

A RECONSIDERATION OF SYSTEMATICS IN THE MOLLUSCA (PHYLOGENY AND HIGHER CLASSIFICATION)

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ABSTRACT

A reconsideration of phylogenetic interrelations in molluscs with respect to several more recent studies on different groups of various taxa leads to a somewhat revised presentation of presumed molluscan evolution. Taking into consideration not only the quantitatively predominant shelled groups, adequately documented as fossils, but allowing also for the minor, yet comparative-anatomically equivalent aplacophoran molluscs, the synorganizationally relevant characters and organ systems reflect distinct anagenetic pathways. This analysis evidences a homogeneous frame of continuous evolution along a phylogenetic main line of archimolluscs—Placophora—Conchifera, and an early sidebranch of Scutopoda. Four essential steps of progressive differentiation are obvious which separate a) the Scutopoda (Caudofoveata) from the Adenopoda (all other molluscs), b) the Solenogastres from the shell-bearing adenopods (Testaria), c) the Placophora from the Conchifera, and d) the conchiferan groups among each other; herein, the Placophora and Solenogastres are synapomorphously tied together in contrast to the merely symplesiomorphous characters in Solenogastres and Caudofoveata ("Aplacophora"). A correspondingly modified higher classification is proposed.

INTRODUCTION

Increase in the knowledge of comparative anatomy and increase in the number of species frequently cause systematic problems. This is especially obvious when a major group of organisms is thoroughly studied and revised, or when some aberrant organization is introduced and/or brought to general knowledge. Since systematics should—as far as possible—coincide with the respective relationships of different organization with an adequate classification (to get a 'natural' system), all taxa within a group as well as the higher taxa should be arranged according to equivalent morphological or other quality—but not with respect to quantity (of species, etc.) or scientific importances (actual or seeming). In the endeavour to present phylogenetic relationships, only monophyletic groups can be classified together; this, however, can only seldomly be confirmed within a linear system (cf. Mayr, 1974). Therefore, a compromise must be accepted which intervenes between evidenced phylogenetic course and usable praxis.

Such systematic discrepancies and problems have more recently been raised in various aspects and levels within the Mollusca, and especially with regard to differences in zoological and paleontological points of view.

Most molluscan classifications suffer from domination by the—generally well-investigated—conchiferan groups, which are sometimes even uniquely regarded as "true" molluscs (cf. Fretter & Graham, 1962, etc.). This often results also in the proposition to accept purely conchiferan conditions as ancestral for molluscan organization: the Conchifera—or even the mere Gastropoda—are misinterpreted so as to represent the organizational standard for all Mollusca (cf. e.g. Yonge, 1947; compare also Runnegar & Pojeta, 1974; Yochelson, 1978). Respective to these conditions, the present contribution tries to present and discuss those various discrepancies for the higher taxa within all molluscs, and to synthesize them for a classification that is adequate phylogenetically as well as for practical systematics.

CAUDOFOVEATA AND SOLENOGASTRES

Several more recent studies (S. Hoffman, 1949; Boettger, 1955; Salvini-Plawen, 1969, 1972) have especially dealt with the organization of the so-called aplacophoran molluscs, resulting in the evidence that they constitute "two long-separate lines" (Stasek, 1972: 40) which diverged at the basic level of archimolluscan organization. When thoroughly com-

pared in their organ systems, the Caudofoveata (the former Chaetodermatina/Chaetodermomorpha / Chaetodermoidea) and the Solenogastres (also Neomeniina/Neomeniomorpha/Neomenioidea) are similar primarily in the symplesiomorphous mantle structure and muscle systems, as well as in the convergently reduced true gonoducts. The alimentary tract in Caudofoveata could be derived from the more primitive one in the Solenogastres (the latter having the most conservative configuration within all mollusca; cf. Salvini-Plawen, 1969, 1972, 1979). All other organ systems (foot, mantle cavity, reproductive system, also nervous system and circulatory system), however, are not synorganizationally derivable from each other in both groups, consequently resulting in the cognition of early convergence of both evolutionary lines.

The Caudofoveata already deviated at the most primitive level of common molluscan organization in adapting to a burrowing way of life. The elaboration of the cerebrally-innervated section of the ventral gliding surface to the actual pedal shield, the reduction of the other gliding surface with the mid-ventral fusion of the lateral mantle rims, and the elaboration of the body wall musculature to a hydrostatic muscular tube are distinct results of that adaptation. The differentiation of the strong longitudinal musculature in the anterior body (including the regression of other muscle systems) must be understood with respect to the antagonistic body fluid for burrowing locomotion in the sediment. And the feeding on microorganisms resulted in a brushing radula of the distichous type (and later on a forceps-like seizing organ), as well as in the separation of a ventral midgut gland including, in higher members only, the differentiation of a proto-style and a gastric proto-shield (primitive stomach; cf. Salvini-Plawen, 1979).

