

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

Importance of the shell and distribution.¹⁾

By

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With 5 figures.

I. Shell.

It is necessary to examine the importance of the shell for the classification of the Stylommatophora, since it was formerly the basis of this classification and plays an important and yet overvaluated part in the most recent systems, too²⁾. A comparative study of the shells of all stylommatophoran groups which was carried out for this purpose had the following result: Most Stylommatophora and Orthurethra have a shell; slugs resp. semi-slugs, i. e. a. reduction of the shell, can be found in several unrelated groups, as in Elasmognatha, several groups of achatinid Sig-murethra (Orthalicoidea, Punctoidea, Rhytidoidea, Oleacinoidea) and helioid Sig-murethra (zonitid superfamilies, Arionoidea, Helicoidea). The presence of a shell is therefore without doubt a plesiomorphous character. The question, what structure of the shell is the plesiomorphous one, is more difficult to solve. Most characters of the shell, especially the external ones (size, shape, color, embryonic and other sculpture, formation of aperture and umbilicus etc.), vary considerably within higher taxa so that they have only little taxonomic value; more important are the internal characters, especially the wall-folds of the adult and juvenile shell.

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²⁾ Examples for an overvaluation of the shell in the system of PILSBRY-BAKER are the purely conchological division of the Orthurethra and the combination of all groups with zonitoid shells in the Limacacea (cf. SOLEM 1978), in the system of SCHILEYKO the combination of various high-spined groups in the Clausilioidea and of various groups with depressed shells in the Endodontinia (cf. SCHILEYKO 1979).

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The folds of the interior walls (lamellae) and those of the exterior ones (plicae) are developed in many groups of Stylommatophora and most groups of Orthurethra; the majority of European Stylommatophora of the Upper Cretaceous and Lower Tertiary have them, too. They can also be found in many other euthyneuran groups; the fold systems of shelled opisthobranchs, such as Pyramidelloidea, Acteonoidea, of other pulmonates, such as Ellobioidea, and of orthurethrous and sigmurethrous Stylommatophora, such as Achatinelloidea, certain Pupilloidea, Clausilioidea, Orthalicoidea and Punctoidea, are so similar that a multiple parallel evolution is very improbable. Thus the presence of a fold system has to be evaluated as a plesiomorphous character³). By a comparison of the fold systems of euthyneurans in general four stages of development can be recognized which may be stages of evolution in the following order: 1) fold system developed continuously in juvenile and adult shells (as in Nerineidae); 2) fold system developed in juvenile and adult shells but resorbed from within, developed continuously (as in Carychiidae, Achatinellidae, Orculidae, Megaspiridae, certain Punctidae) or discontinuously (as in certain Punctidae, Gastrodontidae and Zonitidae); 3) fold system developed only in certain stages of shell growth, mostly in the adult shell (as in Chondrinidae, Clausiliidae, certain Urocoptidae and Subulinidae); 4) fold system absent (as in Helicoidea and many other groups). In the Stylommatophora the fold system is developed more frequently in orthurethrans as in sigmurethrans and in the latter especially in groups with high-spined shells. All groups have lamellae and many groups plicae; a complete fold system consists of several lamellae (in elevated shells 1-2 parietal and 2-3 columellar lamellae, in depressed shells more parietal and less columellar lamellae, the difference probably resulting from a change of position) and a different number of palatal plicae (mostly 2-6, in depressed shells more, possibly by a change of position of columellar lamellae). Since several groups of Ellobioidea and Orthurethra have a complete fold system which is developed continuously and resorbed from within, it can be concluded that the stem form of Stylommatophora (fig. 1) had such a system, too.

Another character of the shell which is found in the Ellobioidea, several Orthurethra (Achatinelloidea, Cochlicopoidea) and Sigmurethra (e.g. Achatinoidea, Oleacinoidea) is a gutter at the base of the aperture, i. e. a weakly developed siphon which is delimited by the lower columellar lamella. This character (siphonostomy) may be a plesiomorphous one and thus a character of the stem form, too. Taking into account that most orthurethrans have a more or less elevated shell, it can be assumed that the stem form had such a shell, too (fig. 1).

There may hardly be an apomorphy of the shell which characterizes a major group of the Stylommatophora; most apomorphies have evolved several times in various groups. An apomorphous shell form, i. e. a depressed shell, occurs in many

³) SCHILEYKO (1979) regards the presence of lamellae as a plesiomorphous character, while the plicae shall have evolved independently, i. e. be apomorphous; this different valuation is based on the earlier appearance of the lamellae in the ontogeny. It must be emphasized, however, that the presence of lamellae and plicae, irrespective of their appearance, must be evaluated as plesiomorphous, since the ancestors of the Stylommatophora (Ellobioidea, shelled opisthobranchs) already had both. For the same reason the opinion of SCHILEYKO that the lamellae of his Endodontinia and Helixinia are not homologous with those of his Pupillina and Achatinina cannot be accepted.

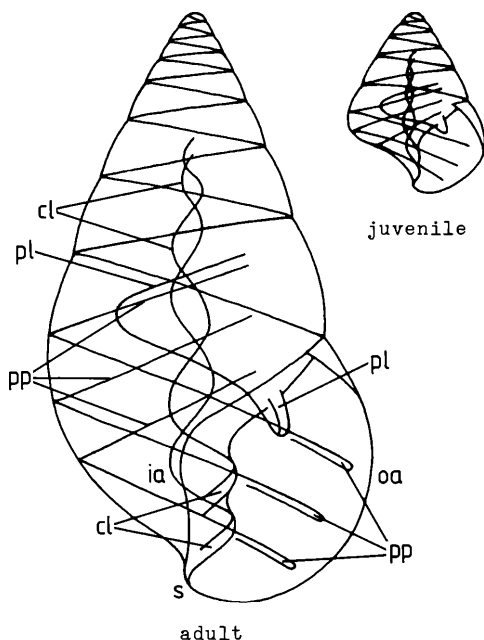


Fig. 1. Shell of Stylommatophora (plesiomorphous condition) (drawn as transparent). cl = columellar lamellae, ia = inner margin of aperture, oa = outer margin of aperture, pl = parietal lamella, pp = palatal plicae, s = siphon.

groups, the majority of them belonging to the helcid Sigmurethra. An apomorphic i.e. incomplete fold system resp. its absence can be stated in many groups, too. In the groups in which a fold system is developed it is more or less modified, in each group in a different way. Most apomorphic but totally different fold systems have the Clausiliidae and Urocoptidae. The fold system of the Clausiliidae has changed into a closing apparatus of the last whorl (clausiliar, cf. H. NORDSIECK 1982), while that of the Urocoptidae is characterized by more or less modified columellar lamellae in several whorls. Such apomorphic fold systems are evidence for the monophyletic origin of the respective groups, but they are restricted to a few families; there is no major stylommatophoran group which can be characterized by a particular apomorphic fold system.

It can be summarized that the shell has only little importance for the higher classification of the Stylommatophora, i.e., in general, major taxa cannot be defined by shell characters. At best it is possible to recognize frequencies of apomorphies which are characteristic of higher taxa, e.g. a depressed shell and the absence of the fold system are more frequent in the helcid Sigmurethra than in the other groups.

II. Distribution.

Geographical distribution.

