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The system of the Stylommatophora (Gastropoda), with special regard to the systematic position of the Clausiliidae, I.

Importance of the excretory and genital systems.

By

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With 6 figures.

Investigations concerning the evolution of the Clausiliidae, which were carried out to improve the system of the family worked out in the last decade (H. NORDSIECK 1978, 1979), made necessary a clarification of their systematic position within the Stylommatophora. This already became obvious, when an effort was made to reconstruct the evolution of the closing apparatus of the family (H. NORDSIECK 1982).

Study of literature shows that the opinions as to the systematic position of the Clausiliidae differ greatly. Conchyliologists of the last century classified the family with other groups having high-spired shells with columellar lamellae, too. In the

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system of P. FISCHER (1883), for instance, the Clausiliidae stand together with Megaspiridae, Coeliaxidae, some Urocoptidae and Ceriidae in his family Pupidae. WIEGMANN (1893), who was the first to examine the anatomy of the family, supposed relations to the Urocoptidae on the one hand, and to the Pupillidae and Buliminidae on the other. PILSBRY (1904) thought the Clausiliidae to be nearly related to the Megaspiridae, judging from the intermediate appearance of the fossil group *Palaeostoa* of this family; a classification with the Orthurethra was out of the question, since WIEGMANN had assigned a sigmurethrous excretory system to the family. The classification of PILSBRY was followed by C. BOETTGER (1926) and ZILCH (1960). A. J. WAGNER (1921) and STEENBERG (1925), who had examined particularly the genital system of the Clausiliidae, assumed, however, close relationships to the Orthurethra. WAGNER placed the Clausiliidae with regard to shell, radula and genitalia near to the Pupillidae and Buliminidae; this opinion was followed by THIELE (1931, 1935), who supposed the nearest relations to the latter family. STEENBERG believed *Lauria* (Pupillidae) to be most closely related to the Clausiliidae, because this group, according to his investigations, has a similar structure of the genitalia. H. B. BAKER (1961) found that the Clausiliidae have an excretory system without ureter like that of *Cerion*: he therefore united Clausiliidae and Ceriidae in a superfamily Clausilioidea, which he classified with his suborder Mesurethra. This classification was accepted in the systems of TAYLOR & SOHL (1962), FRANC (1968) and SOLEM (1978). SCHILEYKO (1979), however, united the Clausiliidae with regard to shell and genitalia with Megaspiridae and Urocoptidae in a superfamily Clausilioidea, which he placed into his suborder Achatinina.

The cause for these different opinions of the systematic position of the Clausiliidae are, after all, different opinions of the taxonomic importance of characters, e. g. of the excretory or genital system, to the classification of the Stylommatophora. It was therefore necessary to examine this importance more carefully. During this examination it became evident that the "American" system of PILSBRY and BAKER (last version from SOLEM 1978) generally accepted today as well as the new "Russian" system of SCHILEYKO (1979) need a critical revision, since both systems show serious deficiencies resulting from the use of the taxonomic characters. This revision shall offer a system founded on several taxonomic characters which were carefully examined for this purpose; as I hope it will serve as a basis for a phylogenetic system which has to be elaborated in the future. In the first part of this revision the importance of excretory and genital systems, in the second that of shell and distribution shall be analyzed, while in the third part the system shall be revised in detail.

I. Excretory system.

The system of the Stylommatophora generally used today originates from PILSBRY (1900), who founded it on the structure of the excretory system. Though this system was rejected by SIMROTH (1911) and THIELE (1931, 1935) as not natural, it was developed further by H. B. BAKER (1955), and after adoption by SOLEM (1959) and ZILCH (1960) it was generally accepted. Recently it was called in question again by SCHILEYKO (1976, 1979), in principle with the same argument as SIMROTH and THIELE.

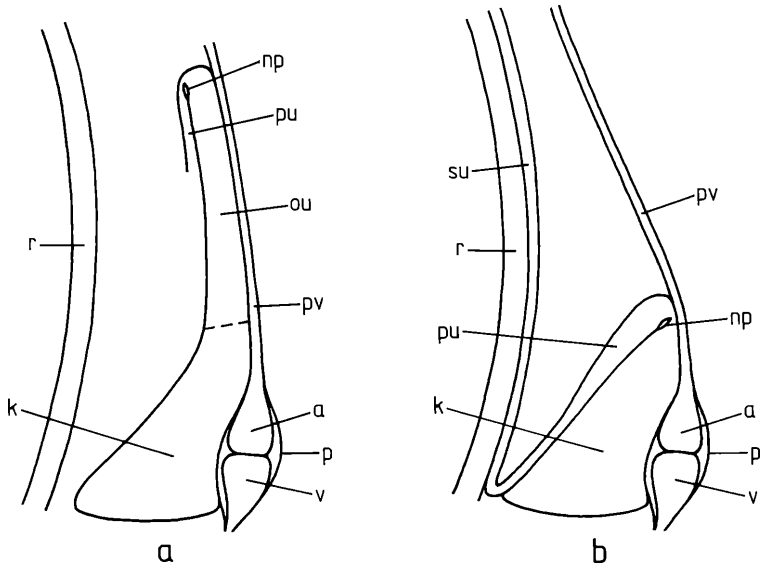

Fig. 1. Excretory system of Stylommatophora: a) orthurethrous system; b) sigmurethrous system (in the strict sense). a = atrium, k = kidney, np = nephridial pore, ou = orthureter, p = pericardium, pu = primary (sigm)ureter, pv = pulmonary vein, r = rectum, su = secondary (sigm)ureter, v = ventricle.

Thus any critical revision of the system of the Stylommatophora has to begin with a question about the taxonomic importance of the excretory system. This can be evaluated only by a comparative examination, which is the condition of revealing its basic phylogeny. It was carried out by a study of the literature referring to the excretory system, especially of some summarizing publications (PILSBRY 1900, SIMROTH 1911, WÄCHTLER 1934, H. B. BAKER 1955, DELHAYE & BOUILLON 1972b, SCHILEYKO 1976, LIKHAREV & WIKTOR 1980) and controlling investigations of may own.

In all Stylommatophora the excretory system (fig. 1) consists of a nephridial sac (kidney) and an ureter if present; the boundary between them is marked by the nephridial pore (cf. WÄCHTLER 1934). There are two different types of kidney as follows: 1) The kidney is long, extending nearly to the mantle collar, and divided into two parts, a broad proximal one (nephridial sac strictly speaking) and a distal one being more or less narrowed. This part is histologically different and functions as an ureter (DELHAYE & BOUILLON 1972b), but cannot be named so, since it is not homologous with that part of the excretory system which usually is called ureter. I therefore use the term orthureter proposed by H. B. BAKER (1935), which is more suited than pseudureter (IHERING 1929) or nephridial pouch (DELHAYE & BOUILLON 1972b)[1]); the true ureter can be called simply ureter or more exactly sigmureter.

[1]) DELHAYE & BOUILLON use the term "uretère" for their "poche néphridienne" and the true ureter, but for the first the term "pseudo-uretère", too. Because this cannot be accepted, I propose to use the terms orthureter and (sigm)ureter, thus reminding of the respective excretory systems.

This kidney is that of the orthurethrous type of excretory system. 2) The kidney is more or less shorter, because the distal part (orthureter) is lacking. This kidney is that of the other types of excretory system.

The ureter (sigmureter) is divided into the primary ureter running back along the kidney and the secondary one running forward along the hindgut to the mantle collar. It is differently developed in the various groups of Stylommatophora; three stages of development can be distinguished, which obviously represent stages of increasing perfection: 1) A real ureter is absent; in place of it a more or less distinct band is visible, which histologically proves to be ciliated, a first stage of ureter. 2) The ureter is a groove separated from the rest of the pulmonary roof by a fold, i. e. the ureter is open. 3) The ureter is a tube developed from the groove which is overgrown by the fold, i. e. the ureter is closed. In many groups more than one type of ureter occurs in the same excretory system, e. g. the primary ureter can be closed and the secondary one open; in general the closure goes on from the nephridial pore up to the ureter pore. It is not always clear from the information given in the literature what type of ureter is developed; total absence of ureter and presence of ciliary band are often not distinguished.

