

On the mono(?)phyly and classification of the *Orthurethra/Pupilloidea*
(*Gastropoda: Pulmonata: Stylommatophora*)

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ABSTRACT. The strict monophyly of the *Orthurethra* is questionable. Large discrepancies between internal classifications of the suborder, as exemplified by the *Pupilloidea*, result mostly from parallel/convergent evolution of characters regarded as taxonomically important: reduction of apertural barriers according to a common pattern and simplification of male genitalia. Broader based comparative studies (poorly known taxa and areas, shell microsculpture, internal structure of copulatory organs, pallial complex, life histories, CNS fusion patterns, infraspecific variation of genitalia, biochemical characters, ecological correlates of evolutionary trends) are advisable.

Key words: Classification, parallel/convergent evolution, monophyly, land snails, *Orthurethra/Pupilloidea*.

Motto: And so, you see, I have come to
doubt all that once I held as true.

(SIMON & GARFUNKEL).

INTRODUCTION

Though systematists do not agree on methods of interpreting facts, many do agree on conditions that should be met by classification. A good classification system should: a/ be natural i.e. reflect phylogenetic relationships defined as a sequence of phylogenetic splittings (cladism) or as a resultant of all evolutionary events in broad sense (evolutionary systematics), b/ be of predictive value and thus falsifiable,

c/ensure a maximally efficient information storage and retrieval. None of the hitherto proposed systems of the *Orthurethra*/*Pupilloidea* meets these requirements.

The system of the *Gastropoda* and *Stylommatophora* changed on various occasions (cf. BIELER 1992 and references contained therein), but the suborder of *Orthurethra* retained a roughly stable composition. Its definition has not changed significantly since PILSBRY (1900), though numerous authors have addressed the question (PILSBRY 1922-1926, THIELE 1931, ZILCH 1959-1960, SHILEYKO 1979, 1984, NORDSIECK 1985, 1986, TAYLOR and SOHL 1962, SOLEM 1978, BOSS 1982, TILLIER 1989). The suborder includes basically the following families: *Achatinellidae* GULICK, 1873; *Tornatellinidae* COOKE and KONDO, 1960; *Amastridae* PILSBRY, 1911; *Cionellidae* (= *Cochlicopidae*) CLESSIN, 1879; *Pupillidae* TURTON, 1831; *Vertiginidae* FITZINGER, 1833; *Orculidae* PILSBRY, 1918; *Chondrinidae* STEENBERG, 1925; *Pleurodiscidae* WENZ, 1923; *Pyramidulidae* WENZ, 1923; *Valloniidae* MORSE, 1864; *Strobilopsidae* PILSBRY, 1918; *Partulidae* PILSBRY, 1900 and *Enidae* (= *Buliminidae*) CLESSIN, 1879 (PILSBRY 1922-1926, STEENBERG 1925, THIELE 1931, ZILCH 1959-1960, SHILEYKO 1979, 1984, NORDSIECK 1985, 1986, TAYLOR and SOHL 1962, SOLEM 1978, BOSS 1982, TILLIER 1989). Additions and subtractions were few; the *Partulidae* and *Pleurodiscidae* were subtracted by SHILEYKO (1979) and the *Partulidae* by NORDSIECK (1985, 1986); the *Clausiliidae* MORCH, 1864 and *Cerastuidae* WENZ, 1923 were added by NORDSIECK (1985, 1986), and the *Cerionidae* (= *Ceriidae*) FLEMING, 1818 by SHILEYKO (1979).

In spite of the relative stability of its limits, the internal classification of the suborder is much more fluid; definitions of superfamilies are virtually nonexistent. This is very well exemplified by the *Pupilloidea* (= *Pupillidae* s.l. sensu PILSBRY 1922-1926 and STEENBERG 1925 = *Vertiginidae* s.l. sensu THIELE 1931). From one to ten families were included in the superfamily by various authors (table; cf. also comparison of land snail classification systems in EMBERTON et al. 1990). In the most splitting system (SHILEYKO 1984) the *Pupilloidea* are monotypic, while in the two most lumping ones (ZILCH 1959-1960, SOLEM 1978) the superfamily includes a majority of the *Orthurethra*. It is perhaps symptomatic that two quite different systems were proposed by the same author with a five year interval (SHILEYKO 1979, 1984).

The classification systems of the *Pupilloidea*/*Orthurethra* were an outcome of a variety of approaches, from a purely phenetic (BOSS 1982) through evolutionary (e.g. SOLEM 1978, SHILEYKO 1979, 1984) or "cladistic-evolutionary" (NORDSIECK 1985, 1986) to "cladistic-phenetic" (TILLIER 1989); theoretical background of some (e.g. TAYLOR and SOHL 1962, THIELE 1931, ZILCH 1959-1960) can be only suspected. Characters employed were gross anatomy of the reproductive system (e.g. SOLEM 1978, NORDSIECK 1985), combined with shell characters and evolutionary tendencies (e.g. SHILEYKO 1979, 1984) or digestive and nervous systems (TILLIER 1989). Attempts at biochemical studies were few, with no effect on the classification below ordinal level (e.g. EMBERTON et al. 1990, TILLIER et al. 1992).

Definitions of the *Pupilloidea* proposed hitherto (e.g. SHILEYKO 1979, 1984, TILLIER 1989) contain at best a combination of plesiomorphous characters, none of which separates the superfamily unambiguously from the remaining *Orthurethra*. No

formal phylogeny of the *Pupilloidea* based on explicitly polarized characters has been proposed to date.

The purpose of this paper is to: a/ re-evaluate some characters commonly accepted as taxonomically important, b/ when possible suggest the direction of their transformation series, c/ indicate some parallel evolutionary tendencies within the group, and d/ suggest possible directions for future studies.

Two basic assumptions are used. 1. Parsimony criterion is applied in the sense that a parallel reduction of structures, especially complex, is more likely than their parallel appearance *de novo*; the more complex a structure, the more likely its unique origin. 2. A transformation series observed within more than one monophyletic (=characterized by joint possession of unique character(s)) taxon is a series of parallel transformations. Parallel evolution of a structure in more than one monophyletic taxon involves the same starting point, the same or similar intermediate stages and the same final outcome. It is distinct from convergence which starts from different points and results in the same final product.