A survey of the geographical distribution of the Stylommatophora is a condition for the reconstruction of the evolution and thus for the classification of the group. It should not be confined to a statement of the ranges and their grouping to certain basic patterns (cf. TE 1972, 1976, PEAKE 1978)⁴⁾, but it is necessary, too, to indicate the centres of distribution and possible vicariances of the groups. The region in which a group has the greatest diversity is regarded as the centre of distribution (= c. o. d.); this can be assumed to be, in general, the centre of origin, too⁵⁾. It can be a smaller or larger area or, if later on separated, more than one area. Allied groups can be vicariant; this vicariance, which for higher taxa need not be a complete one, is an important proof for a common origin. The following synopsis⁶⁾ of the distribution⁷⁾ of the Stylommatophora is founded on the information contained in ZILCH (1959-60) and, with respect to particular regions, additionally on that offered by the

⁴⁾ TE and PEAKE give comprehensive surveys of the distribution of the stylommatophoran families, but take, in my opinion, too little into consideration the kind of distribution and the relationship between the families. This additional information, however, is a condition for recognizing the centres of distribution and possible vicariances.

⁵⁾ Each monophyletic taxon, no matter if arisen by dispersal or vicariance, has a centre of origin and thus a primary centre of distribution. For animals with little mobility as land snails are — in this respect being comparable more to plants than to e. g. higher vertebrates — this is, in general, about the same as the centre of Recent distribution if geological or paleontological information does not contradict this. This opinion is also supported by the fact that the fossil stylommatophoran faunas of Europe and North America from Upper Cretaceous to Recent contained mainly autochthonous groups and did not change considerably in this long space of time (see below).

⁶⁾ The changes which are effected in this synopsis compared to the current classifications (cf. ZILCH 1959-60, TAYLOR & SOHL 1962, FRANC 1968, SOLEM 1978) will be substantiated in part III of this paper.

⁷⁾ The synopsis is confined to the geographical distribution, i. e. the occurrence in certain zoogeographical regions. Ecological information, e. g. on the occurrence in certain climatic zones resp. biomes, is not given, because it has not proved to be important for the phylogeny of the higher taxa. The zoogeographical regions (cf. WALLACE 1876, DE LATTIN 1967) are defined as follows:

Holarctic:

Palaeartic: Western P. = European + Mediterranean of WALLACE; Eastern P. = Siberian + Manchurian of WALLACE.

Nearctic: boundary against Neotropical cf. PILSBRY (1948).

Neotropical: Neotropical s. str. = South America; Middle America.

Ethiopian: Ethiopian s. str.; Malagasy.

Oriental: boundary against Australian LYDEKKER's line, in East Asia Changjiang region and Ryukyu Islands.

Australian: Australian s. str. = Australia, New Guinea, Melanesia, New Zealand (cf. SOLEM 1959: regions D-J, L); Pacific = Micronesia, Polynesia, Hawaiian Islands (cf. SOLEM: regions K, M, N).

respective modern literature⁸); only Recent autochthonous distribution is taken into consideration.

Orthurethra (and Clausilioidea).

Achatinelloidea.

Achatinellidae: Australian (c. o. d. Pacific) with adjacent East Asiatic and western South American islands.

Cochlicopoidea.

Cochlicopidae: Palaearctic (c. o. d. Western Palaearctic), with a group extending to Nearctic; Amastridae: Australian (Hawaiian Isl.).

Pupilloidea.

Pupillidae, Valloniidae, Vertiginidae (with Gastrocoptinae): Holarctic, with groups extending to Ethiopian and other southern regions, some groups (e. g. Nesopupinae, Gastrocoptinae) in nearly all regions.

Orculidae (without *Fauxulus*): Western Palaearctic to Central Asia, with groups extending to Ethiopian s. str.; Pleurodiscidae: southern Western Palaearctic; Strobilopsidae: eastern Nearctic, northern Neotropical, Eastern Palaearctic and adjacent Oriental; Pyramidulidae: southern Palaearctic; Chondrinidae (without Gastrocoptinae): Western Palaearctic and adjacent Ethiopian.

Buliminoidea.

Buliminidae (Enidae): Palaearctic (c. o. d.), Oriental; Cerastuidae: Ethiopian (c. o. d.), Oriental, Australian s. str. Vicariance of both families!

Clausilioidea.

Clausiliidae: Western Palaearctic, with a group extending to eastern Ethiopian s. str., Eastern Palaearctic, Oriental, northern and western Neotropical.

As is shown by the synopsis the Orthurethra are distributed world-wide, but have their centre of distribution in the northern regions of the earth (Holarctic). Some groups of Pupilloidea dispersed in the warm regions all over the world and thus into the southern regions, too. The Achatinelloidea may also originate from the Holarctic (Eastern Palaearctic?), since their distribution pattern (nearly exclusively Pacific, a few species in Australia and New Zealand, cf. COOKE & KONDO 1960) is similar to that of other groups of Asian origin, contradicting an origin from the Australian. The distribution of the Cerastuidae, which more or less continues that

⁸) As complement of ZILCH's information it was especially made use of the work of the following authors: AZUMA (East Asia), H. B. BAKER (Americas, Pacific), EHLMANN (Eurasia), KONDO (Pacific), LIKHAREV (Eurasia), PILSBRY (Americas), SCHILEYKO (Eurasia), B. J. SMITH (Australia), SOLEM (Pacific), VAN BENTHEM JUTTING (Southeast Asia), VAN BRUGGEN (Africa), YEN (East Asia).

of the Buliminidae, points to an origin from the Palaearctic, too (opposing the opinion of MORDAN 1984).

The Clausilioidea are also of Palaearctic origin, which can be proved as follows: The Clausiliidae of the Western Palaearctic are much more diverse than those of East Asia or South America so that the majority of the subfamilies come from this region (cf. H. NORDSIECK 1978, 1981). In the Cretaceous and Tertiary faunas of Europe plesiomorphous groups of the Clausiliidae (cf. H. NORDSIECK 1985) and plesiomorphous families of the Clausilioidea (Triptychiidae, Palaeostoidae) occur (see below). Origin and distribution pattern of the Clausilioidea fits only the classification near to the Orthurethra, not that with the achatinid Sigmurethra.

Achatinid Sigmurethra.

Partuloidea.

Partulidae: Australian (c. o. d. Pacific except Hawaiian Islands).

Orthalicoidea.

Orthalicidae (Bulmulidae) (with Odontostomidae, Amphibulimidae): Neotropical (c. o. d.) and adjacent Nearctic, Australian s. str.

Urocoptidae: northern Neotropical and adjacent Nearctic; Ceriidae: Neotropical (West Indies).

The Megaspiridae of Neotropical s. str. and Coelociidae⁹⁾ of Australian s. str. are provisionally classified with the Orthalicoidea.

Achatinoidea.

Ferrussaciidae: southern Western Palaearctic (c. o. d.), Ethiopian, western Oriental, northern Neotropical; Subulinidae: Ethiopian, Neotropical (both regions c. o. d.), with a group extending to southern Western Palaearctic, Oriental and adjacent Eastern Palaearctic and Australian; Achatinidae, Coeliacidae: Ethiopian s. str.

The Thyrophorellidae of Ethiopian (São Thomé) are provisionally classified with the Achatinoidea.

Aillyoidea.

Aillyidae: Ethiopian (Cameroon).

Oleacinoidea.

(systematic arrangement sensu PILSBRY and H. B. BAKER olim, new one of BAKER not accepted!):

Spiraxidae: northern Neotropical; Oleacinidae: northern Neotropical and adjacent Nearctic, southern Western Palaearctic.

Testacellidae: southwestern Western Palaearctic.

⁹⁾ n. fam., definition see appendix.

Streptaxoidea.

Streptaxidae: Neotropical s. str., Ethiopian (with Canary Islands), Oriental (both regions c. o. d.) and adjacent Eastern Palaearctic.

Acavoidea.