PILSBRY (1900) proposed to divide the Stylommatophora except for the Tracheopulmonata into the groups Orthurethra, Heterurethra and Sigmurethra; BAKER (1955) added the group Mesurethra. The respective types of excretory system can be characterized as follows: 1) Orthurethria: Kidney with orthureter; usually only the proximal part of primary ureter developed as a groove. 2) Mesurethria: Kidney without orthureter; primary and secondary ureter lacking, in place of them ciliary bands developed. 3) Sigmurethria: Kidney without orthureter; both ureters are developed, primary one usually closed, secondary one open or closed. 4) Heterurethria is an ambigous term. It was created by PILSBRY for the excretory system of the Succineidae whose kidney differs from that of the Sigmurethra by being transversely extended, the primary and secondary ureter at right angles with each other. BAKER applied the term to all Stylommatophora having a transverse kidney. This is not only found in snails showing a reduction of mantle cavity in connection with an evolution towards slugs (limacisation), as in Succineidae, Amphibuliminae, Helixarionidae, Vitrinidae, but also in many groups whose mantle cavity is not reduced, e. g. of Achatinoidea, Oleacinoidea, Streptaxoidea, and Punctoidea.

Thus heterurethria would be a form of sigmurethria. DELHAYE & BOUILLON (1972b), however, ascertained further differences between the excretory systems of Succineidae and other Sigmurethra concerning the nephridial pore and ureter, and thought therefore heterurethria in the original sense to be possibly an independent type of excretory system, but the taxonomic importance of these differences has yet to be examined.

Orthurethrous are several groups which except for some of them agree widely in shell and genitalia. In some groups, such as *Pupisoma* (Vertiginidae) and *Acanthinula* (Valloniidae), the primary ureter is closed; the Cerastuidae even have a complete open or closed primary ureter and an open secondary ureter (pseudosigmurethria, SOLEM 1964). There are no transitions between orthurethria and the other types of excretory system; a remarkable exception is the excretory system of the Partulidae, whose kidney has a shortened and more narrowed orthureter.

Mesurethria and sigmurethria, on the contrary, can be found in groups differing very much in shell and genitalia. In this regard the Mesurethra of BAKER are an exceptionally heterogenous group, including besides the Clausiliidae the Ceriidae, which are nearly related to the sigmurethrous Urocoptidae, the Strophocheilidae and Dorcasiidae, which belong together with the sigmurethrous Acavoidea, and the Corillidae, which can be grouped with the sigmurethrous Asian Helicoidea (and are sigmurethrous, too, according to SOLEM 1966)[2]). There are transitional stages between mesurethria and sigmurethria. A mesurethrous system with a short ureter, as in Strophocheilidae, is the first step towards sigmurethria; further steps are sigmurethrous systems without secondary ureter, as in Caryodidae, Haplotrematidae, Endodontidae, and those with a totally or partly open secondary ureter occuring in many groups, as in Orthalicidae (Bulimulidae), Rhytididae, Oleacinidae, and Helicidae. There are transitional stages between sigmurethria and heterurethria (in the sense of BAKER), too, in connection with limacisation, as in Amphibuliminae, Helixarionidae, or not, as in Ferrussaciidae, Punctidae, whose kidneys have various u-shaped forms.

The more or less divergent types of excretory systems of slugs, which are not named (except for clasturethria of SIMROTH), are connected by transitions with sigmurethrous systems, too. The excretory system of the Testacellidae is a sigmurethrous one which is turned backwards; the ureter running behind is not a primary one, as PLATE (1891) and the following authors thought, but the secondary one, because the primary one is represented by the initial part of ureter bent forward over the kidney ("Uretersack" of PLATE). The Athoracophoroidea have an excretory system with an ureter forming a long serpentine duct in which a primary and secondary ureter cannot be well delimited; it is possible to derive it from that of the Succineidae, e. g. *Omalonyx* (DELHAYE & BOUILLON 1972b). The excretory system of Arionoidea is characterized by a kidney surrounding the pericardium and the primary and secondary ureter lying closely together; it is connected with the sigmurethrous one by transitional forms, e. g. in Philomycidae. The same applies to the excretory systems of the different slug groups of Vitrinoidea (Zonitoidea), Limacoidea and Trigonochlamydoidea, which have variously formed kidneys and primary and secondary ureters generally lying less closely together. The only common character of all these excretory systems is the entirely closed ureter; thus slugs demonstrate by their excretory systems that they have evolved several times independently (cf. LIKHAREV & WIKTOR 1980).

It results from this synopsis that there are two basic types of excretory system in the Stylommatophora, the orthurethrous and the sigmurethrous one in the broad sense, since only the development of the kidney is constant, while that of the ureter varies widely. To the sigmurethrous type belong the mesurethrous, heterurethrous and unnamed types of slugs, too, all being somehow connected with the sigmurethrous one.

The orthurethrous and mesurethrous systems, both without ureter, are plesiomorphous, because they can be derived easily from that of the Ellobioidea (cf. DELHAYE & BOUILLON 1972a). It is a question what kind of excretory system the

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[2]) The creation of this group by BAKER was therefore no progress compared to the system of PILSBRY, who classified the mesurethrous groups with the next related sigmurethrous ones, though he knew the structure of their excretory system intimately.

ancestor of Stylommatophora had. DELHAYE & BOUILLON assumed that both forms have evolved from that of the Ellobioidea; this would imply polyphyletic origin of the Stylommatophora. The correspondence of orthurethrous and mesurethrous groups, such as Pupilloidea and Clausilioidea, in shell and anatomy speaks, however, in favour of a common ancestor.

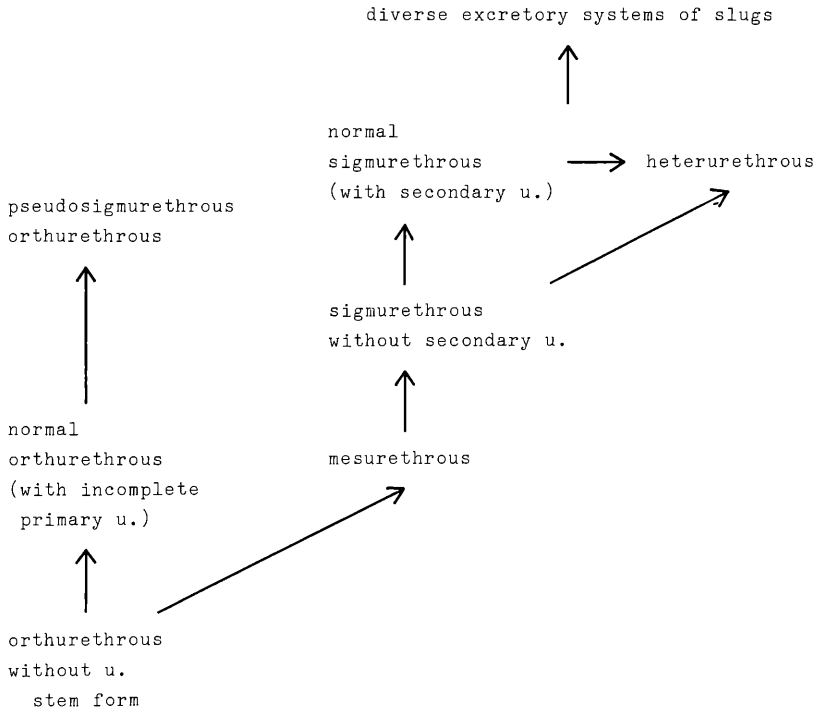

Fig. 2. Phylogenetic diagram of excretory systems of Stylommatophora. u. = (sigm)ureter.