The Solenogastres are conservative members of the alternative evolutionary line within those early molluscs which proceeded in a gliding-creeping locomotion upon the ventral surface, but having already differentiated a peripodal mantle cavity, a rudimentary head (snout), and the pedal gland. They are still provided with the primitive mantle cover and—owing to their early preference for feeding as predators on Cnidaria—with the original configuration of a pouched midgut (and serial dorsoventral muscle bundles). The narrowing of the whole body including the foot, the partial reduction of the mantle cavity and

its partial internalization are adaptations to a winding-wriggling manner of muco-ciliary locomotion on secondary hard bottoms (also coral reefs, littoral, etc.). The manifold modifications of the monoserial radula and/or the differentiation of a pharyngeal sucking-pump are further adaptations for feeding on Cnidaria (cf. Salvini-Plawen, 1979).

The most obvious evidence for these divergent evolutionary pathways in the Caudofoveata and the Solenogastres comes from the comparative analysis of the pedal system and the mantle cavity. Solenogastres, Placophora and Conchifera possess a ventrally-innervated foot and a distinct pedal gland associated with it; on the contrary, the Caudofoveata are only provided with a cerebrally-innervated pedal shield structurally almost identical to the foot of other molluscs. The presence of mucous glandular cells like those along the pedal groove in the Solenogastres (cf. S. Hoffman, 1949), the lack of mantle folds (Fig. 3), and the cerebral innervation of the pedal shield (Salvini-Plawen, 1972) contradict its interpretation as secondarily re-established pedal organ, but positively indicate its primitive condition. The ventrally-innervated section of the ancestral gliding surface in the caudofoveatan line has been reduced from posterior to anterior (as is still obvious in some species of *Scutopus*), so that the mantle edges are midventrally fused (Fig. 3). The mantle cavity coincides in its terminal position with that statement, and it has medially inverted pallial grooves with mucous tracts and with ventrolateral (!) openings of the pericardial outlets (cf. S. Hoffman, 1949; Salvini-Plawen, 1972). That configuration, as well as the total lack of further portions of the mantle cavity essentially serve to contrast the whole organ system of the Caudofoveata to that in the Solenogastres (and other molluscs), both of which cannot be derived from each other.

Also the gonopericardial system of both Caudofoveata and Solenogastres can in no case be derived from each other. Findings in *Phyllomenia* and further arguments (cf. S. Hoffman, 1949; Salvini-Plawen, 1970b, 1972, 1978) clearly indicate that the forerunners of the Solenogastres possessed both pericardioducts as well as gonoducts; the latter, however, are now predominantly in secondary connexion by their upper portion with the pericardium (the lower portions then being reduced). The pericardioducts open into the spawning ducts, i.e. the internalized posterior-lateral sections of the mantle cavity provided