Strophocheilidae: Neotropical s. str.; Dorcasiidae: Ethiopian (western South Africa); Acavidae: Ethiopian-Oriental (Malagasy, Ceylon); Caryodidae (with Macrocyclidae): Australian s. str., Neotropical (Chile); Megomphicidae (Ammonitellidae): western Nearctic. Vicariance of all families!

Rhytidoidea.

Rhytididae: Australian (c. o. d. Australian s. str.) and adjacent Oriental, Ethiopian (South Africa); Chlamydephoridae: Ethiopian (South Africa).

Systrophiidae: Neotropical (c. o. d. Neotropical s. str.); Haplotrematidae: Nearctic (c. o. d. western Nearctic) and adjacent Neotropical. Vicariance of both families!

Plectopylidoidea.

Sculptariidae: Ethiopian (western South Africa); Plectopylidae (Corillidae): Oriental.

Punctoidea.

Endodontidae: Australian (Pacific); Punctidae (with Helicodiscidae, Charopidae, Otoconchidae): Australian (c. o. d.), Oriental and adjacent Eastern Palaearctic, Antarctica (Kerguelen Islands), Ethiopian (South Africa, some islands), Neotropical, Nearctic, with groups extending to Palaearctic and Ethiopian s. str.; Discidae: Holarctic (with Cape Verde Islands, c. o. d. Nearctic); Oreohelicidae: western Nearctic.

Oopeltidae: Ethiopian (South Africa).

The achatinid *Sigmurethra* are thus entirely or predominantly distributed in the southern regions of the earth. Some groups occur in the Nearctic or Palaearctic or even have a holarctic range, but the distribution of the most related groups demonstrates that their ancestors originated from the Neotropical resp. Ethiopian. The transantarctic distribution of some groups leads to the supposition that they formerly occurred in Antarctica, too (see below).

Elasmognatha.

Succineoidea.

Succineidae: All regions, some groups (*Indosuccinea* group, *Quickia*, *Omalonyx*, *Hyalimax*) distributed only in Neotropical, Ethiopian resp. Oriental.

Athoracophoroidea.

Athoracophoridae: Australian s. str. (c. o. d. except Australia).

At first glance the distribution of the Succineoidea seems to say nothing about the origin of the group; if it is taken into consideration, however, that several

groups, especially the higher evolved ones, and the Athoracophoridae, which probably derived from succineoid ancestors, are distributed only in the southern regions of the earth, it can be assumed that the Succineoidea and thus the Elasmognatha originate from these regions.

Helicid Sigmurethra.

Sagdoidea.

Sagdidae: Neotropical (West Indies).

Gastrodontoidea.

Gastrodontidae: Holarctic (c. o. d. eastern Nearctic) and adjacent Neotropical.

Helixarionoidea.

Euconulidae: Oriental and adjacent Eastern Palaearctic, Australian (both regions c. o. d.), eastern Ethiopian s. str., Nearctic, with a group extending to Palaearctic, northern Neotropical; Helixarionidae (with Ariophantidae, Trochomorphidae): Oriental (c. o. d.) and adjacent Eastern Palaearctic, Australian, Ethiopian (Malagasy); Urocyclidae: Ethiopian; Cystopeltidae: Australian (eastern Australia). Vicariance of Helixarionidae and Urocyclidae!

Vitrinoidea.

Vitrinidae: Western Palaearctic, with groups extending to eastern Ethiopian s. str. resp. Nearctic.

Zonitidae: Holarctic (c. o. d. Western Palaearctic and Nearctic) and adjacent Ethiopian and Neotropical, with groups extending to Australian (Hawaiian Islands); Daudebardiiidae: Western Palaearctic.

Parmacellidae: southern Western Palaearctic to Central Asia; Milacidae: Western Palaearctic.

Limacoidea.

Limacidae, Boettgerillidae: Western Palaearctic to Central Asia; Agriolimacidae: Holarctic (c. o. d. Western Palaearctic) and adjacent Ethiopian and Neotropical.

Trigonochlamydoidea.

Trigonochlamydidae: southeastern Western Palaearctic.

Mesodontoidea.

Mesodontidae (Polygyridae): Nearctic (c. o. d. eastern Nearctic) and adjacent Neotropical; Thysanophoridae (without *Microphysula*): northern Neotropical (c. o. d. Central America) and adjacent Nearctic.

Camaenoidea.

Solaropsidae⁹⁾: Neotropical (c. o. d. Neotropical s. str.); Camaenidae: northern Neotropical (c. o. d. except Central America), Oriental (c. o. d.) and adjacent Eastern Palaearctic, Australian s. str.

Helicoidea.

Sphincterochilidae: southern Western Palaearctic.

Hygromiidae (with Halolimnohelicinae): Palaearctic (with Cape Verde Islands, c. o. d. Western Palaearctic), eastern Ethiopian s. str.; Helicidae: Western Palaearctic (with Cape Verde Islands), with a group extending to northeastern Nearctic; Bradybaenidae (without Halolimnohelicinae): Eastern Palaearctic (c. o. d.), with a group extending to Western Palaearctic, eastern Oriental; Xanthonychidae: western Nearctic, northern and western Neotropical, southwestern Western Palaearctic. Vicariance of Western Palaearctic Helicoidea — Bradybaenidae — American Xanthonychidae!

Arionoidea.

Arionidae: western Nearctic (c. o. d.), Palaearctic (c. o. d. Western Palaearctic).

Philomycidae: eastern Nearctic (c. o. d.) and adjacent Neotropical, Eastern Palaearctic, eastern Oriental.

The helcid *Sigmurethra* are thus predominantly distributed in the northern regions of the earth. The groups occurring in the southern regions (higher *Helix*-arionoidea, Camaenoidea) have a distribution pattern different from that of the achatinid *Sigmurethra* of the same regions (diversity more or less decreasing from north to south) and are related to groups having a distribution in the northern regions so that their ancestors can be assumed to originate from these regions, too.

It can be summarized that the centre of distribution of the *Orthurethra* (and *Clausilioidea*) is in the Holarctic, while the other *Stylommatophora* in this respect fall into two groups: the achatinid *Sigmurethra* (and *Elasmognatha*) which have their centre of distribution in the southern continents, and the helcid *Sigmurethra* which have it in the northern ones. This primary distribution can only be explained by the fact that the achatinid *Sigmurethra* (and *Elasmognatha*) arose on the former southern continent Gondwana, the helcid *Sigmurethra* on the northern continent Laurasia; this can be evaluated as strong evidence for both groups being monophyletic ones. That the achatinid *Sigmurethra* are really of Gondwanian origin is supported by the correspondence of their distribution pattern with that of other animal groups from Gondwana: most groups resp. highest diversity in South America (especially southwestern and eastern part), South Africa, southwestern and eastern Australia, New Caledonia and New Zealand, while the remaining parts of former Gondwana are shared to a greater extent with groups of northern origin (cf. VAN BRUGGEN 1980¹⁰⁾).