This ancestor probably had an orthurethrous system (fig. 2), because in many Orthurethra this is combined with a plesiomorphous structure of shell and genitalia, which is not the case in the mesurethrous groups. The orthurethrous system is less perfect than the sigmurethrous one; therefore the Orthurethra remain quite small, and an evolution towards slugs was not possible. The most perfect orthurethrous system is the pseudosigmurethrous one of Cerastuidae with complete ureters. The mesurethrous system occurs in several unrelated groups; therefore it must be concluded that it evolved several times independently. The evolution from orthurethrous to mesurethrous type was realized by the reduction of the orthureter; moving force of it may have been the increase of the respiratory surface of the

pulmonary roof which was achieved by the shortening of the kidney. The mesurethrous system evolved several times further to the sigmurethrous one; in the various respective groups different developing stages of ureter were reached. In several groups evolution went further to heterurethrous systems, in connection with limacisation or not; heterurethria made possible a maintenance resp. an increase of the respiratory surface in the lung. The diverse excretory systems of slugs were derived from different sigmurethrous ones, probably in general by way of heterurethrous ones. The most perfect excretory system of Stylommatophora is the sigmurethrous one with closed ureters; it is not only that of many shelled snails, several of them reaching considerable size, but also that of nearly all slugs.

It can be summarized that orthurethria is a plesiomorphous character, while sigmurethria in the broad sense arose several times by parallel evolution. The groups which PILSBRY and BAKER founded on these characters are therefore paraphyletic (Orthurethra) or polyphyletic (Mesurethra, Sigmurethra), i. e. no natural groups. Thus it is clear that the structure of the excretory system cannot be the basis of the classification of Stylommatophora; apart from this overvaluation it is an important taxonomic character.

As to the excretory system of the Clausiliidae (fig. 3) the following informations can be given: BEHME (1889) and WIEGMANN (1893) stated that it is sigmurethrous with closed ureters. This was repeated by many authors, lastly by LIKHAREV (1962); only MANDAHL-BARTH (1951) described an open secondary ureter in *Boettgeria*. H. B. BAKER (1961) found that the ureter of *Nenia* and other Clausiliidae is lacking, i. e. that the excretory system is mesurethrous. My examination of several species belonging to different subfamilies led to results largely agreeing with those of BAKER. The excretory systems of the various species do not differ considerably. The nephridial pore has a subterminal position (less terminal than can be assumed from BAKER's figure) and free opening; there is no open or closed ureter. From the pore a whitish band is developed along the kidney back to the end of the pulmonary roof and from there along the hindgut forward to the anus; it overlaps somewhat the flanks of these organs. This is the same structure which WIEGMANN thought to be the ureter and BAKER described as "whitish zones (mucus or thickening?) along hindgut and kidney" In fact this is the ciliary band representing the ureter in the Mesurethra (see above). The band in place of the secondary ureter is somewhat more distinct than that of the primary ureter.

II. Genital system.

The great complexity of the genital system of the Stylommatophora requires an examination which has to be extended beyond this group to the other pulmonates and euthyneurans on the whole, so that its plesiomorphous structure and basic phylogeny in the pulmonates can be reconstructed. This extensive outgroup comparison is the prerequisite for recognizing the plesiomorphous condition of the genitalia and their evolutionary changes in the Stylommatophora. Therefore I think it necessary to repeat the most important results I have already published in a former paper concerning the comparative genital morphology of snails (H. NORDSIECK 1966).

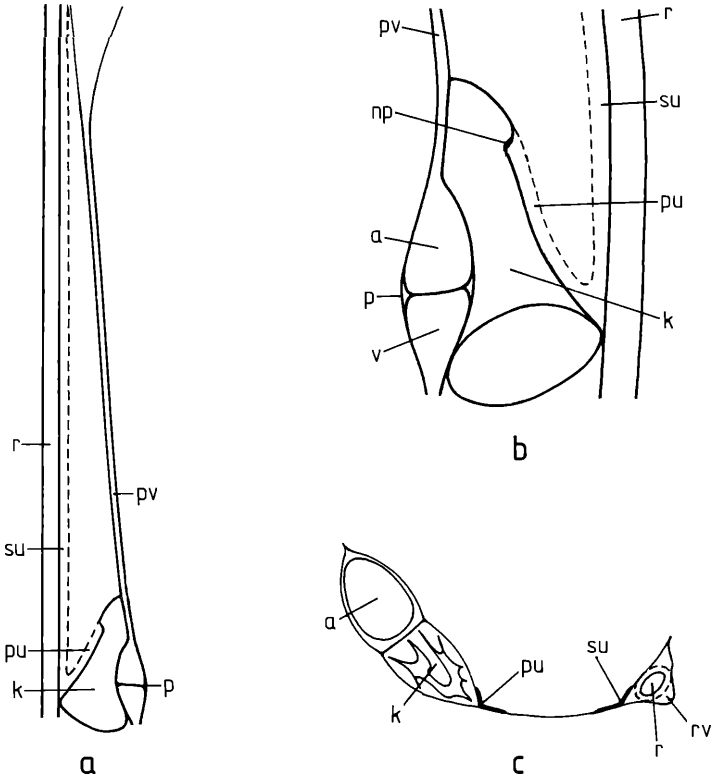

Fig. 3. Excretory system of Clausiliidae: a) from the outside; b) kidney from the inside, enlarged; c) section of b, inside above. pu = band in place of primary ureter, rv = rectal vein, su = band in place of secondary ureter, other abbreviations see fig. 1.

The genital system of higher Prosobranchia (cf. FRETTER & GRAHAM 1962; 1966: fig. 3[3])) consists, besides gonad, of gonadial, renal and pallial gonoduct, and additionally a cephalopodial gonoduct in the males. While gonadial and renal gonoduct are quite similar in both sexes, the following part is differing considerably. In the males there is a pallial spermiduct with prostate and a cephalopodial vas deferens and penis. In the females there is a pallial oviduct with oviducal glands and sperm receptacles, distally (with regard to the gonad) the bursa copulatrix (spermatheca), receiving the allosperm after copulation, and proximally a receptaculum seminis (spermatocyst), serving as a depository of allosperm for fertilization. Both are connected by a groove, which I propose to name allospermiduct[4]); thus the lumen of the female pallial gonoduct is divided into two parts.

[3]) This and other figures of my paper were copied by GÖTTING (1974: fig. 65), but with the incorrect indication "combined from various authors"

The changes in the genital system of the euthyneurans depend on hermaphroditism and the shifting of the gonoduct into the body haemocoele, which is caused by the change of the mantle cavity. The hermaphrodite pallial gonoduct did not evolve from the female gonoduct (PELSENEER 1895, FRETTER 1946) or the male gonoduct (HUBENDICK 1945) alone, but arose from a combination of both gonoducts; this is proved by the fact that it consists primarily of three channels (1966: fig. 6): the outlet-channel for autosperm = (auto-)spermiduct, the outlet-channel for eggs = oviduct and the inlet-channel for allosperm = allospermiduct[4]). This tripartite structure of gonoduct can be found in many shelled opisthobranchs (cf. EALES 1921, FRETTER & GRAHAM 1954, LEMCHE 1956) and pulmonates (cf. BECK 1912, STEENBERG 1914, 1925, RIGBY 1965, LEME 1973, VISSER 1973). The sinking of the gonoduct into the haemocoele makes possible essential evolutionary changes, on the female side an enlargement of the oviducal glands and a shifting forward of the female opening, i. e. a lengthening of the gonoduct, and on the male side an invagination of the penis and the change of the seminal groove into the closed vas deferens. In the pulmonates these changes go further as in the shelled opisthobranchs, which is shown by a comparison of the Ellobioidea with tectibranch groups (cf. MORTON 1955, DUNCAN 1960, 1975).