PURPORTED APOMORPHIES OF THE *ORTHURETHRA*

Orthurethra is a snail with a long kidney built of two parts. One, kidney proper, is homologous with that of the other *Stylommatophora* (= *Sigmurethra* s. lat.). The other has no counterpart in the *Sigmurethra* s. lat., is histologically different and functions as a ureter. NORDSIECK (1985) described the *Orthurethra* as "several groups which, except some of them, agree widely in shell and genitalia". The only author who attempted a new and more profound definition of the suborder was TILLIER (1989). Apart from the "orthurethrous kidney", his *Orthurethra* were characterized by the absence or weak development of oesophageal crop, cylindrical or medially inflated gastric crop, differentiated gastric pouch, generally rather long intestine, visceral and right parietal ganglia not always seemingly fused, right cerebro-pedal connective usually shorter than the left, distinct lateral connectives, and finally by the fact that no member of the group was carnivorous. Some of the characters listed by TILLIER (1989) may be suspected of plesiomorphy (no carnivory, the ganglia just named not always fused, generally long connectives), whereas others (characters of alimentary tract) are present "generally", but not in all the taxa examined, and known only in very few taxa (cf. Appendix B in TILLIER 1989); the direction of their transformation series is hard to establish.

Being orthurethrous with respect to the excretory system is the only known character shared by all the members of the suborder. No transitory forms exist in this respect between the *Orthurethra* and other *Stylommatophora* (except, perhaps, *Partulidae*; SOLEM 1978). NORDSIECK (1985) questioned monophyly of the *Orthurethra* on the grounds that the type of excretory system found in that group could be easily derived from that of the *Ellobioidea* (*Basommatophora*) and was thus plesiomorphous. A few comments should be made on the excretory system in view of its adaptive value. The orthurethrous kidney resembles not only that of the *Ellobioidea*, but generally that

of all the freshwater *Basommatophora*, and differs from that of the prosobranchs in possessing the part which plays the role of ureter (NORDSIECK 1985 and references contained therein). A change from marine to freshwater or land habitat creates osmoregulation problems: necessity to resorb ions. Hence possession of the part of kidney that functions as a ureter might reflect either an adaptation to a similar function, or common ancestry, or else both. The common ancestry would imply that the pulmonates invaded freshwaters via land, which is not unlikely (similar structure of respiratory system in both groups). The other possibility, i.e. that this type of kidney arose twice, as a response to similar osmoregulation needs, is supported by small but constant histological differences between ureters of both groups (DELHAYE and BOUILLON 1972). On the other hand, such differences may well be those of adaptation, not of origin. Besides, kidney has been histologically examined only in very few members of these groups. The *Sigmurethra* s. l. have a secondary (= pallial; NORDSIECK 1993) ureter instead of the "orthurethrous ureter", of a different structure and origin. Thus they would originate from an orthurethrous stock that lost the part of kidney which played the role of ureter (less likely), or (more likely) directly from some marine pulmonates. The latter is supported by the results of histological studies on the excretory system (DELHAYE and BOUILLON 1972) and by the presence of an incipient pallial ureter in the *Orthurethra* (NORDSIECK 1993). In such a case the suborder would not be monophyletic in the strict (Hennigian) sense i.e. holophyletic, since it would not include all the descendants of the most recent common ancestor.

Another rarely considered character is the position of eyes. The *Basommatophora* retain the primitive eye/tentacle arrangement of the prosobranchs (BISHOP 1981). In the *Orthurethra* and *Sigmurethra* s. lat. eyes are situated on ommatophores. Assuming this as an apomorphy, the *Orthurethra* should be defined as such *Stylommatophora* that retained the ancestral ellobioid kidney, which would turn them into a typical "non A group" (ELDGREDGE and CRACRAFT 1980). Though no other characters are available at present to solve the problem, the strict (Hennigian) monophyly of the suborder *Orthurethra* is questionable. However, an analysis of character distribution within a paraphyletic group is the only way to find out about its phylogeny.

CLASSIFICATION AND SYSTEMATIC POSITION OF THE PUPILLOIDEA

There is an enormous discrepancy of opinions on the composition of the *Pupilloidea* (cf. table). Reasons for the virtual lack of resolution of phylogenetic relationships are many, the most important being probably: a/ small size and similar shell shape causing clustering of genera, irrespective of other characters, into the *Pupillidae* s. l., b/ lack of anatomical data on many taxa, and very simplified structure of the reproductive system in other taxa, c/ various significance attributed to characters by various authors, and - most important - d/ lack of unequivocal distribution of characters.

Table. Families included in the *Pupilloidea* by various authors.

Family/Author:	1	2	3	4	5	6	7	8	9	10	Total
<i>Pupillidae</i>	+	+	+	+	+	+	+	+	+	+	10
<i>Chondrinidae</i>	+	+	+	+	+	+	+	-	+	-	8
<i>Vertiginidae</i>	+	+	+	+	+	+	+	-	+	-	8
<i>Pyramidulidae</i>	+	+	+	+	+	+	+	+	-	-	8
<i>Vallonidae</i>	+	+	+	+	+	-	+	+	-	-	7
<i>Orculidae</i>	+	+	+	+	+	+	-	-	+	-	7
<i>Pleurodiscidae</i>	+	+	+	+	+	+	-	-	-	-	6
<i>Enidae</i>	+	+	+	+	-	-	+	-	-	-	5
<i>Strobilopsidae</i>	-	+	+	-	+	-	+	+	-	-	5
<i>Cochlicopidae</i>	+	-	-	-	-	+	-	-	+	-	3
<i>Amastridae</i>	+	-	-	-	-	-	-	-	-	-	1
<i>Achatinellidae</i>	-	-	-	-	-	-	-	+	-	-	1
<i>Tornatellidae</i>	-	-	-	-	-	-	-	+	-	-	1
<i>Partulidae</i>	-	+	-	-	-	-	-	-	-	-	1
total	10	10	9	8	8	7	7	6	5	1	

1 - ZILCH 1959-10160, 2 - SOLEM 1978, 3 - BOSS 1982, 4 - TAYLOR and SOHL 1962, 5 - NORDSIECK 1985, 1986, 6 - THIELE 1931, 7 - SHILEYKO 1979, 8 - TILLIER 1989, 9 - PILSBURY 1922-1926, 10 - SHILEYKO 1984.

Two groups of characters and evolutionary trends are considered below:

1. apertural barriers - a major trend for their reduction to loss, and a minor trend for their further complication, 2. genitalia - an "evolution by loss" of various components of originally complex genital system, and a minor trend for ovoviviparity.

- Apertural barriers

The *Ellobioidea* (*Basommatophora*) have been selected as an out-group for comparisons, since: a/ they probably stand closest to the hypothetical common ancestor of the *Stylommatophora*, and b/ they (and other *Basommatophora*) share the kidney structure with the *Orthurethra*. The ellobioids have teeth in their aperture. Some orthurethrous snails (*Orculidae*, *Lauriinae*) still have the most ancestral, ellobioid pattern of ontogenic development of columellar and parietal teeth. Such teeth appear first on the border between the embryonic and definitive whorls, and grow with the shell while their older (i.e. deeper situated) parts are gradually resorbed (fig. 1, top row). Those orthurethrans, like many others, have in addition teeth on the basal/palatal wall of the shell, the latter teeth forming during sexual maturation and being also a part of the ellobioid heritage.