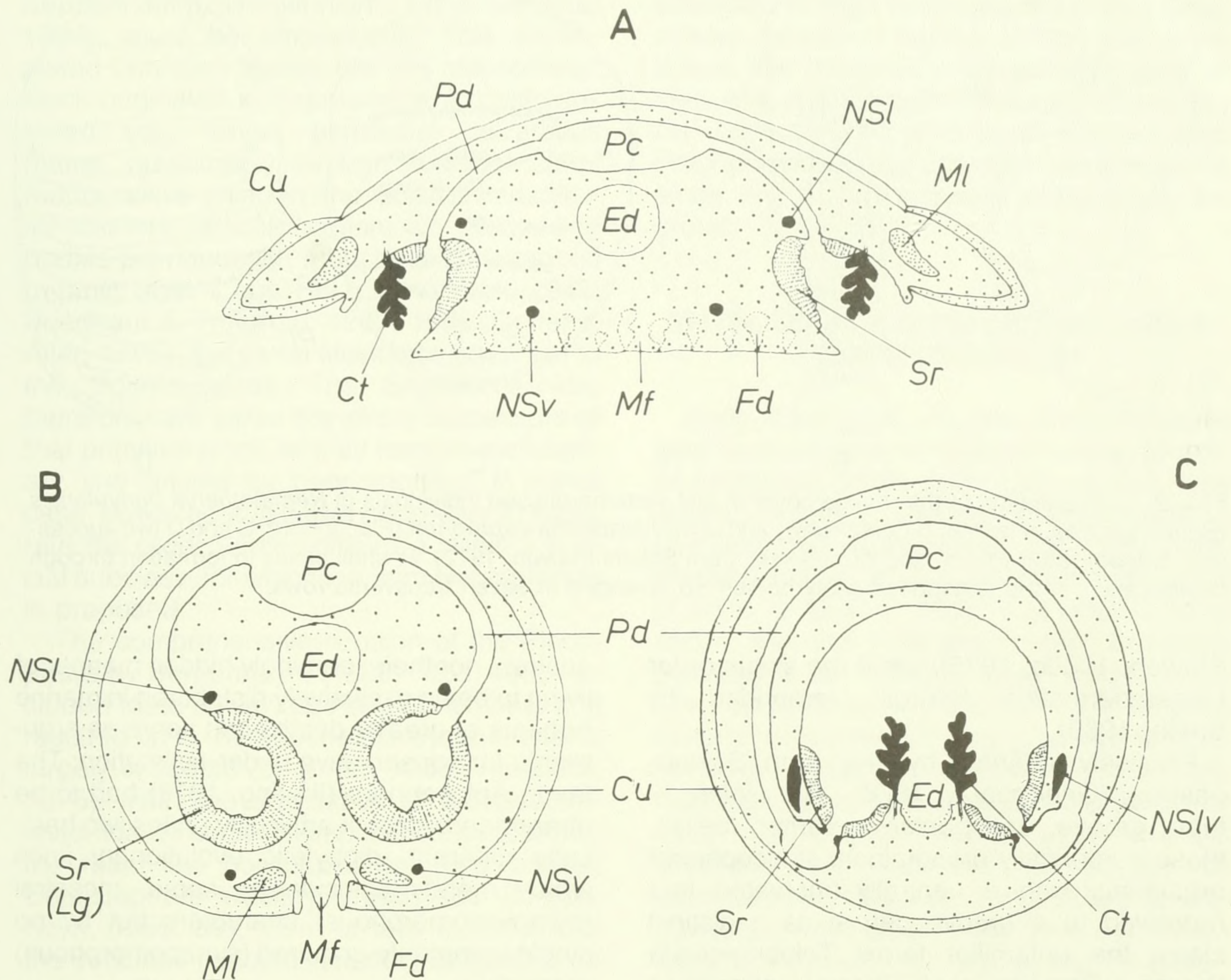


FIG. 1. Comparative arrangement of the pallio-pericardial system in A Placophora-Lepidopleuridae, B Solenogastres, and C female Caudofoveata (after Salvini-Plawen, 1972). Ct ctenidium, Cu mantle-cuticle, Ed hind gut, Fd sole glands, Lg spawning duct, Mf foot, MI longitudinal muscle, NSI/NSv/NSIv lateral and ventral nerve cords, Pc pericardial cavity, Pd pericardioduct, Sr mucous tract.

with the mucous tracts (S. Hoffman, 1949; cf. Fig. 1). In contrast, the pericardioducts in the Caudofoveata open into ectodermal glandular ducts (cf. Fig. 1) which, owing to their configuration as well as to their structure, neither belong to the pericardioducts nor to the mantle cavity (into which they open ventrolaterally by means of a narrow opening with strong sphincter). Since there are no real gonoducts in the Caudofoveata, these glandular ducts may possibly constitute the altered lower portions of the original gonoducts (cf. Salvini-Plawen, 1972: 251 ff.).

Such outlined conditions, and properties in further organ systems synorganizationally considered in Caudofoveata and in Soleno-

gastres (cf. Salvini-Plawen, 1972; Salvini-Plawen & Boss, 1980), cannot be derived from each other and hence obligatorily prove the basically independent evolutionary differentiation of both groups from an ancestral organization common to all molluscs (see Figs. 3-5).

Following knowledge of the "diphyletic Aplacophora" (Stasek, 1972: 19),¹ the Caudofoveata (Boettger, 1955) have been separated from the solenogastrid aplacophorans and raised to the rank of an independent class, equivalent to Solenogastres and Placophora (Salvini-Plawen, 1967, 1968b, 1975). The some 65 described species are grouped in three families (Salvini-

¹Although Stasek (1972: 19 & 40) is well aware of the "long-separate," "diphyletic" aplacophoran molluscs, he takes this knowledge not into account and inexplicably classifies both groups again under one single taxon. There are no comments here on the mis-conceived interpretation by Scheltema (1978) as concerns commonly inherited (symplesiomorphous) and phylogenetically specialized (apomorphous) characters.