To understand the Recent distribution of the *Stylommatophora* an attempt must be made to reconstruct the evolution of the high taxa, i. e. of the *Orthurethra* (and *Clausilioidea*), achatinid *Sigmurethra* (and *Elasmognatha*) and helcid *Sigmurethra*,

¹⁰⁾ It must be emphasized, however, that not only the "Gondwanaland elements" of VAN BRUGGEN but all achatinid *Sigmurethra* and *Elasmognatha* probably originate from Gondwana.

and thereby the genesis of their distribution. The earliest fossils which probably belong to the Stylommatophora are known from the Upper Carboniferous; they are rather diversified so that an origin of Stylommatophora some time ago must be assumed. From the Mesozoic up to the Upper Cretaceous no fossil Stylommatophora are known. In the faunas of the Upper Cretaceous and Lower Tertiary, which are better known only from the northern continents, there are groups of all high taxa; consequently their evolution was already accomplished in the Upper Cretaceous, and their distribution at least on the northern continents was, on the whole, not different from the Recent one. The reconstruction of evolution using fossils alone is not possible, since the gap of fossil record is too great; it must be supported by paleogeographic and paleoclimatological data which are offered by the rapidly advancing geology of the last decades (cf. HALLAM 1973, SCHWARZBACH 1974, SEYFERT & SIRKIN 1979, SMITH, HURLEY & BRIDEN 1981).

The Stylommatophora arose in the Devonian or Lower Carboniferous from some pulmonate of Laurasia and spread over the Pangaea which has formed since the Carboniferous; this dispersal was certainly favoured by the warming of Gondwana at the end of the Paleozoic (fig. 2). In the Permian and Triassic, under favourable climatic conditions, an adaptive radiation into the available ecological niches took place, especially an adaptation to more arid conditions (evolution of the sigmurethrous excretory system). In the Jurassic, in connection with the separation of Pangaea into Laurasia and Gondwana by the broadening Tethys, the sigmurethrous groups were separated, too, those of Gondwana becoming the achatinid *Sigmurethra* and those of Laurasia the helicid *Sigmurethra* (fig. 3). In the Cretaceous, when Gondwana fell into several continents, among which South America and Africa more or less contacted Laurasia, a spreading of groups of southern continents into Laurasia and vice versa occurred, e.g. of *Acavoidea* and *Punctoidea* into North America, *Oleacinoidea* into Europe, *Clausilioidea* into South America and so on (fig. 4). The union of Antarctica, Australia and New Zealand in one continent and its connection with South America until the Lower Tertiary led to the transantarctic distribution of some groups of achatinid *Sigmurethra* (*Orthalicoidea*, *Rhytidioidea*, *Punctoidea*). In the Tertiary, in connection with the close contact of the southern continents Africa and India and the less close one of South America and Australia with the northern continents, a further spreading of groups of the northern and southern continents to the opposite ones occurred, especially an invasion of the higher evolved helicid *Sigmurethra* into the southern continents, e.g. of the *Helixarionoidea* into India, Africa and Australia, and of the *Camaenoidea* into South America and Australia (fig. 5). This invasion was the larger, the closer the contact of the continents was; therefore the percentage of helicid *Sigmurethra* in Africa and especially India is high, while several groups of achatinid *Sigmurethra* can only be found in the south of these continents. This applies to a lower degree also to South America and Australia, while in New Zealand and New Caledonia, which in the Tertiary had no contact with northern continents, no (autochthonous) helicid *Sigmurethra* occur. By the same way achatinid *Sigmurethra* spread into the northern continents, e.g. the *Achatinoidea* into Europe and Asia and the *Streptaxoidea* into Asia. In the Neogene also the non-continental Pacific Islands were settled by groups of all high taxa from neighbouring continents, the origin of which has to be found out for each individual case; thus Micronesia was colonized by *Orthurethra* and helicid *Sigmurethra* from Asia and by

achatinid *Sigmurethra* from Australia, while in the Hawaiian Islands also Nearctic groups were added¹¹). By the Neogene glaciation of Antarctica its autochthonous fauna which probably consisted of present-day transantarctic groups was destroyed. The Plio-Pleistocene climatic deterioration resulted on the Northern Hemisphere, too, in an impoverishment of the stylommatophoran fauna, especially in Europe; the respective groups receded into neighbouring regions or became extinct; in this way from a former Holarctic distribution a North American-East Asian disjunction could result, as in *Strobilopsidae* and possibly in *Philomycidae*.

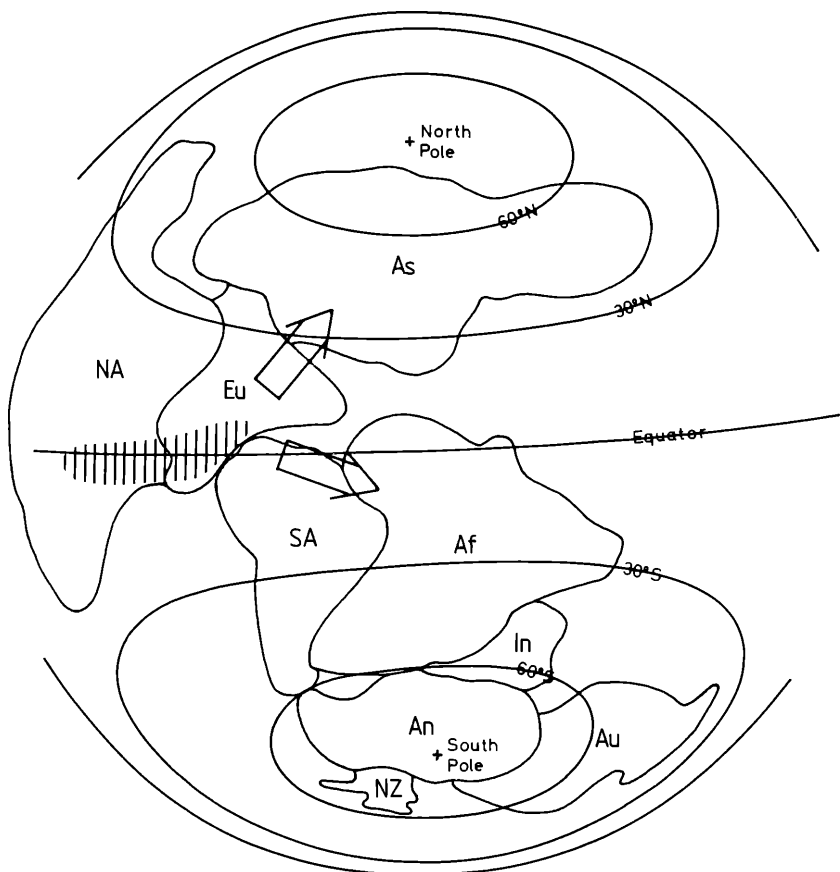
Fossil record.

The proposed hypotheses concerning the evolution of the Stylommatophora can only be verified, if extensive fossil material from the Mesozoic which fills the above-mentioned gap can be obtained. But necessary, too, is a revision of the fossil Stylommatophora of all ages found until now, since the current classification of several groups seems to contradict these hypotheses. This revision was recently carried out for that purpose, but only with regard to the family taxa.

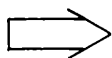
For the classification of Paleozoic land pulmonates it should be considered which group may be the stem group of the Stylommatophora. Among the pulmonates and the euthyneurans in general the Ellobioidea are, with respect to shell and anatomy, most related to the Stylommatophora; in comparison with them they show in most characters the plesiomorphous condition. The stem form should therefore be sought within or near to the Ellobioidea. This seems to be contradicted by the fact that fossil Ellobioidea are not found until the Upper Jurassic (cf. SOLEM & YOCHELSON 1979), but arguing so, it is overlooked that the Soleniscidae, known from Devonian to Permian, which are usually classified with the Subulitoidea, resemble the Ellobioidea so much that they can be classified with them as well. The Subulitoidea, known since the Ordovician, may belong to an early mesogastropod stock arisen from some archaeogastropod ancestor group (cf. KNIGHT et al. 1960); just as plesiomorphous Opisthobranchia and Pulmonata they are characterized by the presence of columellar lamellae and siphonostomy, and may therefore represent or be close to the stem group of euthyneurans¹²). To sum up, the Stylommatophora

¹¹) The Orthurethra and helcid *Sigmurethra* which came from Asia to the Pacific islands are part of the "Palaeo-Oriental fauna" of SOLEM (1959), while the achatinid *Sigmurethra* from Australia resp. New Zealand represent his "Southern Relict fauna". An independent "Pacific Island fauna" sensu SOLEM should not be defined, because its land pulmonates belong to the above-mentioned groups, too, although the origin of some endemic groups (*Achatinellidae*, *Amastriidae*, *Partulidae*) cannot be as easily demonstrated as in the other groups; a third source for Pacific Stylommatophora, except for the Nearctic origin of some Hawaiian groups, does not exist.