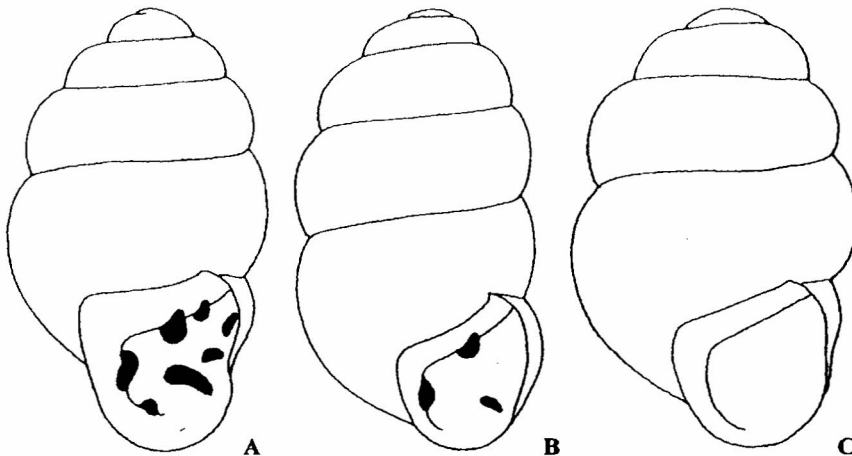
This original version of apertural barriers becomes subsequently modified. The formation of the columellar and parietal is delayed until subadult stage, and as a result all teeth (not only basal and palatal) form during sexual maturation (fig. 1, bottom row). Then the teeth (all or some of them) get shortened i.e. they reach less and less deep inside the shell, and lower, thus decreasing the degree of aperture occlusion. Next they get reduced to the form of small, vestigial nodules, subsequent to which they may disappear. Another possibility is a further complication of original apertural barriers by adding new components or by particular alterations of those already existing.



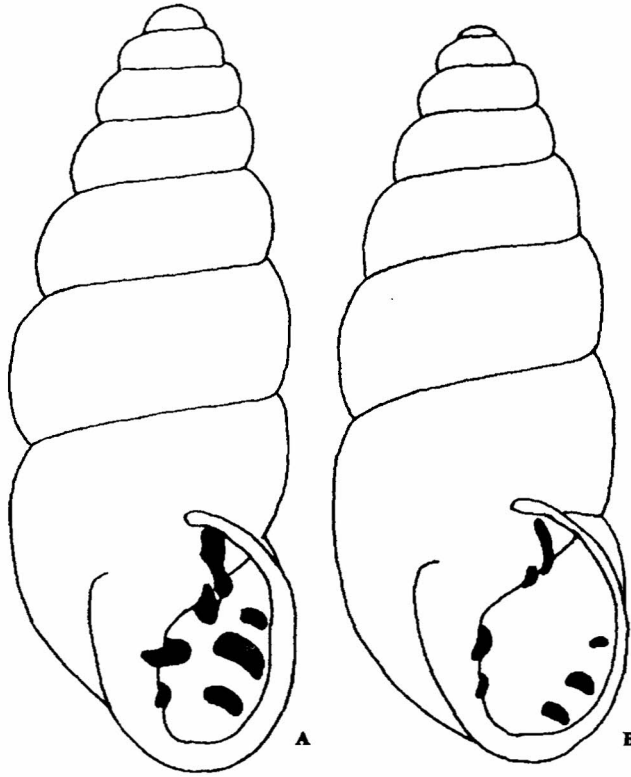
1. Ontogenetic development of apertural barriers: top row - plesiomorphous, ellobioid-like pattern in a pupilloid *Sphyradium* (modified from SHILEYKO 1984); bottom row - most common pupilloid pattern in *Vertigo pusilla* O. F. MÜLLER. Outline of adult shell marked with thin line

Teeth formed during sexual maturation are the most common among the orthurethrans. Almost any monophyletic group in which they are found, includes also toothless species; such teeth are a prelude to loss. There is no reason to doubt the original presence of teeth in the *Orthurethra*. Likewise, there is no reason to assume that the shift of teeth formation to later ontogenic stages happened more than once. However, once the shift took place, the teeth reduction and/or loss must have

proceeded independently in more than one group. "Experiments" with teeth reduction are found in many genera, subfamilies or families otherwise well defined by joint possession of unique apomorphies and thus monophyletic. In two vertiginid genera, *Vertigo* O. F. MÜLLER and *Truncatellina* R. T. LOWE, each defined by its own apomorphies, there are species having apertural barriers (in some species of *Vertigo* even complex), almost reduced barriers and no barriers at all (fig. 2). The loss must have happened after the generic characters were acquired and thus independently. In some species of e.g. *Vertigo* the process may be caught red-handed, and these are species with both inter- and intrapopulation variability of the number of teeth (POKRYSZKO 1990a). The same is true of *Gastrocopta* WOLLASTON (*Gastrocoptinae* - a monophyletic pupilloid subfamily of uncertain familial position). *Pupilla* TURTON (*Pupillidae*) comprises both toothed and toothless species, and species with variable apertural barriers. Some members of *Chondrina* REICHENBACH (*Chondrinidae*) (fig. 3) differ in the degree of aperture occlusion. Populations of other species of that genus (fig. 4) differ only in apertural barriers (GITTENBERGER 1973). The same is true of another chondrinid - *Solatopupa* PILSBRY (GITTENBERGER 1973). Within the lauriins (*Pupillidae*) *Leiostyla* R. T. LOWE comprises mostly well toothed species though also here some shy attempts at teeth reduction are observed, while within *Lauria* GRAY only two weak teeth are left. It is noteworthy that within species with well developed and complex apertural barriers the latter are little variable; in species with short, low and poorly developed teeth, their number and degree of development vary widely (e.g. *Vertigo alpestris* ALDER, *ronnebyensis* (WESTERLUND), *arctica* (WALLENBERG), *Chondrina tatrica* LOŽEK). In taxa comprising both toothed and toothless species there are always also species with teeth only weakly developed.

