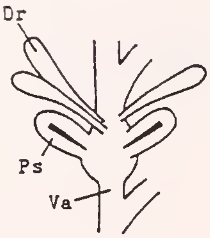
Epiphragmophora



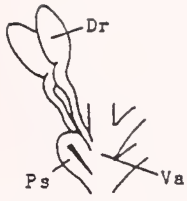
Trichodiscina
(= Averellia)



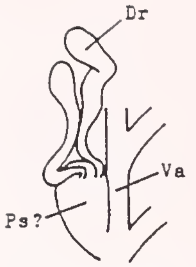
Leptarionta



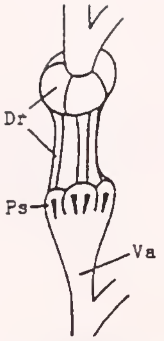
Lysinoe



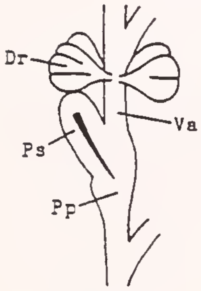
Xanthonyx



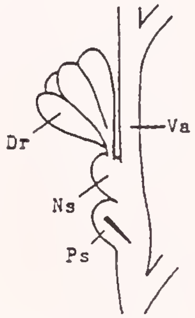
Metostracon



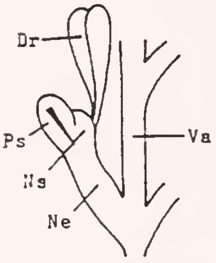
Humboldtiana



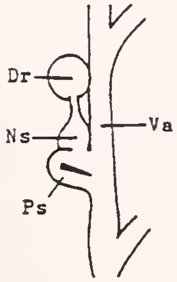
Elona



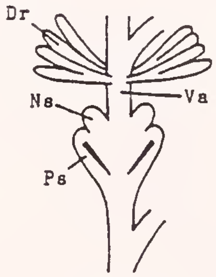
Fruticicola
(= *Bradybaena*)