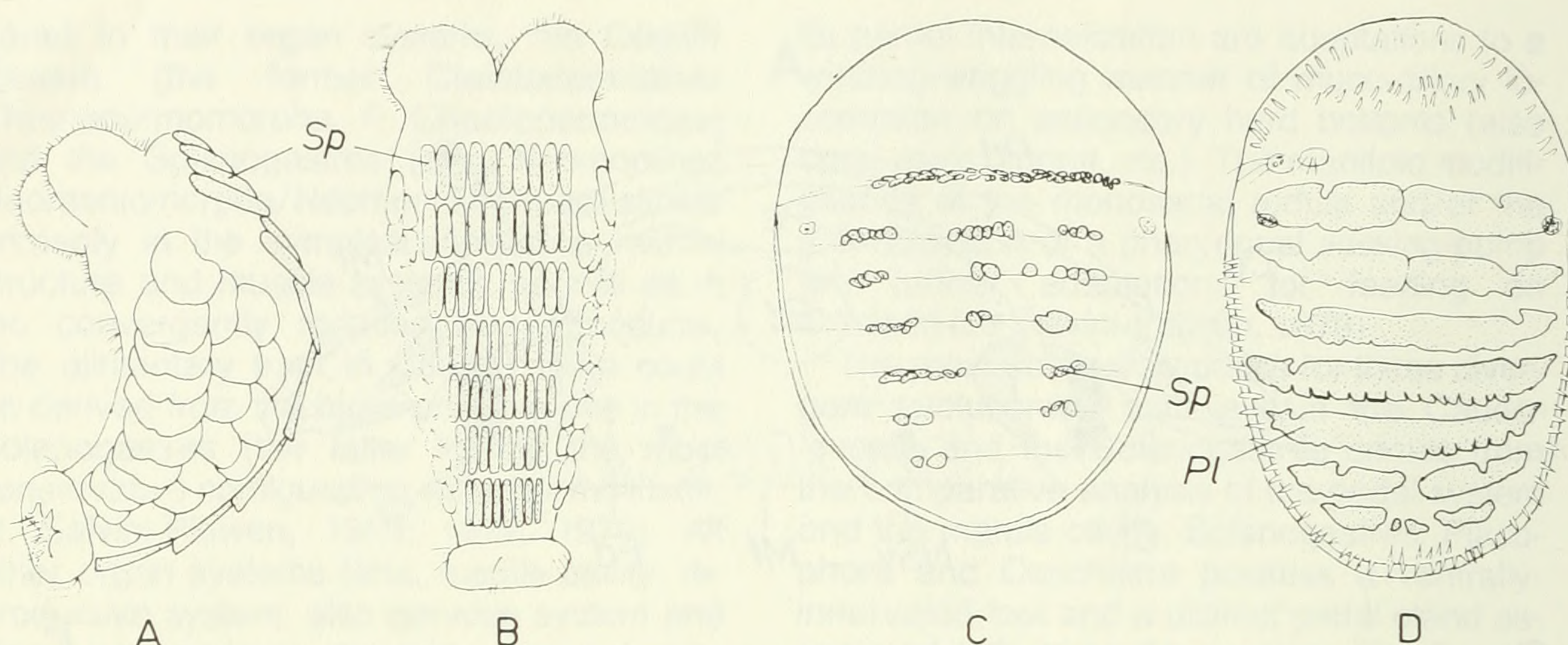


FIG. 2. Differentiation of the mantle cover in just metamorphosed individuals of *Nematomenia banyulensis* (Solenogastres; A lateral, B dorsal view) and of *Middendorffia caprearum* (Placophora; C and D two successive stages) (after Pruvot and Kowalevsky from Salvini-Plawen, 1972). *Pl* shell plates in formation through coalescence of the juxtaposed scaly bodies *Sp* arranged in seven transverse rows.

Plawen, 1968b, 1975) within the single order Chaetodermatida Simroth (emended by Smith, 1960).

Precisely defined by the term Solenogastres (Gegenbaur, 1878: 139; *solen* = tube, groove, and *gaster* = venter, 'belly'), these numerically predominant aplacophoran organisms with a ventrally-innervated foot narrowed to a groove persist as a distinct class; the unfamiliar terms Telobranchiata (Koren & Danielssen, 1877) and Ventroplicida (Boettger, 1955) hence can be disregarded. A comprehensive analysis of the 180 Recent species (Salvini-Plawen, 1978) brought about the establishment of four orders (Pholidoskepia, Neomeniomorpha, Sterrofustia, and Cavibelonia) within two higher levels of organization (supraorders Aplotegmentaria and Pachytegmentaria).