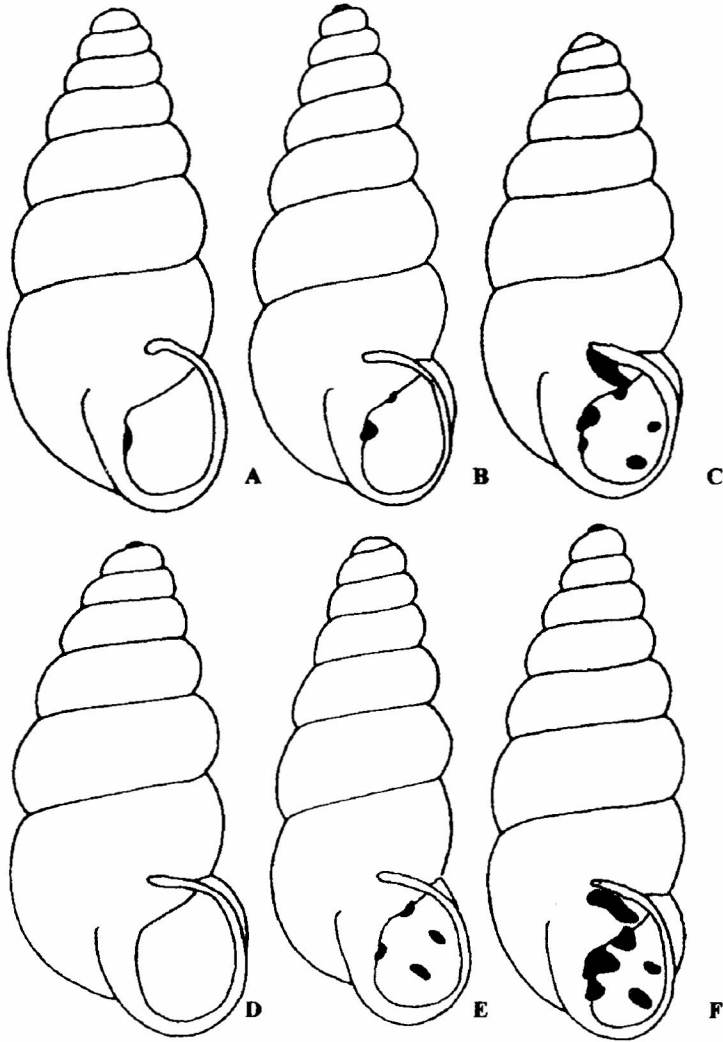


2. Examples of apertural barriers in the genus *Vertigo*: A - *moulinsiana* (DUPUY), B - *ronnebyensis* (WESTERLUND), C - *genesii* (GREDLER)



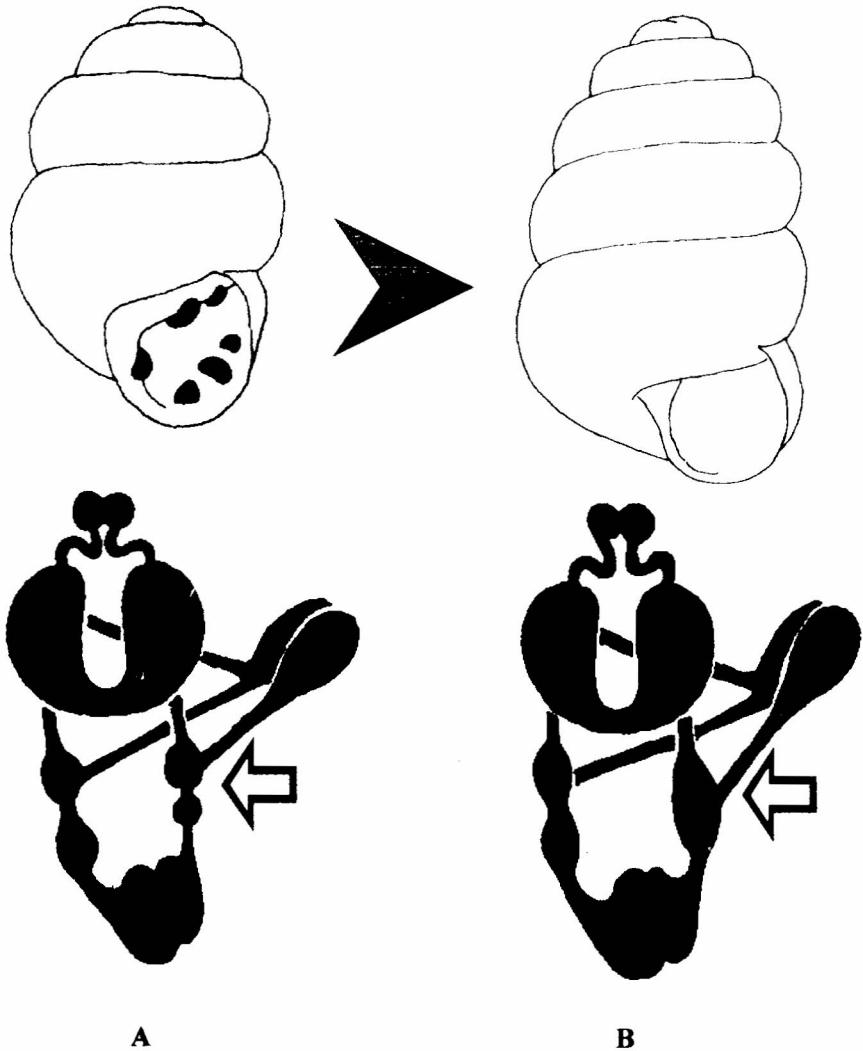
3. Apertural barriers of two closely related species of *Chondrina*: A - *clienta* (WESTERLUND); B - *tatrlica* LOZEK

Apart from comparison with the ellobioids, the degree of fusion of ganglia of the central nervous system (CNS) confirms the proposed direction of the transformation series (fig. 5) (POKRYSZKO 1990a). The reduction or loss of teeth is prerequisite to forming hard-shelled eggs or to ovoviviparity, the characters not found in the ellobioids (see below), and to growth continuation once the sexual maturity has been attained (POKRYSZKO 1990a). Since the presence of teeth is plesiomorphous and their reduction took place parallelly and independently in many taxa, characters of apertural barriers should be regarded as useless from phylogenetic viewpoint above family level. However, considering the process instead of its final product(s) may suggest the opposite. To use the mere tendency to reduction of a structure as a "good character" to define a group would be a circular reasoning, since monophyly should be established prior to recognizing the tendency. To use the reduction pattern