¹²) It is surprising that the authors who have recently discussed the origin of the euthyneurans (e.g. FRETTER 1975, GOSLINER 1981, HASZPRUNAR 1985) look for it only in Recent plesiomorphous mesogastropodan groups and pay no attention to the fossil ones coming in question, such as the Subulitoidea. Because heterostrophy is probably an important synapomorphy of the euthyneurans (*Heterobranchia* sensu HASZPRUNAR), it should be checked up if any or all Subulitoidea have a heterostrophous shell, too. The earliest groups with such a shell which are known originate from the Lower Carboniferous (*Streptacidae*, *Acteonina* group) so that the heterostrophous ancestor of the euthyneurans had at least Devonian age.



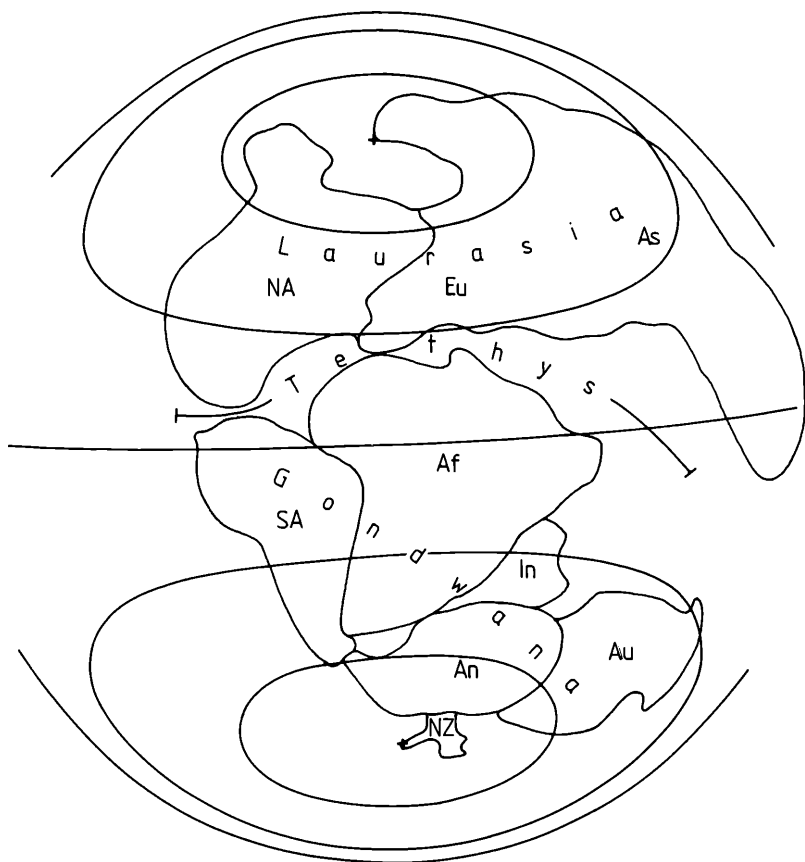
range of known Paleozoic Stylommatophora



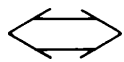
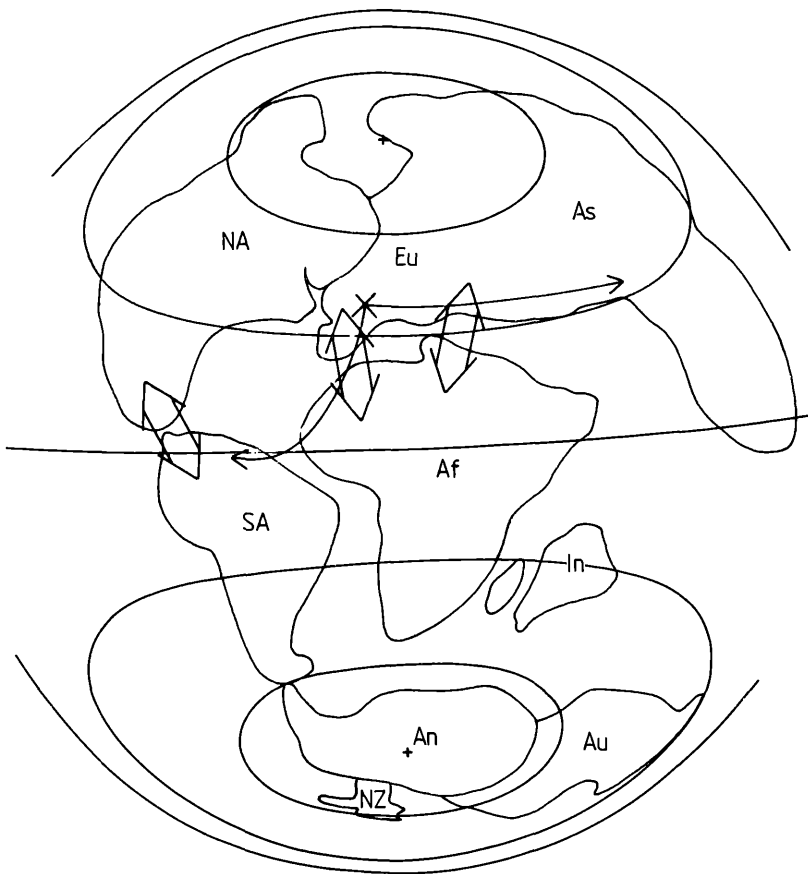
assumed spreading of Stylommatophora over Pangaea
in the Permian

2

Fig. 2-5. History of the distribution of Stylommatophora (paleogeography cf. SMITH, HURLEY & BRIDEN 1981). 2: Lower Permian, 3: Upper Jurassic, 4: Upper Cretaceous, 5: Upper Eocene. Af = Africa (with Arabia), An = Antarctica, As = Asia (without Arabia and India), Au = Australia, Eu = Europe, In = India, NA = North America, NZ = New Zealand, SA = South America. Further explanation in the text.