The genital system of the Pulmonata can therefore be divided into the following parts: ovotestis, hermaphrodite duct with vesicula seminalis, fertilization chamber and receptaculum seminis (carrefour + talon = FPSC[5])), spermoviduct[6]) resp. spermiduct and oviduct if separated, i. e. spermiduct with prostate, oviduct with albumen gland and oviducal gland(s), and allospermiduct with its gland, further on the female side bursa copulatrix and vagina, on the male side vas deferens and penis, consisting of penial sheath and penis itself (penial sheath is called penis if real penis is more or less reduced).

For a comparison of the genital systems of Pulmonata it is necessary to distinguish the various combinations of gonoducts and genital openings which are denoted by the endings -auly and -tremy (1966: fig. 7-8[3])). The genital system is monaulic if the male and female gonoducts are combined up to the genital opening; this condition can be regarded as plesiomorphous, because it is found in most shelled opisthobranchs (cf. GHISELIN 1965). The genital system is semidiaulic if the male and female gonoducts are distally more or less separated; this is the case if the seminal groove is closed forming the vas deferens, and the female opening is shifted forward, so that a vagina is developed. The genital system is diaulic if the pallial gonoducts are totally separated; it is triaulic if oviduct and allospermiduct are separated, too. The genital openings can be separated (diatremy) or united (syntremy); this is not simply correlated with the combination of gonoducts. In the monaulic genital system the genital openings must be separated; this is the plesiomorphous condition (see above). In the semidiaulic, diaulic and triaulic genital

[4]) In my opinion, this term is the most suitable, since the term vaginal groove of FRETTER leads to confusion with the vagina (and is not correct, too, because it is no part of the copulatory organs), and the term seminal duct of VISSER does not emphasize enough the differences to the (auto-)spermiduct.

[5]) This term of TOMPA (1984) is an abbreviation of fertilization pouch-spermatheca complex, which should be correctly named f. p.-spermatocyst complex.

[6]) The term uterus often used for the female part of the spermoviduct should be restricted to that part of the female duct which in ovoviviparous resp. viviparous snails retains the ova.

systems they can be separated or united; the uniting of the openings is probably connected with the change from non-reciprocal to reciprocal copulation.

In the lower Basommatophora (Archaeopulmonata) and the Pulmonata in general, as far is known, only *Pythia* (Ellobiidae) is monaulic, with open seminal groove to the penis. The other Ellobioidea are more or less semidiaulic resp. diaulic and diatrematic. The genital systems of other Basommatophora are very diverse: The Trimusculidae are semidiaulic and diatrematic, the Amphibolidae and Siphonariidae secondary-monaulic (spermoviduct opening into penial sheath) and thus syntrematic; both patelliform groups are obviously not closely related. The higher Basommatophora (Hygrophila) are diatrematic; some groups, such as the Chilinidae, are semidiaulic, most groups, however, diaulic. The Systellommatophora (Onchidioidea and Soleolifera) are semidiaulic or diaulic and diatrematic.

The Stylommatophora are syntrematic; most groups are semidiaulic, some diaulic, such as the Achatinelloidea and many Elasmognatha. Since in the pulmonates in general the monaulic condition is plesiomorphous, in the Stylommatophora it must be the semidiaulic one; this is supported by the fact, too, that most Orthurethra are semidiaulic.

The genital system of the Stylommatophora (fig. 4) is additionally provided with organs for producing and receiving spermatophores and an auxiliary copulatory organ (stimulatory organ). The spermatophore is made by the distal part of the vas deferens, which has a special structure and is named epiphallus. If the vas deferens does not insert terminally, it has an appendage named flagellum; this term must be restricted to this part of the epiphallus, which often has a somewhat different structure (e. g. the lime sac in the Helixarionoidea) and forms a part of the spermatophore. The appendage of the bursa copulatrix which receives the spermatophore after copulation is named diverticulum; this term, too, should not be used for other appendages of the genital system. Sperm transfer by spermatophores is an adaptation to terrestrial life and is characteristic of the Stylommatophora. An epiphallus is developed in most Orthurethra and several other unrelated groups of Stylommatophora, so that its presence can be regarded as plesiomorphous. A flagellum and diverticulum occur less frequently but also in several unrelated groups; thus their development may be a plesiomorphous character, too.

Stimulatory organs can be found in many groups of Stylommatophora; they are obviously an adaptation to reciprocal copulation. There are different opinions concerning the evolution of these organs; some authors, such as IHERING (1892), SIMROTH (1912), SCHILEYKO (1979), think all or only a part of them to be homologous, others, such as THIELE (1935), SOLEM (1978), TOMPA (1984), think them to have evolved independently. The latter base their opinion on the different structure of these organs and their development in different parts of the genital system. The homology of the stimulatory organs, however, is very probable for the following reasons:

1) Basic structure and functioning of the organs are the same (REMANE's criterion of special quality of the structure). They consist of a papilla (stimulator) in a sheath with or without a hardened tip and one or more adjoining glands leading out their secretion through or next to the papilla. During copulation the sheath is evaginated, so that the papilla is protruded, and with its aid the secretion of the gland is put on resp. into the mating partner, obviously in order to synchronize

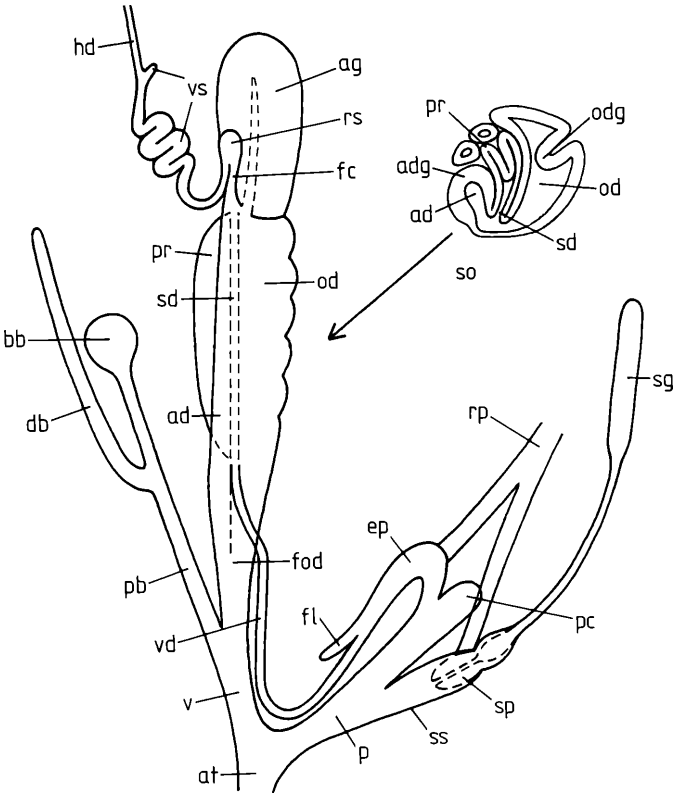

Fig. 4. Genital system of Stylommatophora (plesiomorphous condition) (with a section of spermoviduct). ad = allospermiduct, adg = allospermiducal gland, ag = albumen gland, at = atrium, bb = bursa of bursa copulatrix, db = diverticulum of bursa copulatrix, ep = epiphallus, fc = fertilization chamber, fl = flagellum, fod = free oviduct, hd = hermaphrodite duct, od = oviduct, odg = oviducal gland, p = penis, pb = peduncle of bursa copulatrix, pc = penial caecum, pr = prostatae, rp = penial retractor, rs = receptaculum seminis, sd = spermiduct, sg = gland of stimulatory organ, so = spermoviduct, sp = papilla of stimulatory organ, ss = sheath of stimulatory organ, v = vagina, vd = vas deferens, vs = vesicula seminalis.

reciprocal copulation resp. sexual activity in general (cf. TOMPA 1984). The organ is modified by reduction of parts, either of the stimulator while the gland is left over or vice versa, or by multiplication of parts or of the whole organ.