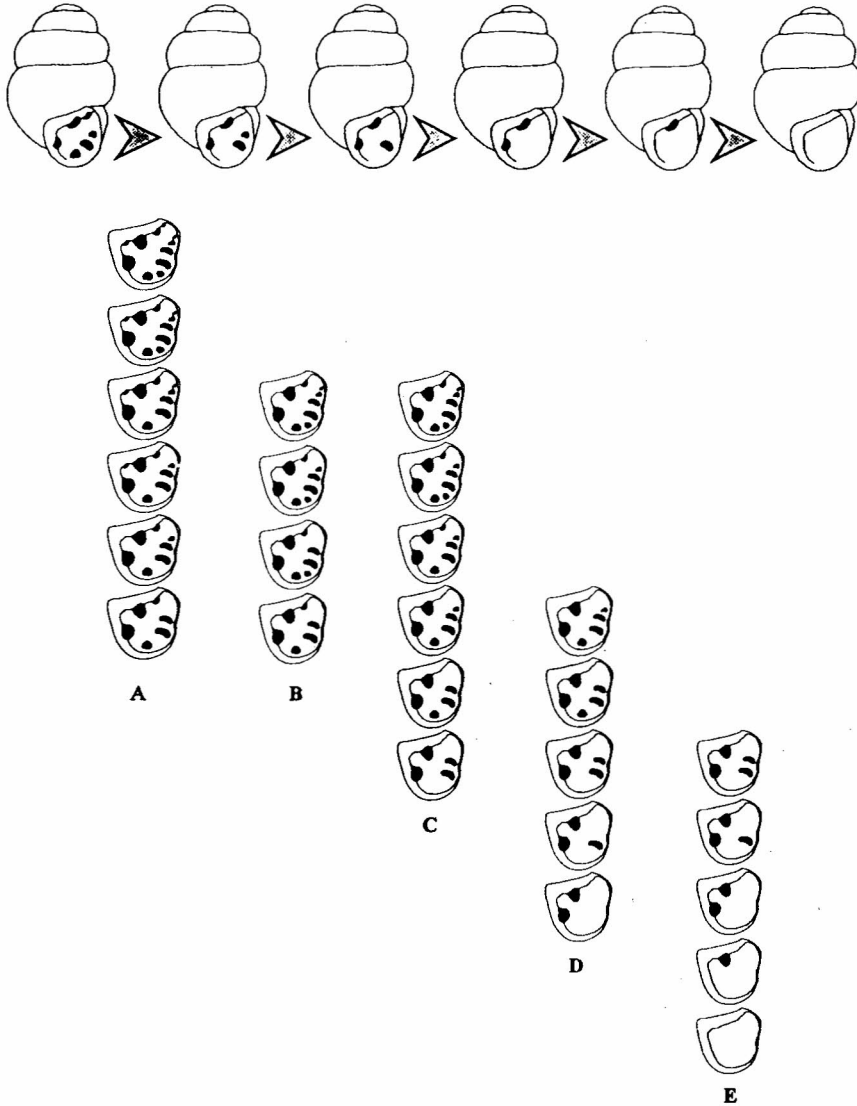
4. Examples of apertural barriers in populations of *Chondrina farinesii* (Des Moulins): A - La Preste, Pyrenees, France; B - Torres, E of Seo de Urgel, Spain; C - Cornudella, Tarragona, Spain; D - Aras de Alpuente, Valencia, Spain; E - Desfiladero de Collegats, Lerida, Spain; F - Alentorn, Montsec de Rubies, Lerida, Spain (all modified from GITTENBERGER 1973)

(i.e. common pattern of variability between and within taxa and populations; cf. VAVILOV 1922), supported additionally by evidence from an independent data set, seems acceptable. The reduction nearly always starts with teeth of the basal and palatal



5. Apertural barriers and CNS of two closely related vertiginid genera: A - *Vertigo*, B - *Columella*; solid arrow indicates the direction of transformation series; hollow arrows indicate the two ganglia (right pleural and right parietal) separate in *Vertigo* and fused in *Columella*

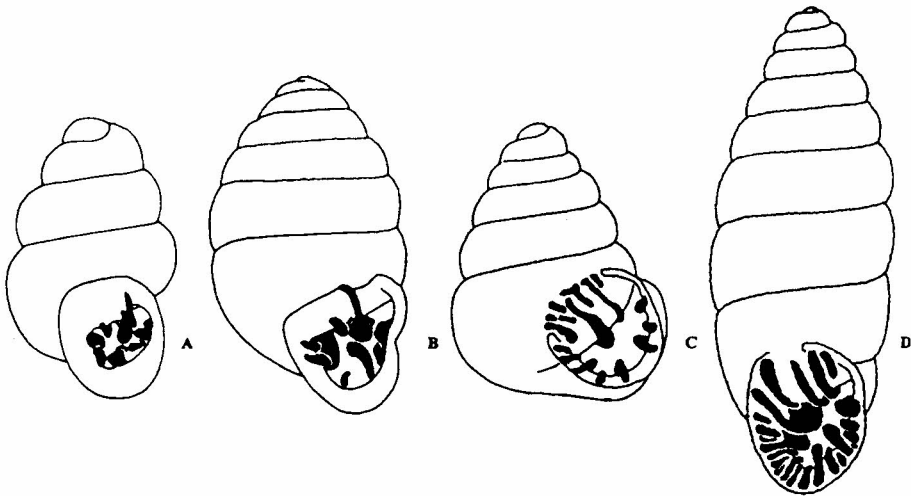
walls, leaving the columellar and parietal teeth as the very last to be reduced (fig. 6). This common pattern is repeated by the individual variability of apertural barriers in many species, such as e.g. *Vertigo alpestris*, *arctica*, *ronnebyensis*, some species of



6. Reduction sequence of pupilloid apertural barriers (top row) compared with their individual variation in selected species of *Vertigo*, represented by columns below: A - *antivertigo* (DRAPARNAUD), B - *pusilla* O. F. MÜLLER (converted to dextrous), C - *mouliinsiana* (DUPUY), D - *lilljeborgi* (WESTERLUND), E - *arctica* (WALLENBERG)

Gastrocopta, *Truncatellina*, *Pupilla*, *Chondrina*. There are also species, as a rule devoid of teeth, in which e.g. parietal tooth appears rarely and as a vestige (e.g. *V. genesii* (GREDLER)). The above reduction sequence is found in the vertiginids, lauriins, orculids, pupillids, enids, chondrinids etc., i.e. in nearly any taxon showing a tendency for teeth reduction. There exist, though, taxa completely devoid of apertural barriers (e.g. valloniids). The reduction is the most common but by no means the only tendency within the suborder.