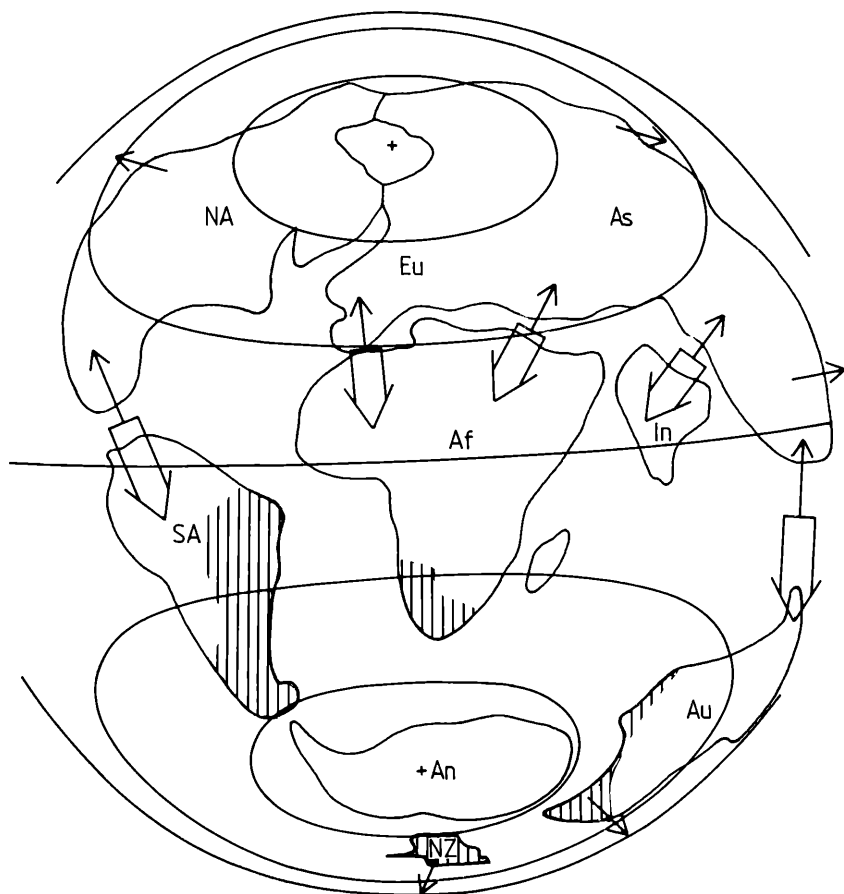
—Tethys— assumed separation of the sigmurethrous groups
by the Tethys in the Jurassic

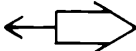



assumed spreading of the different groups from
northern into southern continents resp. vice versa
in the Cretaceous




centre of origin and main dispersal of
the Clausiliidae



 assumed invasion of helioid *Sigmurethra* into the southern continents and spreading of achatinid *Sigmurethra* into the northern ones in the Tertiary

 spreading of the different groups into the Pacific

 regions in which Gondwanian groups are still dominant

can be assumed to have arisen from subulitoid resp. ellobioid ancestors in the Devonian or Lower Carboniferous.

All known groups of land pulmonates from the Upper Carboniferous and Lower Permian, *Anthracopupa* WHITFIELD, *Dendropupa* OWEN, *Protodiscus* SOLEM & YOCHELSON and "*Pupa*" (cf. SOLEM & YOCHELSON 1979), may have been orthurethrans. *Anthracopupa* is possibly a transitional group between Ellobioidea and Orthurethra, because it corresponds with the Ellobioidea, especially the Carychiidae, more than SOLEM & YOCHELSON admit¹³). It is therefore appropriate to recognize the Anthracopupidae as an independent family which can be placed at the base of the Stylommatophora. *Dendropupa* is characterized by a shell having two columellar lamellae in the lower whorls which is more like that of the Cyllindrellinidae of Upper Cretaceous and Paleogene (see below) than that of the Enidae (= Buliminidae) or Urocoptidae with which it has been compared until now; the Dendropupidae should therefore be regarded as an independent family of the Orthurethra. *Protodiscus* is similar to the Punctoidea, especially the Discidae (cf. SOLEM & YOCHELSON), with respect to shell form and sculpture, but is comparable in the same characters to depressed orthurethrans with similar sculpture, e.g. the Pleurodiscidae; thus there is little evidence that it was a sigmurethrous snail. It is highly improbable that sigmurethria should have already been evolved in the Carboniferous, when the earliest Stylommatophora lived, as far as is known, in a humid tropical climate (fig. 2).

The revision of the classification of the extinct land pulmonates of European Upper Cretaceous and Paleogene (cf. ZILCH 1959-60)¹⁴) has led to results which can be summarized as follows¹⁵):

Palaeostoa ANDREAE, classified until now with the Megaspiridae. The group is characterized by a high-spined shell with a complete fold system, which consists of parietal and columellar lamellae and palatal folds, developed continuously and resorbed from within, in the adult shell being present only in the lower whorls.

¹³) Only two of the differences between *Anthracopupa* and the Ellobioidea to which SOLEM & YOCHELSON refer really exist, if the Carychiidae are taken for comparison. The latter differ from *Anthracopupa* in the lower position of the upper lamella and the resorption of the inner walls of the shell, but there are no differences in the shell form, apertural angle and formation of the columellar lamella. The difference in the position of the upper lamella is understandable since in the Carychiidae it is really an upper columellar lamella which should not be compared with the parietal lamella of *Anthracopupa*. The presence of such a lamella cannot be evaluated either as proof against a relationship with the Carychiidae, because certain fossil Carychiidae also have a parietal lamella. On the other hand, the characteristic palatal barriers of *Anthracopupa* can be evaluated as proof of this relationship, because the Carychiidae have similar barriers.

¹⁴) The earliest fossils of the European Cretaceous which were described as land pulmonates originate from the Lower Cenomanian (REPÉLIN 1902); shell characters and occurrence, however, suggest nearly all of them to be freshwater prosobranchs. This work of REPÉLIN was obviously overlooked by WENZ (1923, 1940) and ZILCH (1959-60).

¹⁵) The definitions of the Cenozoic epochs are the most recent ones of the marine stratigraphy (cf. BERGGREN & VAN COUVERING 1974, HARDENBOL & BERGGREN 1978, BERGGREN, KENT & VAN COUVERING in press).

Thus the fold system differs much from that of the Neotropical Megaspiridae, the only common character of both being the presence of this system. *Palaeostoa* (Maastrichtian to Upper Eocene) is not related to the Megaspiridae but to the Tertiary Triptychiidae, i. e. to the Clausilioidea (H. NORDSIECK unpubl.); therefore a new family, Palaeostoidae n. fam.¹⁶⁾, must be erected.

Cylindrellina group (Santonian to Middle Eocene)¹⁷⁾, classified until now with the Coeliacidae. The group is characterized by a turreted shell with columellar lamellae developed only in lower whorls and, except one, reduced up to the aperture and with palatal plicae but lacking a parietal lamella. Thus the fold system is very different from that of the Ethiopian Coeliacidae, the only common character being its presence; the group must therefore be regarded as an independent family Cylindrellinidae.

Scalaxis PILSBRY (Upper Paleocene), classified until now with the Achatinidae. As is demonstrated mainly by the fold system (columellar lamella forming the columella), it may be a freshwater snail and belong to the lymnaeid Basommatophora. The related genus *Berellaia* LAUBRIÈRE & CAREZ of equal age has already been taken, though with doubt, for a basommatophoran group by WENZ (1923); thus until further investigation the *Scalaxis* group should be eliminated from the Stylommatophora.

Anadromidae (Turonian to Upper Eocene), regarded by WENZ (1940) as an independent family related to groups of southern continents. The family is characterized by a bulimoid shell generally lacking a fold system; it contains several groups, among them the Vidaliellinae n. subfam.¹⁶⁾ with a normal shell (including e. g. *Vidaliella* WENZ and *Romanella* JODOT), and the Anadrominae with a ascending resp. ascending and descending last whorl (including *Anadromus* SANDBERGER and *Lychnus* MATHERON). The Vidaliellinae were classified until now with Orthalicoidea, Acavoidea or bulimoid Helicoidea, the Anadrominae especially with certain groups of Orthalicoidea; this similarity, however, is only superficial, caused by the shell form and in the Anadrominae also by the particular formation of the last whorl¹⁸⁾. More important may be common characters of the Vidaliellinae with the Tertiary European Triptychiidae (H. NORDSIECK unpubl.) which suggest relations rather to the Clausilioidea than to the mentioned groups of southern continents.