2) The position of the organs is different (penial sheath, atrium, vagina), but is always on the cephalopodial part of the genital system (REMANE's criterion of sameness of position). The organs of various groups of Stylommatophora replace each other, i. e. in the same species they cannot occur e. g. on penial sheath and vagina. The organ, however, can more or less fuse with adjoining parts of the genitalia, even to such a degree that it cannot be recognized any more.

3) Organs with similar structure can be found also in other pulmonates and shelled opisthobranchs, but only on the penial sheath, as in Systellommatophora

(cf. SIMROTH 1912), Basommatophora (wrongly named prostate or flagellum, cf. SIMROTH 1912, HUBENDICK 1978) and Tectibranchia (wrongly named prostate, cf. GHISELIN 1965). The insertion on the penial sheath is obviously the plesiomorphous condition; only in case of syntremy (opisthobranch slugs, Stylommatophora) the organ can shift from the penial sheath over the atrium to the vagina. In the Stylommatophora this shifting can be demonstrated in several groups, such as Helixarionoidea and Helicoidea, where nearly related groups with different insertion occur (REMANE's criterion of linkage of intermediate forms).

Thus neither the differing structure nor the differing position of these organs is an argument against homology; on the contrary, a multiple parallel evolution of such a complex organ with the same basic structure and functioning on neighbouring parts of the genital system is very improbable.

That the homology of the auxiliary copulatory organs in the various pulmonate groups was not recognized until now can be explained by the fact, too, that this organ is lacking in most Basommatophora (as in the Ellobioidea, too), in connection with their non-reciprocal copulation. If it is present (as in Amphibolidae, Siphonariidae, Ancylidae), it is more or less modified. This is quite different in the less known Systellommatophora, especially in Onchidiidae and Veronicellidae, which have reciprocal copulation and therefore a stimulatory organ. This resembles so much that of stylommatophoran groups (cf. SIMROTH 1912) that their can be little doubt about their homology. Since Systellommatophora and Stylommatophora are no monophyletic group, this is a strong proof of the homology of the auxiliary copulatory organs of all euthyneurans. The striking resemblance of the organs, too, is the reason why only SIMROTH, the great authority on terrestrial slugs, recognized this homology (his "Pfeildrüse"), though his derivation of the organ from SIMROTH's gland of the Rathouisiidae (he was evidently not familiar with the occurence of the organ in opisthobranchs) and his occasional mingling of stimulatory organ and epiphallus cannot be accepted.

Stimulatory organs of Stylommatophora which are homologous are the penial appendix of Orthurethra and the sarcobelum resp. gypsobelum with gland or the dart apparatus of higher Stylommatophora, but also the various modified organs in aulacopod groups, such as the ligula with gland of Arionidae, the stimulator with gland of Agriolimacidae or Milacidae, the perivaginal gland of Zonitidae and the glandula amatoria of Vitrinidae, and so on. There belongs, too, the penis of *Limax* (Limacidae) which corresponds to the combined penis and stimulatory organ (see below). The penial appendix can be regarded as the plesiomorphous condition of the organ, because in other pulmonates and euthyneurans in general only penial organs occur. It has the characteristic structure of an ejectory apparatus (BECK 1912, STEENBERG 1925, H. B. BAKER 1935, SCHILEYKO 1979) and functions probably in the same way as the other stimulatory organs[7]).

[7]) The hypothesis of SCHILEYKO (1979, 1984) that the penial appendix receives sperm in order to fill the envelope of the spermatophore cannot be accepted. It is founded on the occasional occurrence of sperm in the ampulla of the appendix; this is not astonishing, since the ejected spermatophore passes near to the sheath of the appendix. In all probability the spermatophore is always completed in the epiphallus, and the penial appendix ejects its secretion and not sperm. By the way, the hypothesis of SCHILEYKO is already disproved by the fact that the Achatinelloidea have no epiphallus but a fully developed penial appendix.

The penial appendix must not be confused with the other appendages of the male end ducts, flagellum and caeca. The penial caecum is the appendage of the penial sheath which results from a subterminal insertion of the epiphallus; it occurs in many groups of Stylommatophora, among others in the Clausiliidae, where it was named penial appendix until now (cf. H. NORDSIECK 1978). A non-terminal appendage of the epiphallus occuring e. g. in Buliminidae and Helixarionoidea can be named epiphallial caecum; it contributes to the formation of the spermatophore and is not homologous with flagellum or penial caecum.

The plesiomorphous structure of the genital system of the Stylommatophora (fig. 4) thus can be characterized as follows: FPSC simple; semidiaulic, i. e. spermoviduct developed, consisting of spermiduct, oviduct, and allospermiduct with their glands, the latter a continuous open groove running from free oviduct to FPSC; epiphallus and stimulatory organ present, the latter developed as penial appendix consisting of a perforated papilla in a sheath and an adjoining gland.

Diauly is not the plesiomorphous condition in the Stylommatophora, as SOLEM (1976, 1978) believes, but is as apomorphous as in the Basommatophora, because both groups evolved from monaulic resp. semidiaulic ancestors. There are more plesiomorphous groups of Stylommatophora and especially of Orthurethra which are semidiaulic than those which are diaulic. The plesiomorphous genital system of Stylommatophora has no simple structure without appendages, as SCHILEYKO (1979) believes, but complex copulatory organs with a stimulatory organ, because the ancestor of Stylommatophora and Pulmonata in general already had them. The opinion of SCHILEYKO that the genitalia of Orthurethra are apomorphous, since they have a penial appendix, is therefore wrong, too. These and other wrong phylogenetic hypotheses are of great importance, because they have more or less influence on the system accepted or conceived by the respective authors.

Additional remarks concerning the allospermiduct of the Stylommatophora are necessary. It is differently developed in the various groups: In some groups it is a more or less continuous open groove with surrounding gland cells, as in Buliminidae, Clausiliidae ("canal séreux", STEENBERG 1914), Ceriidae, Strophocheilidae (*Megalobulimus:* "accessory genital gland", LEME 1973), or without these, as in Subulinidae, Succineidae, or developed only in a part of the gonoduct, as in Helicidae; in other groups it is closed and glandular, connected proximally with the gonoduct, as in Streptaxidae, or not, i. e. developed as a blind appendage, as in Chondrinidae ("cul-de-sac de l'oviducte", STEENBERG 1925) and other Streptaxidae ("seminal duct diverticulum", VISSER 1973); in other groups it seems to be absent, as in some slug groups. The genital system with closed allospermiduct cannot be termed triaulic (VISSER 1977, TOMPA 1984), but only semitriaulic, since in the triaulic one, e. g. in some groups of opisthobranch slugs, the allospermiduct is separated as an independent duct up to the genital opening (1966: fig. 7d).

The allospermiducts and (auto-)spermiducts of all pulmonates are homologous, because they have all been derived from the homologous parts of the ancestors, i. e. shelled opisthobranchs resp. prosobranchs. It is improbable that the allospermiduct of any pulmonate group should have changed into the (auto-)spermiduct, as VISSER (1973, 1977) believes. His arguments for this change are based on informations of RIGBY (1965) concerning the spermoviduct of *Succinea*, which VISSER obviously has

misunderstood[8]). This change should have happened, according to VISSER, whenever a semidiaulic group of Stylommatophora has evolved towards diauly; this hypothesis can easily be disproved, since each comparative examination of semidiaulic and diaulic species, which, by the way, in some groups, such as Athoracophoridae, are connected by transitions, shows the completely corresponding structure of their gonoducts. There is no reason to doubt the homology of spermiducts and allospermiducts of all Stylommatophora and Pulmonata in general, since, and this is overlooked by VISSER and other authors, their ancestor had a tripartite and not a bipartite pallial gonoduct (see above).