Evolution of some taxa proceeded in the opposite direction, and also apparently independently (fig. 7). Some species of *Chondrina* and *Leiostylia* developed numerous extraapertural basal and palatal folds or nodules (situated outside the aperture proper, on the reflexed part of lip), absent in the ellobioids; the chondrinids have acquired the



7. Examples of complex apertural barriers: A - *Gastrocopta kessneri* (SOLEM), B - *Leiostylia adolfi* POKRYSZKO, C - *Odontocyclas kokeili* (ROSSMÄSSLER), D - *Abida polyodon* (DRAPARNAUD)

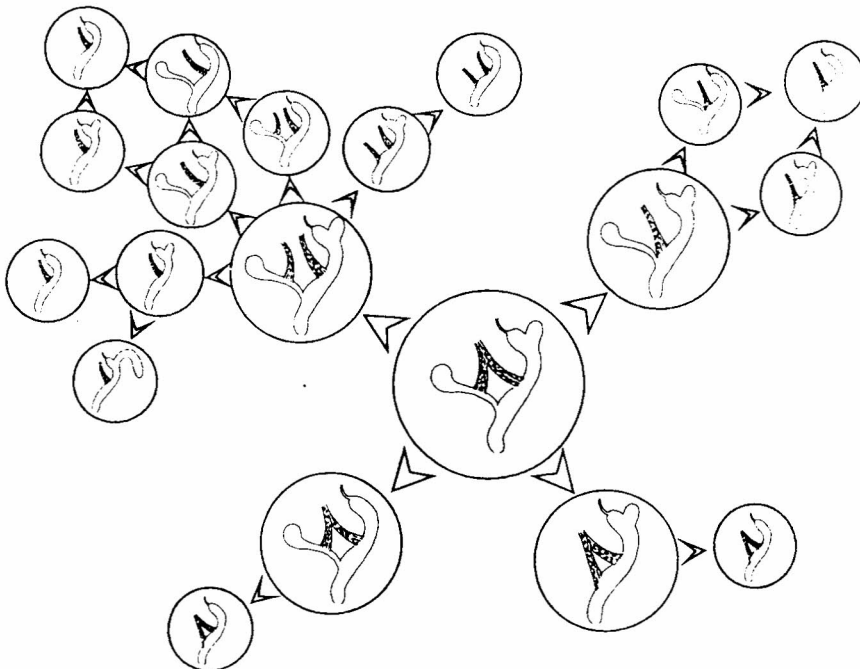
so called spiralis, subgenus *Vertilla* MOQUIN-TANDON within *Vertigo* a long, bent palatal, various gastrocoptins and members of *Leiostylia* complicated their apertural barriers in various ways. *Pagodulina* CLESSIN builds its teeth 1/2 whorl before shell completion and leaves them there. It is worth notice that neither reduction nor complication of the apertural barriers seem to be size-correlated; both tendencies are found among very minute and rather large snails.

- Genital organs

It is argued that either 1. complex copulatory organs consisting of penis plus epiphallus, penial appendix, forked retractor and possibly also epiphallial caecum are plesiomorphous, on the grounds that a penial appendage - flagellum - is found also within the *Basommatophora* (NORDSIECK 1985), or 2. such organs are apomorphous

because so complicated and not found anywhere else (SHILEYKO 1984). In a sense both views are partly right and partly wrong. The flagellum found in the *Basommatophora* is different from the appendix of the *Orthurethra* (HUBENDICK 1978, DUNCAN 1960), and even if both structures are homologous (though convincing arguments in favour of this view are lacking) it is not the same. To maintain that homology alone is an evidence for plesiomorphy (NORDSIECK 1985) is an obvious nonsense.

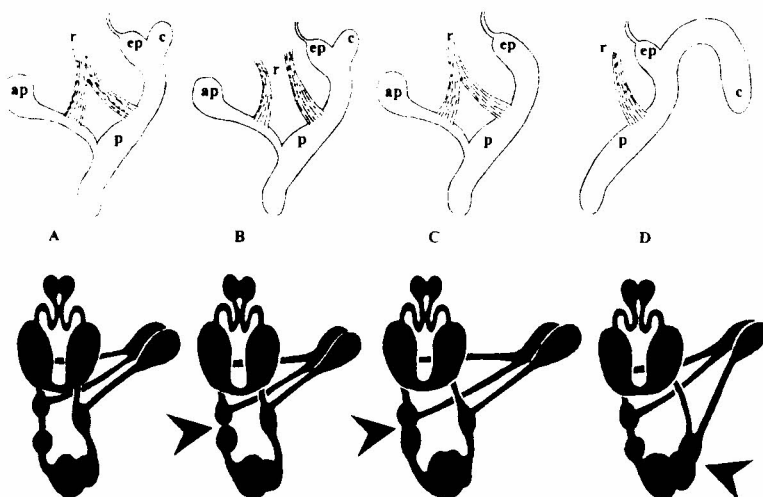
The *Basommatophora* (including *Ellobioidea*) have no bifid retractor (HUBENDICK 1978); such a retractor is found in some clausiliids (Nordsieck 1985) where it may evidence some kinship with the *Orthurethra*, and in some zonitids where it arose independently (RIEDEL 1966). The combination of penial appendix with bifid retractor and epiphallial caecum is present only in the *Orthurethra*. It seems thus likely that the presence of those complex copulatory organs originally characterized all the orthurethrans, or at least their majority, and it is most likely that the character arose once only. It follows that this is an apomorphy of a group of snails (all or most *Orthurethra*) some of which later resigned that apomorphy partly or wholly. Numerous monophyletic orthurethrous taxa provide evidence for this.



8. Plesiomorphous male copulatory organs and some of their possible transformations; original combination in the dotted circle in the centre consists of penis, epiphallus, penial appendix, epiphallial caecum and forked genital retractor

Assuming the complex copulatory organs as a point of departure, the following may happen (fig. 8): 1. Retractor, originally bifid, divides in two separate muscles. 2. After the retractor has divided, its branch inserted on the appendix disappears. 3. Branches of the originally bifid retractor fuse gradually. Once completed, the process can not be distinguished from '2'. 4. The appendix disappears, after: a/ the retractor has divided and one branch disappeared, b/ the retractor has completely fused and thus become single, and c/ together with its retractor branch. Once accomplished, these pathways can not be distinguished. 5. The appendix disappears after the retractor has divided, leaving its retractor branch (result: penis with two retractors). 6. The appendix disappears without any preceding retractor division (result: penis with no appendix and with bifid retractor). 7. After the appendix has disappeared, the epiphallial caecum assumes a large size. 8. The epiphallial caecum disappears as the only organ, or as one of those that are reduced. There are many more possible things that may be invented to happen to the originally complex copulatory organs; those listed above are the possibilities actually observed, or easy to envisage based on what is assumed to be their final outcome.

1. Within the otherwise well defined genus *Leiostylia* there are species with bifid retractors and with two separate muscles. The direction of the transformation series is additionally testified to by the fusion of the CNS ganglia (fig. 9) (POKRYSZKO and WALDÉN 1991). The retractor division took place also in the enids (SHILEYKO 1984). The process was parallel in those two groups.