The long ignored investigation of aplacophoran molluscs, their seemingly small numbers, their lack of a shell, and their worm-like shape unfortunately led to a misunderstood interpretation until a few years ago in regarding them either as vaguely mollusk-like or as aberrant Mollusca. Only a few authorities (e.g. H. Hoffmann, C. R. Boettger), according to their general knowledge, took a neutral point of view independent of hypertrophic information on Conchifera and evaluated the molluscan organizations comparatively according to differentiated quality. As a consequence of the more recent organizational-evolutionary elucidations, neither the superficially similar appearance of Caudofoveata and Soleno-

gastres, nor their seemingly hidden manner of living in being exclusively distributed in marine habitats of greater depths can serve as arguments for conservative under-estimation: The taxon Aplacophora (Ihering, 1876) had to be abandoned, since it artificially unites two basically different, diphyletic evolutionary lines which merely coincide by some ancestral (symplesiomorphous) characters but by no single commonly-acquired (synapomorphous) property.

PLACOPHORA

In considering the (Poly-)Placophora, one condition has generally not been taken sufficiently into account, viz. the ontogenetic differentiation of initially only seven shell plates (cf. summary in Smith, 1966). That peculiarity is underlined by the predominant 'abnormality' in adults, i.e. the formation of only seven plates (cf. H. Hoffmann, 1929/30: 173; Taki, 1932). A further particularity is met within the Solenogastres, where the metamorphosed stage of *Nematomenia banyulensis* (a member of the most conservative Pholidoskepia) is provided dorsally with seven transverse rows of juxtaposed scaly bodies; this coincides exactly with an occasional condition in the Placophora (Fig. 2), where the formation of the plates results from the coalescence of calcareous granulations arranged in seven transverse rows.² Finally, the record of fossil Placophora with seven plates, described as

²"formation des plaques par la coalescence de granulations calcaires" (Kowalevsky, 1883: 33).

Septemchiton (Bergenhayn, 1955; Sanders, 1964), must be emphasized. This seven-plated condition shows that the placophoran stock originated in organisms which differentiated only seven primordial calcareous plates, presumably through coalescence of the formative anlagen (the isolated-intracellular centers of calcification) of juxtaposing bodies provided with a basal quinone-tanned organic layer ("cup"; cf. S. Hoffman, 1949; Beedham & Trueman, 1967, 1968; Carter & Aller, 1975); the same stock also gave rise to the Solenogastres. The Septemchitonida, therefore, are either the direct successors of that primitive stock, or they form an evolutionary line arising by paedomorphy. In either case, however, it appears necessary to separate the order Septemchitonida within a special subclass, for which the term Heptaplacota is proposed.

The comprehensive revision of the Placophora by Bergenhayn, (1930, 1955, 1960) included fossil as well as Recent members and resulted in a homogeneous system that is largely accepted (cf. Smith, 1960, Van Belle, 1975). With the separation of the Septemchitonida as a special subclass Heptaplacota, the main line constitutes the (hypothetical) Eoplacophora (Pilsbry, 1893; see Bergenhayn, 1955: 39), more or less identical with the subclass Loricata including Bergenhayn's orders Chelodida, Lepidopleurida, Ischnochitonida (= Chitonida), Acanthochitonida, and Afossochitonida³). Only the Chelodida are hence included with the supraorder Palaeoloricata and contrasted to the other orders = Neoloricata; the latter, however, do not form a monophyletic group but have, according to Bergenhayn (1960: 176), a diphyletic root within the Chelodida. The Neoloricata constitute therefore an artificial group to be avoided. Starobogatov & Sirenko (1975) discuss in a short article the classification within the Neoloricata and reclassify them in accepting the articulamentum-bearing orders Scanochitonida nov., Lepidopleurida including Bergenhayn's Afossochitonidae, and Chitonida including Ischnochitonina and Acanthochitonina; the dubious *Llandeilo-chiton* is omitted (cf. also Van Belle, 1975), and the Palaeoloricata anyway remain identical with the order Chelodida.

The first term given for the chitons as an independent group was that of Ducrotay-Blainville in 1819 as Polyplaxiphora; it was

amended in 1821 to Polyplacophora by Gray. It was, however, Ihering, (1876) who introduced the group in a comparative point of view with respect to the molluscs; accordingly his—also familiar, and even simpler—term Placophora may be preferred, even more so since there is no problem in confusing the group.

TRYBLIDIIDA AND BELLEROPHONTIDA: GALEROCONCHA

Early Cambrian univalve molluscs have long been a cause for scientific debate whether planispiral shells belong to untorted (exogastric) or torted (endogastric-gastropod) organization (cf. Runnegar & Jell, 1976; Berg-Madsen & Peel, 1978). Recent investigations (Rollins & Batten, 1968, and others) have shown that the exogastric tryblidiids already possessed a marked shell sinus, since *Sinuitopsis acutilira* (Hall) with its three pairs of symmetrical muscle scars, as well as other similarly organized species unequivocally must be regarded as untorted-exogastric. The sinus in *Sinuitopsis* therefore proves that this shell character (and even the shell slit) has been evolved adaptively long before gastropod torsion took place. Thus there is no further argument in favour of considering the Bellerophontida, provided with a sinus and/or shell-slit and with one symmetrically-arranged pair of dorsoventral muscle bundles (cf. Knight, 1947), as belonging to the gastropods; the sinus or slit merely demonstrates the symmetrical (paired) arrangement of the pallial organs (cf. also Fretter, 1969).