There is another hypothesis concerning the allospermiduct, which led to some confusion. VISSER (1977) and HOCHPÖCHLER & KOTHBAUER (1979) think that the diverticulum and the allospermiduct are homologous; this hypothesis is based on the fact that the allospermiduct of *Helix* (Helicidae) is developed only in the proximal part of the spermoviduct (above diverticulum). But in several other groups, as in Buliminidae, Clausiliidae, Ceriidae, a continuous allospermiduct and a diverticulum are present in the same genital system, so that the diverticulum cannot be homologous with any part of the allospermiduct. This is quite clear because it is a part of the bursa copulatrix and not of the pallial gonoduct in the strict sense such as the allospermiduct.

The comparative examination of the genital system of the Stylommatophora, which was carried out recently, is based on a study of the literature referring thereto and my own investigations of groups which were available. The literature is very extensive, so that the studied papers cannot be itemized in the bibliography; it concerns the following authors: H. B. BAKER, BERRY, BREURE, BURTON, FORCART, GITTENBERGER, GIUSTI, GROSSU, HESSE, HOFFMANN, HUDEC, KONDO, LIKHAREV, MEAD, MINATO, ODHNER, PATTERSON, PILSBRY, QUICK, RIEDEL, SCHILEYKO, SIMROTH, SOLEM, STEENBERG, VAN MOL, WÄCHTLER, WEBB, WIKTOR, and WURTZ. Histological information was got from the following papers: BECK (1912), DASEN (1933), GHOSE (1963), JAENICKE (1933), KUGLER (1965), LEME (1973), NOYCE (1973), RICHTER (1926), RIGBY (1963, 1965), SCHILEYKO (1978), SIRGEL (1973), STEENBERG (1914, 1925, 1929), VAN MOL (1968, 1971, 1973), VISSER (1973), WILLE (1915); my own histological investigations of Clausiliidae were carried out some time ago (cf. H. NORDSIECK 1978).

According to this examination the following parts of the genital system offer important taxonomic characters: vesicula seminalis, FPSC, spermoviduct resp. spermiduct and oviduct in diaulic groups, allospermiduct, bursa copulatrix (with diverticulum), vagina, epiphallus (with flagellum), penis and stimulatory organ.

The proximal parts of the genital system, which especially need histological investigation, are examined only in rather few species resp. groups (e. g. FPSC, cf. SCHILEYKO & SCHILEYKO 1975), so that the phylogenetic evaluation of characters is not yet possible; consequently they cannot be as important for classification as

[8]) The spermiduct and allospermiduct of *Succinea* have the same position as in other Stylommatophora. The supposition of VISSER (1973) that their position is exchanged may result from a wrong interpretation of RIGBY's fig. 6, since there is no further information concerning this position in her text. This figure, however, ensues from a combination of transversal and longitudinal sections allowing no conclusion as to the position of the spermiduct.

would be desirable. The distal parts (end ducts), however, are more important, because they have been examined in many species and groups; they are complex enough to offer many characters easy to examine and different enough in the various taxa without being influenced too much by environmental factors. But a taxonomic use of them can only be successful on condition that a standardized terminology is reached; this concerns especially the appendages of the male ducts, flagellum, caeca and appendix, which are clearly defined (see above) and must not be confused.

The results of the comparative examination of the end genitalia can be summarized as follows:

The Orthurethra resemble more or less the reconstructed plesiomorphous (stem) form of Stylommatophora; their stimulatory organ, if present, is a penial appendix. The various groups of Pupilloidea are characterized by different apomorphies, especially in the male ducts; there are more plesiomorphous groups, such as Pupillidae, Valloniidae, Orculidae, Buliminidae, and more apomorphous ones, such as Vertiginidae, Chondrinidae, and Pleurodiscidae. The Achatinelloidea are more apomorphous, too, because they are diaulic and characterized by the reduction of the epiphallus.

The Clausilioidea are similar to the Orthurethra; their male ducts are as apomorphous as those of Vertiginidae or Chondrinidae (see below).

The other non-orthurethrous groups are, compared to the Orthurethra, more or less apomorphous, especially concerning the male ducts and the stimulatory organ. An exception are the Sagdoidea, which have a sigmurethrous kidney and a penial appendix like the Orthurethra. The other characters of this group, however, do not allow a classification with the Orthurethra[9]), but point toward nearer relations to the following group.

Several groups, i. e. Partuloidea, Orthalicoidea (Bulimuloidea), Acavoidea, Rhytidoidea, Achatinoidea, Oleacinoidea, Testacelloidea, Streptaxoidea, and Punctoidea (Endodontoidea), can be provisionally united as achatinid Sigmurethra[10]), because their stimulatory organ has been reduced; if present, it is simplified and inserts on the penis. This organ, which must not be confused with a penial caecum, is named penial appendage or penial gland and occurs in several groups, such as Orthalicidae, Ferrussaciidae, Oleacinidae, Testacellidae, and Punctidae. The male ducts of achatinid Sigmurethra are, compared to those of most Orthurethra, simplified, too (at least externally); in some groups the sheath around the penis is rather voluminous with the vas deferens more or less bound to it.

The male ducts of the Partulidae are not similar to those of the Buliminidae, with which they were grouped by SOLEM (1978), or of any other orthurethrous group, but are very like those of the Orthalicidae, which is true for their shell, too; thus their special systematic position is justified only by the structure of their excretory system (see above). The Ceriidae have male ducts differing much from those of the

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[9]) SCHILEYKO (1979) classifies the Sagdoidea with his Pupillina (= Orthurethra), as he does not recognize the essential differences between the orthurethrous and the sigmurethrous kidney. It must be emphasized, however, that the orthurethrous kidney is not merely longer than the sigmurethrous one, but has also another structure (see above).

[10]) This group is about equivalent to the Holopodopes of H. B. BAKER (1955, 1962), but includes, too, the related mesurethrous groups and the Punctoidea, whose relations to the Holopodopes are emphasized by BAKER in the former paper.

Clausiliidae, with which they were classified by H. B. BAKER (1961), but resembling those of the Urocoptidae, especially of the Holospirinae, which they resemble in shell, too. The genital system of the Strophocheilidae and Dorcasiidae is not like that of any other mesurethrous group, but is similar to that of other Acavoidea, especially with regard to the female ducts (presence of an appendicula). The Punctoidea belong to the achatinid Sigmurethra, because they have no stimulatory organ (except rarely a simplified one) and simplified male ducts; this classification is supported by the tendency to heterurethria which is similar to that of other achatinid Sigmurethra (see above). They have no nearer relations to the Arionoidea, with which they were grouped until now; the characters which both have in common are plesiomorphous or due to convergence.

The genital systems of the elasmognathous groups, Succineoidea and Athoracophoroidea, have common apomorphous characters proving the relationship of these groups: tendency to diauly, stimulatory organ absent, sheath around penis, if present, rather voluminous, thus except the first similar to the achatinid Sigmurethra. One group of Succineidae has a simplified stimulatory organ on the penis like many groups of achatinid Sigmurethra. The hypothesis that the Elasmognatha (Heterurethra) are an isolated plesiomorphous group of Stylommatophora is not supported by the structure of the genitalia; more probable is a common origin with the achatinid Sigmurethra.

In this connection *Aillya* (Aillyidae), which was classified by H. B. BAKER (1955) with the Heterurethra, has to be mentioned. VAN MOL (1978), however, found considerable differences leading him to the supposition that it may be related to the Helixarionoidea; with regard to the genital system (nearly diaulic, without stimulatory organ, penial retractor inserting on the flagellum) it is better classified with the achatinid Sigmurethra. Besides, the genital morphology of Elasmognatha and *Aillya* demonstrates that the separation of these groups from other Stylommatophora as three independent orders by MINICHEV & SLAVOSHEVSKAYA (1971) is quite unacceptable.