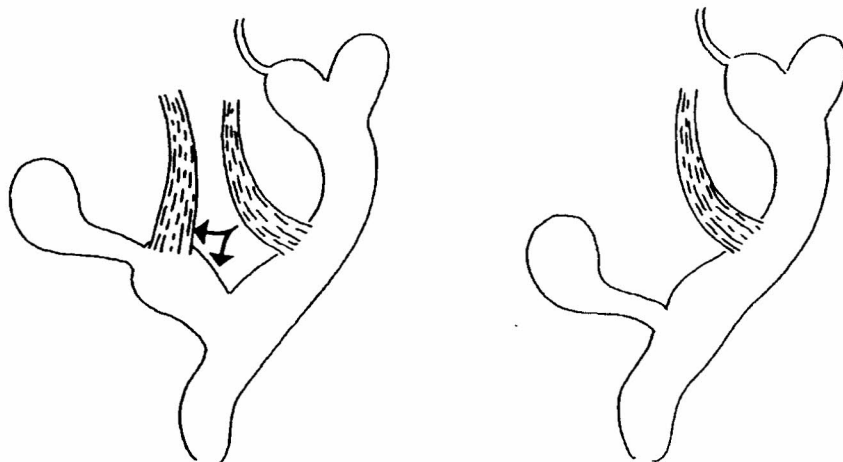
9. Transformation of male copulatory organs and CNS in selected members of the genus *Leiostylia*: A - *adolphi* POKRYSZKO, B - *silicea* (SHILEYKO), C - *anglica* (WOOD), D - *calathiscus* (LOWE); p - penis, ep - epiphallus, ap - penial appendix, c - epiphallial caecum, r - genital retractor; arrows indicate fusing ganglia: in B and C left pleural and left parietal ganglion, in D visceroparietal and right pleural ganglion

2. In some enids one of those separate retractors becomes lost, most probably according to the pattern '2', as the group comprises also species with two retractors. Furthermore, within an enid subfamily *Multidentulinae* there are three closely related genera, two of which: *Multidentula* LINDHOLM and *Improvisa* SHILEYKO, have the penial appendix and two retractors, while the third - *Senaridenta* SHILEYKO - is devoid of both those structures (SHILEYKO 1984). In single-retractored orculids the way to loss might have been the same.

3. That the retractor may get less and less bifid is evidenced by e.g. *Argna* COSSMANN (*Pupillidae*), some of which (*bielzi* (ROSSMÄSSLER)) have only insignificantly forked muscle. The opposite direction of the transformation series seems unlikely, since it implies that the muscle was originally single, and became bifid parallelly in at least three well defined taxa (enids, orculids, lauriins) subsequent to which in some of them it got completely divided (enids, lauriins), also parallelly.

4. The appendix disappears along with its retractor branch at the same or different time, in a part of enids, orculids (*Pagodulina pagodula* (DES MOULINS)), some chondrinids, pyramidulids, gastrocoptins, vertiginids, and it could happen in any of the ways described. As indicated by the other characters, the process should be regarded as parallel at least in the vertiginids, gastrocoptins, pyramidulids and chondrinids on the one hand, and in the enids and orculids on the other.

5. In some orculids the appendix most likely disappeared leaving after it its retractor. In *Sphradium doliolum* (BRUGUIÈRE) there are two separate retractors and

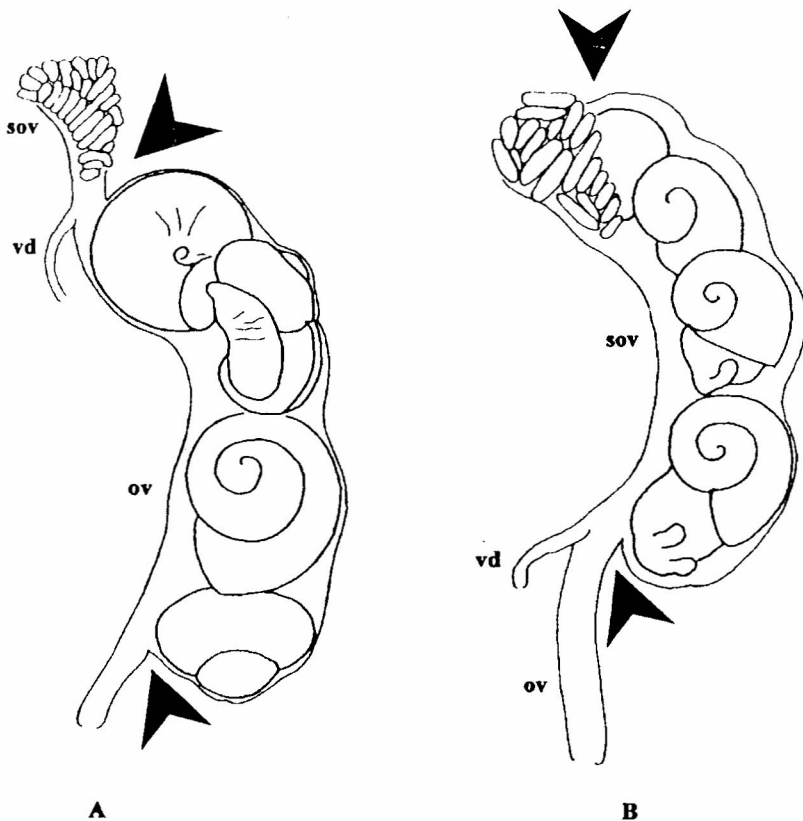


10. Individual variation of genitalia in an enid *Brepulopsis bidens* (KRYNICKI) (modified from SHILEYKO 1984): appendix retractor and basal part of appendix indicated with an arrow

a vestige of appendix. In related *Pagodulina lederi* (O. BOETTGER) there are two separate retractors with no trace of appendix (SHILEYKO 1984) (curiously, in other members of *Pagodulina* the genitalia evolved according to a different pattern).

6. The disappearance of appendix in bifid-retractored species has not been caught red-handed. But why a bifid penial retractor with no appendix in e.g. *Abida* TURTON?

7. The increase in size of the epiphallial caecum after the appendix had been lost happened at least twice, and maybe even three times. Among the lauriins *Leiostyla calathiscus* (R. T. LOWE) has such a caecum, and the condition is more apomorphic than the small caecum found in other members of *Leiostyla* (fusion of the CNS ganglia) (fig. 9). In the genus *Pagodulina* (Orculidae), *P. pagodula* has such a caecum; the same is found in *Sphyradium doliolum* but this does not have to be parallel with *Pagodulina*.