Anostomopsis group (Turonian to Maastrichtian), classified by WENZ (1940) with the Streptaxidae, by HRUBESCH (1965) partly with the Streptaxidae, partly with the Corillidae (= Plectopylidae). The shell of the group is conical to depressed, partly with ascending last whorl, in most groups with a fold system, in those which are well known with a complete one, developed continuously and resorbed from within. This plesiomorphous fold system resembles that of certain Punctoidea more

¹⁶⁾ Definition and genera belonging there see appendix.

¹⁷⁾ WENZ (1923) recognized the genera *Cylindrellina* MUNIER-CHALMAS and *Distoechia* CROSSE; COSSMANN (1924) revised this classification by dividing the group into the genera *Cylindrellina* (= *Distoechia*) and *Paradistoechia* COSSMANN, which was obviously overlooked by ZILCH (1960). The systematic position of *Coeliaxis* COSSMANN non ADAMS & ANGAS which WENZ wrongly united with *Cylindrellina* remains doubtful, since the respective species of Upper Paleocene resp. Middle Eocene are insufficiently known.

than that of Streptaxidae¹⁸⁾¹⁹⁾ or Plectopylidae, which makes nearer relations to these families improbable. The group should therefore be regarded as an independent family, Anostomopsidae n.fam.¹⁶⁾; for the present its systematic position remains uncertain, since a plesiomorphous fold system in this regard does not admit any decision.

The classification of extinct Stylommatophora is difficult, because the shell has only little taxonomic value (see above); that those of the Upper Cretaceous and Paleogene of Europe were classified until now with non-European achatinid Sigmurethra is mainly due to the fact that their shell is a more or less plesiomorphous one, i. e. elevated and (or) provided with a fold system. A more detailed examination shows, however, that these groups cannot be classified with those achatinid Sigmurethra but are related to other Palaearctic groups or have an isolated resp. uncertain systematic position. Thus their occurrence in this space and time cannot be evaluated as evidence against the evolution of the two sigmurethrous groups in Gondwana resp. Laurasia.

The history of the stylommatophoran fauna of Europe from Upper Cretaceous to Recent can be described as follows: At the Cretaceous-Tertiary limit the Anostomopsidae and Anadrominae disappeared. The fauna of the Paleocene and Eocene contained, besides the above-mentioned extinct groups, some of all high taxa. Up to the Eocene-Oligocene limit ("Grande coupure" of mammals = Terminal Eocene Event) several groups disappeared, e.g. the Cyllindrellinidae, Palaeostoidae, Vidaliellinae and some groups of Clausilioidea and Vitrinoidea. In the Oligocene the yet absent groups of the Recent fauna appeared so that the composition of the Neogene fauna with regard to higher taxa differed little from that of the Recent one. A considerable change was effected by the Plio-Pleistocene climatic deterioration at the Lower-Middle Villafranchian limit (~ 2.5 Ma): the Strobilopidae, Triptychiidae and some groups of Clausiliidae, Subulinidae, Zonitidae and Helicoidea became extinct, while in the other groups the great faunal change on the species level took place. After the extinction of some further groups up to the end of the Villafranchian (~ 1 Ma) the fauna had the Recent composition with regard to lower taxa, too.

¹⁸⁾ The Anadromidae and Anostomopsidae were classified with the mentioned groups of achatinid Sigmurethra also on account of the ascending last whorl of some groups belonging there. This character which I propose to name anostomy occurs in several non-related Recent groups of Stylommatophora (e.g. in Nesopupinae, Gastrocoptinae, Odontostominae, and Streptaxidae) and even of land prosobranchs (Diplommatinidae) which all live in tropical regions; in fossil groups it is found, except in the Anadromidae and Anostomopsidae, in the Grangerellidae of North American Paleocene and the prosobranch Ferussininae of European Eocene and Oligocene. Anostomy is an apomorphy of yet unknown biological importance which apparently originated several times in different land snail groups and can therefore be no proof of relationship.

¹⁹⁾ Nearly all fossil groups which WENZ (1940) classified with the Streptaxidae do surely or probably not belong to this family; besides the Anostomopsidae and *Rillya* MUNIER-CHALMAS in FISCHER which is a clausiliid (cf. H. NORDSIECK 1985) *Lychnopsis* VIDAL may belong to the Anadromidae, *Paracratricula* OPPENHEIM to the Orculidae, while *Granoennea* WENZ is an *Argna* (TRUC 1971). Only *Gibbulinella simplex* OPPENHEIM may be a streptaxid if it belongs to this present-day Canarian genus which came from Africa.

Concerning the composition of the European Upper Cretaceous and Tertiary fauna, it is of importance that not only the different main groups but also their subgroups are autochthonous ones, i. e. of Western Palaearctic origin, even if the groups are distributed far beyond Europe. This is true, e. g., for the Clausiliidae, Zonitidae and Helicoidea. The fossil Clausiliidae of Europe (H. NORDSIECK 1981, 1985) belong to several subfamilies all of which, extinct or not, are restricted to the Western Palaearctic (except the Mentissoideinae which extend into the Ethiopian); this proves, too, that the non-European groups of Clausiliidae were already separated from the European ones during the Cretaceous (fig. 4). For the Tertiary Zonitidae of Europe PFEFFER (1929) proposed a division into subfamilies all of which are autochthonous. The Helicoidea of European Tertiary (H. NORDSIECK 1986) can all be classified with families resp. subfamilies which are distributed today only or mainly in the Western Palaearctic.

To sum up, the stylommatophoran fauna of Europe from Upper Cretaceous to Recent was composed mainly of autochthonous groups and changed within this period only gradually, i. e. the evolution of these groups took place in situ. This is also true for the corresponding fauna of North America which, indeed, is less known than that of Europe. It follows that the Tertiary faunas of these continents can contribute only little to the reconstruction of the evolution of the higher stylommatophoran taxa, but also that the distribution of the Stylommatophora in space changes so slowly in time that it is an important basis for this reconstruction.

Appendix: New family taxa.

Coelociidae n. fam.

Type genus: *Coelocion* PILSBRY.

Diagnosis and distribution: Differing from the Megaspiridae especially by the fold system (if fully developed with palatal plica, columellar lamellae simple); NE-Australia, New Guinea.

The genera *Coelocion* and *Perrieria* TAPPARONE-CANEFRI which were classified by PILSBRY (1904) with the Megaspiridae should be separated as an independent family, since they have in common with them only plesiomorphous characters, i. e. a turreted shell, the presence of a fold system and a non-achatinoid radula, while they differ much by the development of the fold system and the distribution. The examination of other anatomical characters is yet outstanding so that the systematic position of the family is doubtful.

Solaropsidae n. fam.

Type genus: *Solaropsis* BECK.

Diagnosis and distribution: Differing from the Camaenidae by the genital system (diverticulum present, male end ducts partly with penial appendix and forked penial retractor); c. o. d. Neotropical s. str.

The systematic position of this group is not at all as certain as IHERING (1912) thought. The few species of *Solaropsis* which have been examined have a jaw and kidney like those of the Camaenidae but a genital system with the above-mentioned plesiomorphous characters which are not found in that family. The Solaropsidae

comprise only the genera *Solaropsis* and *Psadara* MILLER, while *Polygyratia* GRAY with the same c. o. d. differs much by shell characters and possibly belongs to the achatinid Sigmurethra. The insufficient knowledge of both Neotropical groups makes further research necessary.

† *Palaeostoidae* n. fam.

Type genus: *Palaeostoa* ANDREAE.