The other sigmurethrous groups, i. e. Gastrodontoidea, Helixarionoidea, Vitrinoidea (Zonitoidea), Limacoidea, Trigonochlamydoidea, Mesodontoidea (Polygyroidea), Arionoidea, and Helicoidea, can be provisionally united as helicid Sigmurethra, because they have mostly a stimulatory organ, which inserts on the penis, atrium or vagina and, if complete, consists like the penial appendix of a stimulator and adjoining gland(s). The former is unarmed (sarcobelum) or provided with an additional more or less mineralized (calcified) tip called dart (gypsobelum resp. dart sac). Like in Orthurethra, there are in all groups taxa with reduced or lacking stimulatory organ.

The structure and position of this organ make possible phylogenetic conclusions as follows:

Groups with a stimulatory organ inserting on the penis can be regarded as plesiomorphous, such as Gastrodontidae, Euconulidae, and Mesodontidae. The Gastrodontidae have a gypsobelum with gland, named dart sac and coronal gland. The Euconulidae have a simplified organ named penial appendage, while in the Mesodontidae only few groups have a stimulatory organ of the same name; as in achatinid Sigmurethra these simplified organs must not be confused with a penial caecum.

The stimulatory organ of the other groups has mostly shifted to the atrium and further to the vagina. More plesiomorphous are the higher Helixarionoidea with a sarco- or gypsobelum with gland inserting mostly on the atrium and complex male ducts. More apomorphous are the Vitrinoidea which have a stimulatory organ inserting on the atrium or vagina and simplified male ducts. In the Vitrinidae the stimulatory organ is a more plesiomorphous sarcobelum with gland on the atrium (as in *Semilimax*) or a more apomorphous glandula amatoria[11]) on the vagina (as in *Phenacolimax*). The Zonitidae are more apomorphous, since as rest of the stimulatory organ only the perivaginal gland[11]) is developed.

More apomorphous, too, are the different slug groups; the particular changes of their stimulatory organ prove as well as those of their excretory system that slugs have evolved several times independently (cf. LIKHAREV & WIKTOR 1980). The Parmacellidae and Milacidae have a modified stimulatory organ inserting mostly on the atrium. In the Limacoidea the stimulatory organ inserts primarily on the atrium, too, but has secondarily more or less fused with the penis. This fusion is still recognizable in such groups as *Lehmannia* (Limacidae) and *Deroceras* (Agriolimacidae), the penes of which bear a modified stimulatory organ, but no more in *Limax* (Limacidae), where the penis and stimulatory organ have become an unity. In the Trigonochlamydoidea the stimulatory organ is wanting. The Arionoidea have a stimulatory organ on the penis, atrium or vagina. In the Arionidae it is represented by a modified organ (stimulator named ligula) in the penis, as in *Hemphillia* or *Anadenus,* or in the atrium resp. the adjacent female ducts, as in *Arion*. In the Philomycidae *Philomycus* has a gypsobelum with gland on the vagina and atrium, while in *Meghimatium* only the gland is left over.

The Helicoidea are as apomorphous as the Vitrinoidea, because their stimulatory organ is mostly inserting on the vagina; it consists of the dart sac and the so-called mucous glands and is named dart apparatus. This group is characterized also by complex male ducts, especially the generally well developed flagellum. More plesiomorphous are the groups with a stimulatory organ on the atrium, such as Sphincterochilidae with a sarcobelum with gland and Xanthonychidae with a dart apparatus, more apomorphous the other groups with a dart apparatus on the vagina, such as Bradybaenidae, Hygromiidae, Helicidae, or without stimulatory organ, such as Camaenidae. In several groups, i. e. Xanthonychidae and Hygromiidae, the dart apparatus has multiplied (maximum quadrupled), with dart sac and glands more or less separated; this is an apomorphous condition (opposite to the opinion of SCHILEYKO 1978), since a singular apparatus must be regarded as plesiomorphous.

It can be summarized that the Stylommatophora, according to the end genitalia, can be divided into three main groups which are provisionally named by terms of the current system based on the excretory system (fig. 5): Orthurethra (with Clausilioidea), achatinid Sigmurethra (with Elasmognatha), and helicid Sigmurethra. The Orthurethra have plesiomorphous end ducts and are therefore a paraphyletic group like the group of the same name based on the kidney. It is a question whether the two other groups with apomorphous end ducts are monophy-

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[11]) The glandula amatoria and perivaginal gland are probably not homologous with the gland around the free oviduct of Helixarionoidea (named uterus by VAN MOL), which has another structure (VAN MOL & VAN BRUGGEN 1971) and may not belong to the cephalopodial gonoduct.

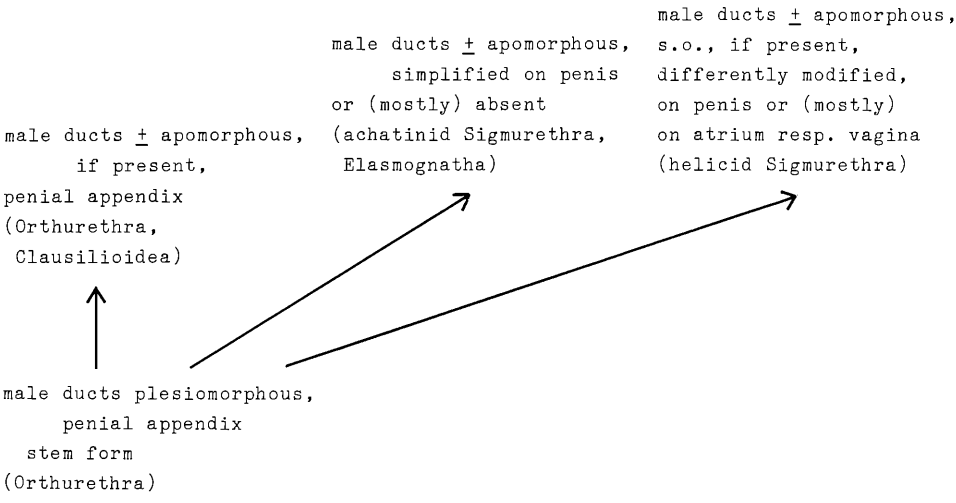

Fig. 5. Phylogenetic diagram of end genitalia of Stylommatophora. s.o. = stimulatory organ.

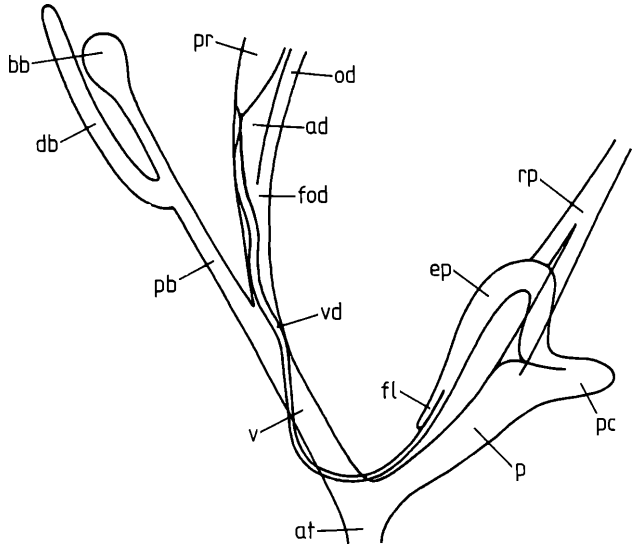

Fig. 6. End genitalia of Clausiliidae (plesiomorphous condition). Abbreviations see fig. 4.

letic ones; an attempt to solve this problem by examination of further important taxonomic characters will be made in the following parts of this revision.