11. Ovoviviparity-related transformations of the pupilloid reproductive system: A - *Lauria*, B - *Pupilla*; sov - spermoviduct, ov - free oviduct section, vd - vas deferens; section transformed into uterus indicated with arrows

8. The epiphallial caecum as the only or one of the organs disappeared parallelly in a few lineages. Within the lauriins (*Leiostyla*) there are species with no caecum, other species with a small caecum and some with caecum of considerable size. That the character is apomorphic is evidenced by the degree of fusion of the CNS ganglia (fig. 9). The caecum has also been lost in the cochlicopids, valloniids, pyramidulids, gastrocoptins, vertiginids, amastrids, chondrinids, though not necessarily in parallel in all those groups; it was parallel at least in those taxa on the one hand and in some lauriins (*Pupillidae*) on the other.

There exist groups in which the reduction of particular parts, like that of apertural barriers, can be caught red-handed. Populations of two enid species, *Brephulopsis bidens* (KRYNICKI) and *Geminula isseliana* (BOURGUIGNAT), are dimorphic: some individuals have two retractors, others have one (penial) retractor only. The other retractor together with the basal part of appendix is absent (fig. 10). Another example, though not pertaining to male copulatory organs, is an enid *Adzharia renschi* HESSE. Some individuals of that species have a spermatheca duct diverticle, others are devoid of it (SHILEYKO 1984). The aphallism, so common in e.g. valloniids and vertiginids, and observed in some lauriins and chondrinids (WATSON 1923, RIEDEL 1953, POKRYSZKO 1987, GITTENBERGER and PIEPER 1988), may be of a similar nature, the only difference being that no groups completely devoid of penis resulted.

There are very few (or no) cases where parallel evolution of apertural barriers and male copulatory organs can be excluded. Groups in which only a final stage of a purported transformation series is represented, i.e. where all members are devoid of e.g. penial appendix or apertural barriers, are especially problematic. In such cases it is impossible to reconstruct the pathway of reduction, and to tell if the character(s) was/were acquired parallelly. This renders the hypothesis of their parallel evolution practically untestable, while it needs testability badly since the alternative - that groups having such characters had them from the beginning - is equally plausible.

It should be pointed out that there are other characters rarely taken into account, often misinterpreted and/or known for only very few orthurethrans. These are e.g. kind of eggs laid, oviparity versus ovoviviparity, the number of clusters and acini in the gonad and the length of prostate gland. The *Basommatophora*, including the ellobioids, lay soft, gelatinous eggs (HUBENDICK 1978, GERAERTS and JOOSSE 1984, TOMPA 1984, BULMAN 1990). Hard-shelled eggs appear in many land snails, among others in those *Orthurethra* that have reduced or lost their apertural barriers. Well-toothed *Orthurethra* lay soft, gelatinous eggs (POKRYSZKO 1990b and unpublished). In view of these facts TOMPA's (1984) suggestion that hard-shelled eggs, as an adaptation to life on land, are plesiomorphous seems to be ungrounded. Ovoviviparity also becomes possible after the teeth have been considerably reduced or lost. It is thus apomorphic and was acquired independently in a few lineages. In ovoviviparous *Pupilla*, some valloniids (*Acanthinulinae*) and *Pyramidula* FITZINGER the uterus is a partly or wholly transformed spermoviduct. In *Lauria* the role is played by the free oviduct section (fig. 11). Most probably the ovoviviparity was acquired independently at least twice. It seems that the prostate gland originally occupied the entire length of

the spermoviduct - the situation found in many members of various orthurethrous taxa. In many, however, it got reduced to a short section, which is an apomorphous condition. In two cases, though, it must be regarded as correlated: a/ when it results from a shortening of entire spermoviduct (*Lauria*) and b/ when it results from a transformation of spermoviduct into uterus (*Pupilla*, *Acanthinulinae*, *Pyramidula*). The short prostates of *Vallonia* RISSO, vertiginids, strobilopsids and gastrocoptins are apomorphous but may well be size-correlated. Similar is the case with the number of clusters and, consequently, acini in the gonad. Comparison with the *Basommatophora* (HUBENDICK 1978, DUNCAN 1960) indicates that originally the orthurethran gonad consisted of numerous acini grouped in several (8-10) clusters. In some groups, e.g. pupillids, valloniids, pyramidulids, gastrocoptins and vertiginids, there are 1-3 such clusters with rather few acini. This condition, though most probably derived, seems to be size-correlated.

IS A PHYLOGENETIC CLASSIFICATION POSSIBLE?

Based on available characters and the above considerations, it may be said that the data at hand are not sufficient to propose an internal phylogenetic classification of the *Orthurethra*. When the kidney structure is rejected, it can be only stated that a/ the suborder is characterized by a tendency to reduce the apertural barriers according to a certain pattern, and b/ male copulatory organs of most of its component taxa were originally complex, and then in some were subject to a parallel/convergent "evolution by loss", showing no common pattern. Of taxa comprising only species of uniform and simple structure of male copulatory organs it can not be said if they arose from the original complex-organelled lineage, or from the same ancestor on another occasion. Unequivocal apomorphies characterize only taxa of family or lower rank. The common pattern of reduction of apertural barriers may suggest parallel evolution as well as common ancestry. Two hypotheses are equally plausible. I. The *Pupilloidea/Orthurethra* arose once only, originally characterized by complex copulatory organs, subsequently partly lost by some of them. Such groups as vertiginids and chondrinids would be extreme examples of the process. II. The *Pupilloidea/Orthurethra* arose more than once, some characterized by complex copulatory organs (components of which were later lost), others - as a group with originally simple copulatory organs. Each hypothesis generates predictions on the distribution of other (unknown? overlooked?) characters. If 'I', then the group as a whole should bear a unique, joint character. A failure to find such a character does not, however, automatically reject the hypothesis. Evidence that a thing does not exist is hard to come by, especially if we do not know what to look for. Thus 'I' is hardly falsifiable. If 'II', then two (or more) groups should be characterized each by its own evolutionary novelty, and one (or more) may share some apomorphies with the other *Stylommatophora*. Though the problems with falsifying 'II' are the same as those given for 'I', at least actions aimed at corroborating or falsifying 'I' and 'II' are the same. The following supplementary studies can be proposed: 1. analysis of other characters poorly studied to date

(embryonic shell microsculpture, internal structure of copulatory organs, structure of pallial complex including kidney, details of life histories), 2. study of poorly known taxa and areas, 3. analysis of CNS fusion pattern (cf. VAN MOL 1967, BISHOP 1978) within more taxa which may give a clue to directions of transformation series and help discover parallel evolution, albeit with a provision that ganglionic fusion may not be irreversible (EMBERTON 1991), 4. analysis of infraspecific (individual and inter-population) variability of genital organs which may give a clue to still not well studied ways of reduction of parts (cf. SHILEYKO 1984). 5. enzyme and DNA analysis in doubtful cases (cf. EMBERTON et al. 1990, TILLIER et al. 1992), 6. looking for ecological (or other) correlates of the evolutionary trends.

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