Pojeta & Runnegar (1976: 24 ff.) likewise discuss most arguments and come to the conclusion that the Bellerophontida as well as the Helcionellacea were untorted organisms with an exogastric shell (cf. also Runnegar & Jell, 1976). The symmetrical arrangement of one single pair of muscle scars in adults, however, might also be due to regulative migrations of the muscles during larval development (compare Scissurellidae, and cf. Crofts, 1937, 1955); but additional conditions refute the arguments of Knight (1947, 1952); Cox & Knight, (1960); Berg-Madsen & Peel (1978); and also Stasek (1972):

a) Gastropod torsion occurs in two phases, and loss of equilibrium in the pelagic larva after the first phase because of the heavier

³The suffix -ina generally designates a suborder, whereas for orders the ending -ida should be used (cf. also Starobogatov & Sirenko, 1975).

main bulk of the visceral mass at the left side automatically causes an asymmetry of the whole pallio-visceral complex of the larva including the covering shell: only the left set of pallial organs develops (cf. Fretter, 1969) and the shell becomes asymmetrical before (!) the second phase of torsion begins (cf. Crofts, 1937: 242 f, 259). Since that asymmetrical growth is independent of the (endogastric) coiling of the visceral hump, every shell of torted animals principally demonstrates an asymmetrical condition in the larvae (cf. Fretter & Graham, 1962: 447); this however, is not the case within the Bellerophontida.

b) The growth of a more coiled shell in the plantigrade stage of metamorphosing archaegastropods with differential regulative processes causes a posterior overweight (right side of the post-torsional visceral hump with shell) which is compensated by dextral helicoid growth and thus appears to be an indirectly-caused consequence of torsion. Planispiral coiling can therefore generally be considered as proof of an untorted condition (comp. also most Nautiloidea, Ammonoidea, etc.); only rarely is symmetry secondarily reached, e.g. in some exceptional gastropods such as *Caecum*, several Omalogyridae, and others.⁴)

c) Many operculum-bearing gastropods show some very distinct adaptive structures at the shell-aperture in relation to the respective operculum—in contrast to all known Bellerophontida with a more or less symmetrical, homogeneously formed and wholly regular, wide holostornous aperture. This coincides with the negative record of opercula in bellerophontid beds, indicating that the operculum is obviously an evolutionary attribute of the torted condition, the more since its functional secretion takes place asymmetrically (!) by glands at the post-torsional right side of the posterior pedal ectoderm (compare also Crofts, 1937: 240; 1955: 738).

Summing up earlier arguments (cf. Pojeta & Runnegar, 1976) and the above presented additional arguments, we may positively state that the majority of organisms assigned to the Bellerophontida were untorted animals with a planispiral, exogastric shell. Consequently they have to be separated from the torted Gastropoda and classified closer to the cup-

shaped tryblidiids, as already realized by Simroth (1904) and Wenz (1940) and as also discussed by Salvini-Plawen (1972: 272 f). Wenz classified the Tryblidiacea and Bellerophontacea together within the subclass Amphigastropoda, but without separation from the gastropods (the diagnostic definition of the latter, therefore, becoming inaccurate). Today there is no doubt that the Gastropoda are defined by torsion (and presence of an operculum), and that the untorted groups have to be arranged as a distinct class outside the gastropods. Hence, the term Galeroconcha may be suitable to include Tryblidiida and Bellerophontida, since 'Monoplacophora' is (as a synonym) unequivocally tied to the cap-shaped or orthoconic Tryblidiida (= Tryblidiacea Wenz)⁵ and contrasted to the Bellerophontida (= Bellerophontacea Wenz). The class Galeroconcha is defined to consist of fossil and Recent laterally-symmetrical and untorted Conchifera with a cap-shaped to (exogastrically) planispiral shell, devoid of a siphon and covering the whole body, and with symmetrically-paired dorsoventral muscle bundles which may be fused; it includes the two orders (subclasses) Tryblidiida (Monoplacophora) and Bellerophontida (Belleromorpha) (cf. Salvini-Plawen, 1972: 272).