Diagnosis and distribution: Differing from the Megaspiridae especially by the fold system (with palatal plicae, lamellae developed only in the lower whorls, columellar ones simple); Europe, Upper Cretaceous — Paleogene.

To this family possibly belongs, too, the genus *Ptychicula* TAUSCH, which would extend its range down to the Turonian.

† *Anostomopsidae* n. fam.

Type genus: *Anostomopsis* SANDBERGER.

Diagnosis and distribution: Characterized especially by the fold system (if present, as far as known, in juvenile as in adult stage, with several parietal and palatal folds reaching the aperture); Europe, Upper Cretaceous.

In this family can be united the genera *Anostomopsis*, *Enneopsis* WENZ, *Gosavidiscus* HRUBESCH, *Proterocorilla* HRUBESCH, *Pseudostrobilus* OPPENHEIM, *Strophostomella* FISCHER, and possibly *Eoplicadomus* HRUBESCH.

† *Anadromidae* (*Vidaliellinae*) n. subfam.

Type genus: *Vidaliella* WENZ.

Diagnosis and distribution: Differing from the Anadromidae (Anadrominae) by the non-ascending last whorl; Paleogene.

The groups *Vidaliella* and *Romanella* JODOT belonging there can scarcely be separated as genera (cf. PLAZIAT 1973); only *darderi* VIDAL, type species of *Vidaliella* JODOT, but figured by ZILCH (1960) to represent *Vidaliella* WENZ, has a more isolated systematic position. This species has not an Upper Cretaceous but an Upper Eocene or Lower Oligocene age (cf. FALLOT 1922); thus *Vidaliella*—*Romanella* is restricted to the Paleogene. To the *Vidaliellinae* may belong, too, *Vicentinia* JODOT and *Procerastus* WENZ from the Vicentinian Eocene; the similar anadromids of the Upper Cretaceous are too little known to be classified with one of the subfamilies.

Summary

In the second part of the paper on the system of the Stylommatophora the importance of shell and distribution for their classification is discussed. By a comparative study of the shell only a few characters were found which, in this regard, may be important. Plesiomorphous characters, such as an elevated shell, the presence of a fold system, and siphonostomy, make the reconstruction of the shell of the stem form possible. The apomorphous ones evolved several times in a parallel way so that there are no apomorphies of the shell which characterize major groups. As concerns especially the fold system, it was modified resp. reduced in many

groups independently; most apomorphous fold systems can be found in the Clausiliidae and Urocoptidae. Hence it follows that the shell has only little importance for the higher classification of Stylommatophora.

A synopsis of the geographical distribution of the Stylommatophora had the following result: the Orthurethra are distributed world-wide, but have their centre of distribution in the northern regions of the earth so that the Stylommatophora may have originated there, too. The distribution pattern of the Clausiliidae fits their classification near to the Orthurethra well. The two sigmurethrous groups have an opposite distribution: the achatinid Sigmurethra (and Elasmognatha) have their centre of distribution in the southern regions of the earth, the helcid Sigmurethra in the northern ones. Therefore it can be concluded that the first are of Gondwanian, the latter of Laurasian origin; this can be evaluated as evidence for both groups being monophyletic ones. Based on these results an attempt is made to reconstruct the genesis of the Recent distribution, taking into consideration the findings of modern geology and the fossil record.

The results of a revision of the fossil Stylommatophora carried out in this connection correspond to those obtained from the study of distribution: the Paleozoic groups which are known only from Laurasia can all be classified with the Orthurethra. The only known Mesozoic groups, those of the Upper Cretaceous, and the Tertiary ones are more or less related to those distributed at present in the same region or have an uncertain systematic position; this is true, too, for the extinct European groups which were examined in more detail. In addition, the history of the stylommatophoran fauna of Europe from Cretaceous to Recent is outlined.

The following family taxa are described as new: Coelociidae n. fam. (type genus *Coelocion* PILSBRY), Solaropsidae n. fam. (*Solaropsis* BECK), † Palaeostoidae n. fam. (*Palaeostoa* ANDREAE), † Anostomopsidae n. fam. (*Anostomopsis* SANDBERGER), † Anadromidae (Vidaliellinae) n. subfam. (*Vidaliella* WENZ).

Zusammenfassung.

In Teil II der Arbeit zum System der Stylommatophora wird die Bedeutung von Gehäuse und Verbreitung für deren Einteilung diskutiert. Durch eine vergleichende Untersuchung des Gehäuses konnten nur wenige Merkmale gefunden werden, die in dieser Hinsicht von Bedeutung sein dürften. Plesiomorphe Merkmale, wie erhobenes Gewinde, das Vorhandensein eines Faltenapparats und Siphonostomie, ermöglichen die Rekonstruktion des Gehäuses der Stammform. Die apomorphen entwickelten sich mehrfach parallel, so daß es keine Apomorphien am Gehäuse gibt, die für größere Gruppen kennzeichnend wären. Was speziell den Faltenapparat betrifft, wurde dieser in mehreren Gruppen unabhängig voneinander um- bzw. rückgebildet; stark apomorphe Faltenapparate finden sich bei den Clausiliidae und Urocoptidae. Daraus folgt, daß das Gehäuse für die Großsystematik der Stylommatophoren nur geringe Bedeutung hat.

Eine Übersicht über die geographische Verbreitung der Stylommatophoren ergab folgendes: Die Orthurethra sind weltweit verbreitet, haben ihren Verbreitungsschwerpunkt jedoch in den nördlichen Regionen der Erde, so daß die Stylommatophora dort auch entstanden sein dürften. Das Verbreitungsmuster der Clausiliidae paßt gut zu ihrer systematischen Einordnung in der Nähe der Orthurethra. Die beiden sigmurethren Gruppen haben gegensätzliche Verbreitung: die achatiniden Sigmurethra (und Elasmognatha) haben ihren Verbreitungsschwerpunkt in den südlichen Regionen der Erde, die helcid Sigmurethra in den nördlichen. Daraus kann geschlossen werden, daß die ersteren in Gondwana, die letzteren in Laurasia entstanden sind; dies kann als Beweis dafür gewertet werden, daß beide Gruppen monophyletisch sind. Auf der Grundlage dieser Ergebnisse wird der Versuch gemacht, die Entstehung der rezenten Verbreitung unter Berücksichtigung der Erkenntnisse der modernen Geologie und der Fossilbelege zu rekonstruieren.

Die Ergebnisse einer Revision der fossilen Stylommatophora, die in diesem Zusammenhang durchgeführt wurde, stimmen mit denen überein, die aus der Untersuchung der Verbreitung gewonnen wurden: Die paläozoischen Gruppen, die nur von Laurasia bekannt sind, können ohne Ausnahme zu den Orthurethra gestellt werden. Die einzigen bekannten mesozoischen Gruppen, die der Oberkreide, und die tertiären sind näher oder entfernter mit denen verwandt, die im gleichen Gebiet rezent verbreitet sind, oder haben eine unsichere systematische Stellung; dies trifft auch für die ausgestorbenen europäischen Gruppen zu, die etwas genauer untersucht wurden. Zusätzlich wird die Geschichte der europäischen Stylommatophorenfauna von der Oberkreide bis heute dargestellt.

Folgende Taxa der Familiengruppe werden neu beschrieben: *Coelociidae* n. fam. (Typusgattung *Coelocion* PILSBRY), *Solaropsidae* n. fam. (*Solaropsis* BECK), † *Palaeostoidae* n. fam. (*Palaeostoa* ANDREAE), † *Anostomopsidae* n. fam. (*Anostomopsis* SANDBERGER), † *Anadromidae* (*Vidaliellinae*) n. subfam. (*Vidaliella* WENZ).

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