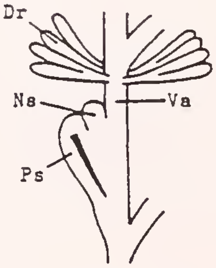
Aegista



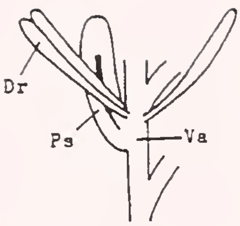
Helicostyla



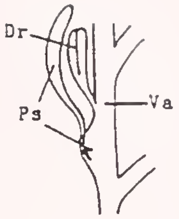
Trichia



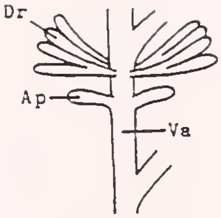
Hygromia



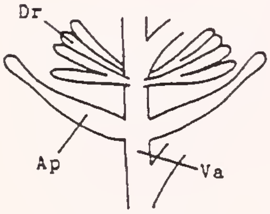
Oestophora



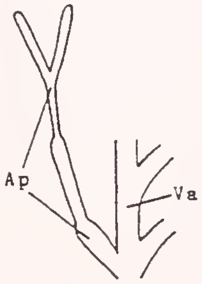
Caracollina



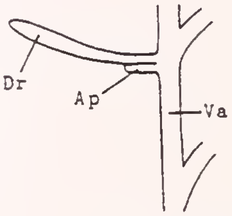
Trochoidea



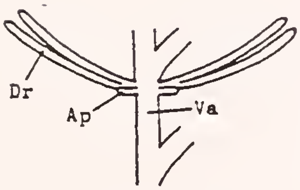
Euomphalia



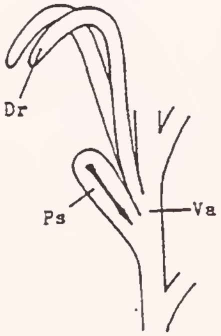
Cochlicella



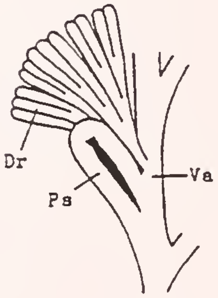
Helicodonta



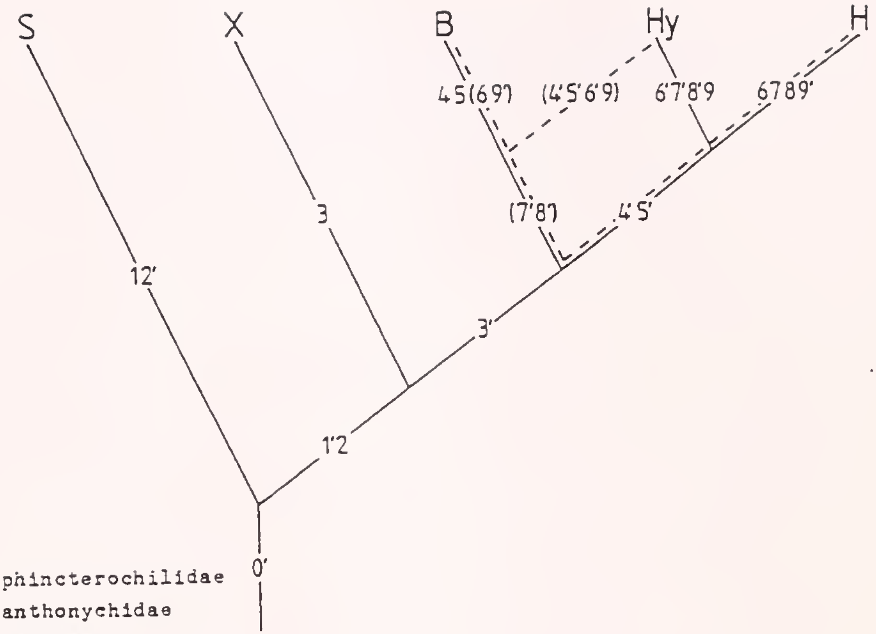
Vicariihelix



Helicigona



Helix



S = Sphincterochilidae
X = Xanthonychidae
B = Bradybaenidae
Hy= Hygromiidae
H = Helicidae

0' = stimulatory organ on atrium resp.vagina
1/1' = other stimulatory organ/dart apparatus
2/2' = hermaphrodite duct without/with accessory ves.seminalis
3/3' = dart glands not divided/divided
4/4' = dart glands not tubular/tubular
5/5' = chromosome number constant/tending to reduction
6/6' = stimulatory organ single/doubled
7/7' = stimulatory organ without/with accessory sac
8/8' = diverticulum present/absent
9/9' = bursa running along spermoviduct/bent off from s..

Fig. 30. Phylogeny of the Helicoidea (a cladogram with plesiomorphic/apomorphic character states, with two alternatives for the Eurasian families).

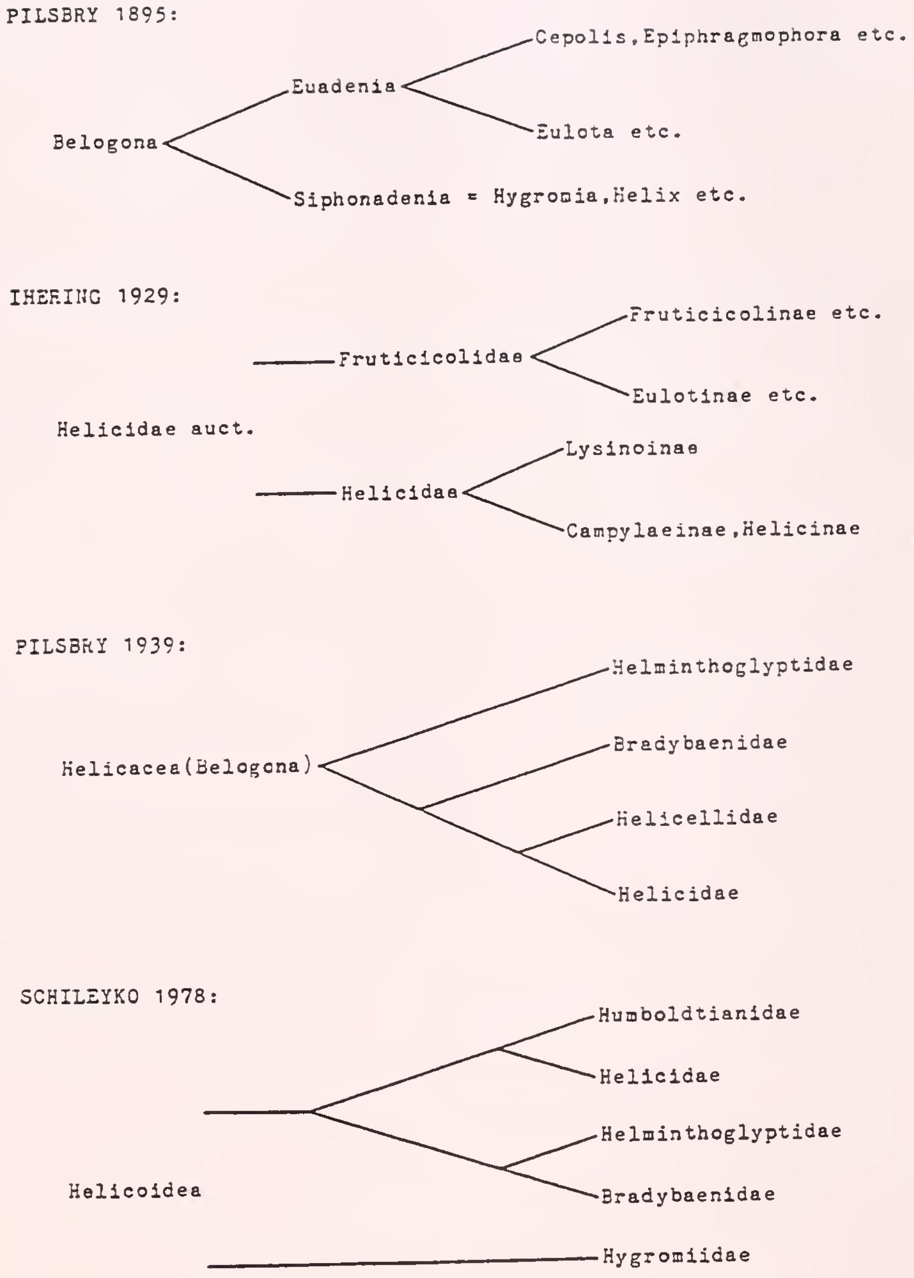


Fig. 31. Various authors' phylogenies of the Helicoidea (not including the Spincterochilidae).