Findings of Recent tryblidiids (*Neopilina*) have led not only to a reactivation of the annelid-theory (derivation of the molluscs from segmented coelomates) which has since been totally refuted by Boettger (1959), Vagvolgyi (1967), Salvini-Plawen (1968a, 1969, 1972), Stasek (1972), Trueman (1976) and others; it also resulted in an increased interest in the whole group, followed, however, by some taxonomic confusion and nomenclatorial misinterpretation (cf. Cesari & Guidastri, 1976; Berg-Madsen & Peel, 1978; Yochelson, 1978). On the one hand, there is a peculiar misuse of the taxon and term Monoplacophora (by Runnegar & Jell, 1976, even assigned to Knight, 1952); most obvious, however, is the trend toward a hypertrophical classification of the fossil genera and families (cf. Knight & Yochelson, 1958; Starobogatov, 1970; Golikov & Starobogatov, 1975, and others) which does not correspond to the degree of morphological differences that are present. Similarly, neither the classification of

⁴The protoconchae in Tryblidiina are mostly bulbous and uncoiled (cf. Menzies, 1968: 7); the slight larval (pretorsional-) dextral coiling in *Neopilina galathea* therefore has nothing to do with the helicoid coiling in plantigrade (postlarval) gastropods.

⁵"man könne die Tryblidiacea geradezu als Monoplacophora bezeichnen" (Wenz, 1940: 5, citing Odhner); compare also Yochelson, 1978.

TABLE 1. Classification of the Galeroconcha.

Classis GALEROCONCHA nov. (pro "Amphigastropoda" Simroth in Wenz, 1940)	
Ordo	Tryblidiida Wenz, 1938 (= Monoplacophora Odhner in Wenz, 1940)
	Subordo Tryblidiina Pilsbry, 1899
	Subordo Cyrtionellina Knight & Yochelson, 1958
	Subordo Archinacellina Knight, 1956
Ordo	Bellerophontida Ulrich & Scofield, 1897 (= Belleromorpha Naef, 1911)
	Subordo Sinuitopsina Starobogatov, 1970
	Subordo Helcionellina Wenz, 1938
	Subordo Bellerophontina McCoy, 1851

some more closely related genera or families in orders, nor a subdivision of the newly defined class Galeroconcha into two subclasses appears to be adequate and hence justified; as evidenced by Yochelson (1967), Pojeta & Runnegar (1976), Runnegar & Jell (1976), or Berg-Madsen & Peel (1978), the morphological variation does not exceed the level of two orders.

With the new concept of Galeroconcha, the classification of Horný (1965) can also be abandoned: his Tergomya are identical with the Tryblidiina (see Table 1), and his Cyclomya are partly incorporated within the Bellerophontida (cf. also Pojeta & Runnegar, 1976; Runnegar & Jell, 1976). To avoid further confusion, we retain the general outline of both orders as presented by Knight & Yochelson (1960), Yochelson (1967), and Berg-Madsen & Peel (1978), which is predominantly based upon the configuration of the concha. Some uncertainty remains only with a few cyrtconic members, and the position of the Archinacellina as well as Helcionellina still needs confirmation (cf. Knight & Yochelson, 1960; Yochelson et al. 1973; Golikov & Starobogatov, 1975; Pojeta & Runnegar, 1976; Yochelson, 1978); the Multifariida Byalyi can be recognized as a separate family within the Sinuitopsina, and the Kirengellida Rozov obviously belong to the Tryblidiina close to *Scenella* (cf. Runnegar & Jell, 1976; Berg-Madsen & Peel, 1978).