The systematic position of the Clausiliidae can be discussed as follows:

The genital system (plesiomorphous structure in Clausiliidae fig. 6, cf. H. NORDSIECK 1969, 1978) corresponds largely to that of the stem form, especially in the development of the allospermiduct and male ducts; the important differences, i. e. the autapomorphies of the family, are the absence of the penial appendix and the reduction of the flagellum to a rudiment. The Clausiliidae do not differ in this regard from the various groups of Pupilloidea more than those from each other (cf. WATSON 1920, STEENBERG 1925, 1929, H. B. BAKER 1935), but they are not closely related to one of these groups, since their male ducts have a characteristic structure occuring in none of them (penial retractor forked though appendix is wanting, one arm inserting on the penis, the other on the epiphallus).

On the other hand, the Clausiliidae differ in the genitalia, especially in the male ducts, much from the Ceriidae (cf. RICHTER 1926, JAENICKE 1933, PILSBRY 1946, H. B. BAKER 1961), with which they were classified by BAKER, or from the Megaspiridae (only *Callionepion* examined, cf. PILSBRY 1904), which PILSBRY thought to be more closely related. The mesurethrous excretory system which Clausiliidae and Ceriidae have in common is due to convergence (see above). The relations between the Clausiliidae and the fossil group *Palaeostoa*, which PILSBRY caused to approach Clausiliidae and Megaspiridae, may really exist, but a careful examination of *Palaeostoa* has proved that this group does not belong to the Megaspiridae (H. NORDSIECK unpubl.). The correspondence in the genitalia between Clausiliidae and Urocoptidae, which SCHILEYKO (1979) stated without foundation, needs no discussion; Urocoptidae and Ceriidae are related, but none of them to the Clausiliidae (see above). Thus by genital characters the Clausiliidae cannot be grouped with the achatinid Sigmurethra, but only with the Orthurethra; if the excretory system and other characters are regarded, too, they have a more isolated systematic position near to the Orthurethra.

The main evolution of the end ducts within the Clausiliidae can be described as follows (cf. H. NORDSIECK 1969, 1978): The plesiomorphous structure occurs e. g. in the Alopiinae; the penial caecum has been reduced several times independently, just as in other subfamilies, too. More important evolutionary changes of the plesiomorphous structure have been:

1) complete reduction of the flagellum, in Phaedusinae and Laminiferinae;

2) change of the diverticulum into a glandular tube, in Neniinae and the subfamily-group of Clausiliinae;

3) change of the vas deferens and epiphallus into pseudoepiphallus and parepiphallus, in Clausiliinae and Baleinae.

The latter two evolutionary processes have taken place only in the Clausiliidae; they are obviously connected with an improvement of sperm transfer and thereby of the reproduction of these groups.

Summary

The original aim of this investigation was the clarification of the systematic position of the Clausiliidae; it made necessary a revision of the system of the Stylommatophora above family level, because the system now in use could not be accepted. This revision will be published in

three parts. In this first part the importance of the excretory and genital systems for the classification of the Stylommatophora is discussed.

The results concerning the excretory system can be summarized as follows: There are two main types of excretory system, the orthurethrous and the sigmurethrous one in the broad sense, to which belong, too, the mesurethrous, the heterurethrous, and various unnamed types of slugs. An orthurethrous type without ureter can be regarded as plesiomorphous, while the mesurethrous one probably evolved several times independently, thus being apomorphous. The latter is, on the other hand, the plesiomorphous type, from which the other sigmurethrous types evolved. Therefore the excretory system though being of great taxonomic importance is not a suitable basis for the classification of the Stylommatophora. The excretory system of the Clausiliidae is of mesurethrous type; additional information as to its structure is given.

The results concerning the genital system are based on those which were published in an earlier paper dealing with the comparative genital morphology of snails (H. NORDSIECK 1966). Together with those of the comparative examination of the genitalia carried out recently they make possible the reconstruction of the plesiomorphous structure of the genital system and its main evolutionary changes. Especially regarded are the allospermiduct and the copulatory organs (end ducts) with the auxiliary copulatory organ (stimulatory organ). The different stimulatory organs of the Stylommatophora are homologous; the penial appendix can be regarded as the plesiomorphous type of the organ, while sarcobelum resp. gypsobelum with gland, dart apparatus and other still more modified organs mainly of slugs are apomorphous. The comparative examination of the end ducts leads to an arrangement of the Stylommatophora into three groups, which is probably more important for the classification than that based on the structure of the excretory system (terms of which still being used provisionally): Orthurethra, achatinid Sigmurethra comprising Elasmognatha, and helicid Sigmurethra. The genital system of the Clausiliidae is a comparatively plesiomorphous one and therefore more like that of the Orthurethra than that of the achatinid Sigmurethra. Considering the genital and excretory systems the Clausiliidae have a somewhat isolated systematic position near to the Orthurethra. Additionally the most important evolutionary changes of the genital system within the Clausiliidae are named.

Zusammenfassung.

Ursprüngliches Ziel dieser Untersuchung war eine Klärung der systematischen Stellung der Clausiliidae; sie machte eine Revision des Systems der Stylommatophora oberhalb des Familienniveaus erforderlich, weil das z. Zt. benutzte System nicht akzeptabel war. Diese Revision wird in drei Teilen veröffentlicht. Im vorliegenden ersten Teil wird die Bedeutung von Exkretions- und Genitalsystem für die Klassifikation der Stylommatophora diskutiert.

Die Aussagen zum Exkretionssystem lassen sich folgendermaßen zusammenfassen: Es gibt zwei Grundformen des Exkretionssystems, die orthurethre und die sigmurethre im weiteren Sinne, zu der auch die mesurethre, die heterurethre und verschiedene unbenannte Formen bei Nacktschnecken gehören. Eine orthurethre Form ohne Ureter kann als plesiomorph angesehen werden, während die mesurethre mehrfach parallel entstanden, also apomorph sein dürfte. Die letztere ist andrerseits die plesiomorphe Form, aus der sich die anderen sigmurethren Formen entwickelt haben. Das Exkretionssystem hat demnach zwar große taxonomische Bedeutung, ist aber als Basis für die Klassifikation der Stylommatophora nicht geeignet. Die Clausiliidae haben ein mesurethres Exkretionssystem; zu dessen Bau werden weitere Angaben gemacht.

Die Aussagen zum Genitalsystem basieren auf denen, die bereits in einer früheren Arbeit zur vergleichenden Genitalmorphologie der Schnecken (H. NORDSIECK 1966) veröffentlicht wurden. Diese ermöglichen zusammen mit einer vergleichenden Untersuchung des Genitalsystems, die jetzt durchgeführt wurde, eine Rekonstruktion der plesiomorphen Ausbildung des Genitalsystems und seiner wesentlichen evolutiven Veränderungen. Besonders berücksichtigt

werden der Allospermidukt und die Kopulationsorgane (Endwege) mit dem Kopulationshilfsorgan (Reizapparat). Die verschiedenen Reizapparate der Stylommatophora sind homolog; der Penisappendix kann als plesiomorphe Ausbildung des Organs angesehen werden, während Sarcobelum bzw. Gypsobelum mit Drüse, Pfeilapparat und andere stärker abgewandelte Formen des Organs besonders von Nacktschnecken apomorph sind. Die vergleichende Untersuchung der Endwege führt zu einer Gliederung der Stylommatophora in drei Gruppen, die größere Bedeutung für die Klassifikation haben dürfte als die auf dem Bau des Exkretionssystems basierende (deren Termini vorläufig noch benutzt werden): Orthurethra, achatinide Sigmurethra, an die sich die Elasmognatha anschließen, und helicide Sigmurethra. Das Genitalsystem der Clausiliidae ist verhältnismäßig plesiomorph und ähnelt deshalb mehr dem der Orthurethra als dem der achatiniden Sigmurethra. Bei Berücksichtigung von Genital- und Exkretionssystem haben die Clausiliidae eine etwas isolierte systematische Stellung in der Nähe der Orthurethra. Zusätzlich werden die wichtigsten evolutiven Veränderungen des Genitalsystems innerhalb der Clausiliidae genannt.

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