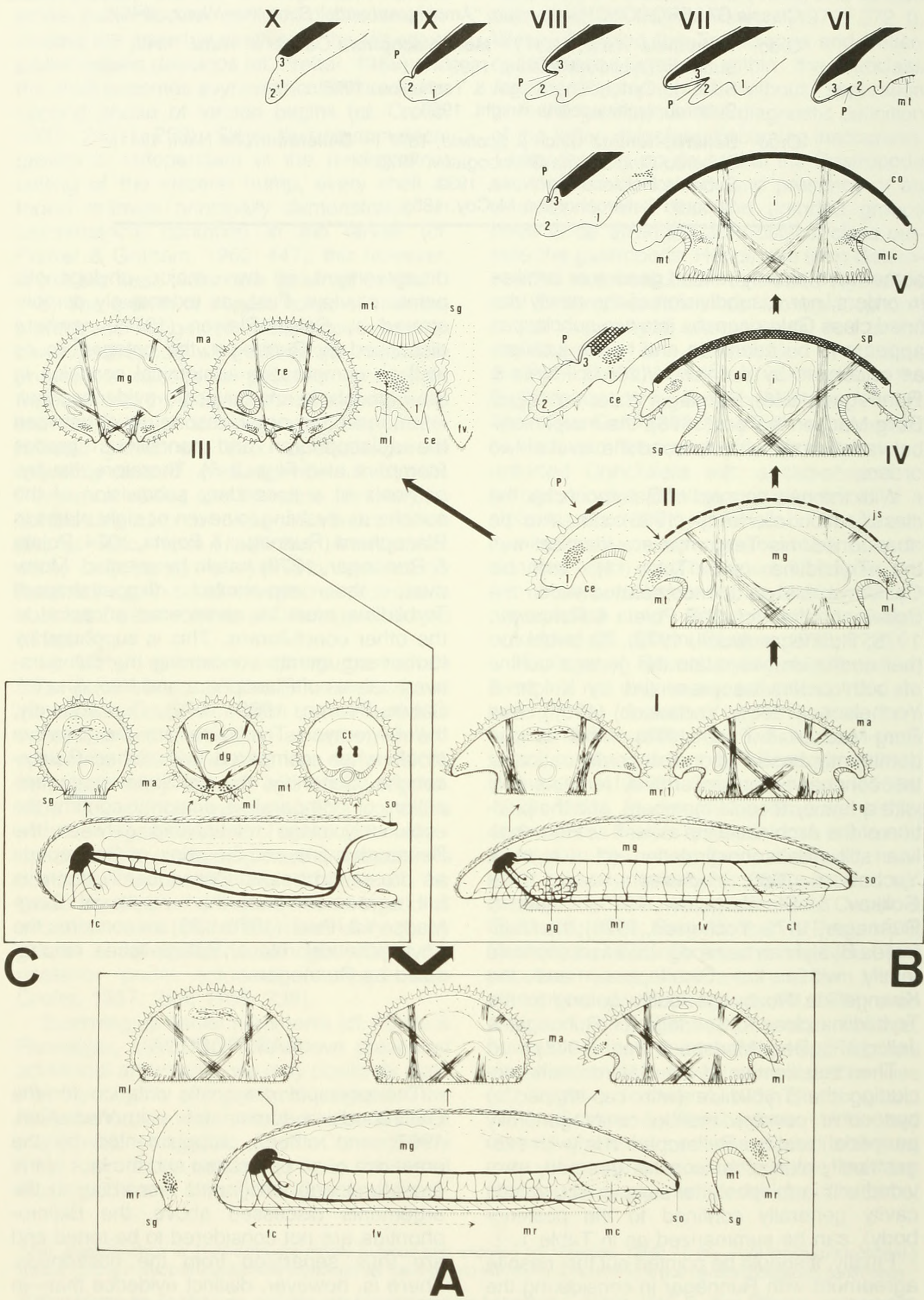
The classification of the Galeroconcha, including the Tryblidiida (with cap-shaped to cyrtconic concha, mantle cavity generally peripedal) and the Bellerophontida (with exogastrically-planispiral concha generally provided with a midposterior sinus or slit, mantle cavity generally confined to the posterior body), can be summarized as in Table 1.

Finally, it should be pointed out that despite agreement with Runnegar in considering the Bellerophontida to be untorted organisms and hence with an exogastric visceral sac, there is

disagreement in two major phylogenetic points of view. First, as extensively demonstrated by Salvini-Plawen (1972), nowhere discussed by Runnegar, the ontogenetic as well as comparative-anatomical condition in the Placophora unequivocally evidences their interconnecting organizational level between the aplacophoran and conchiferan grades (compare also Figs. 3–5). Therefore, the hypothesis of a secondary subdivision of the concha as evolving to seven or eight plates in Placophora (Runnegar & Pojeta, 1974; Pojeta & Runnegar, 1976) has to be rejected. Moreover, the cap-shelled (limpet-shaped) Tryblidiina must be considered ancestral to the other conchiferans. This is supported by further arguments concerning the comparative analysis of Placophora and *Neopilina* (cf. Salvini-Plawen, 1969; 1972). Consequently, the tergomyan Tryblidiina are the primitive stock when compared with other Galeroconcha. Secondly, the functional synorganization of comparative anatomy confirm the evolutively close relationship between the Bellerophontina and the origin of Gastropoda as presented below. Consequently, there is full agreement with the critique of Berg-Madsen & Peel (1978: 123) as concerns the phylogenetical role of Pelagiellacea emphasized by Runnegar.

GASTROPODA

The principal diagnostic criterion for the Gastropoda is torsion (cf. also Yochelson, 1967, and others), supplemented by the presence of an operculum and the lack of the (post-torsional) left gonad. According to the arguments discussed above, the Bellerophontida are not considered to be torted and are thus separated from the gastropods. There is, however, distinct evidence that—in contrast to Runnegar & Jell (1976) or Runnegar & Pojeta (1974)—some Bellerophontina



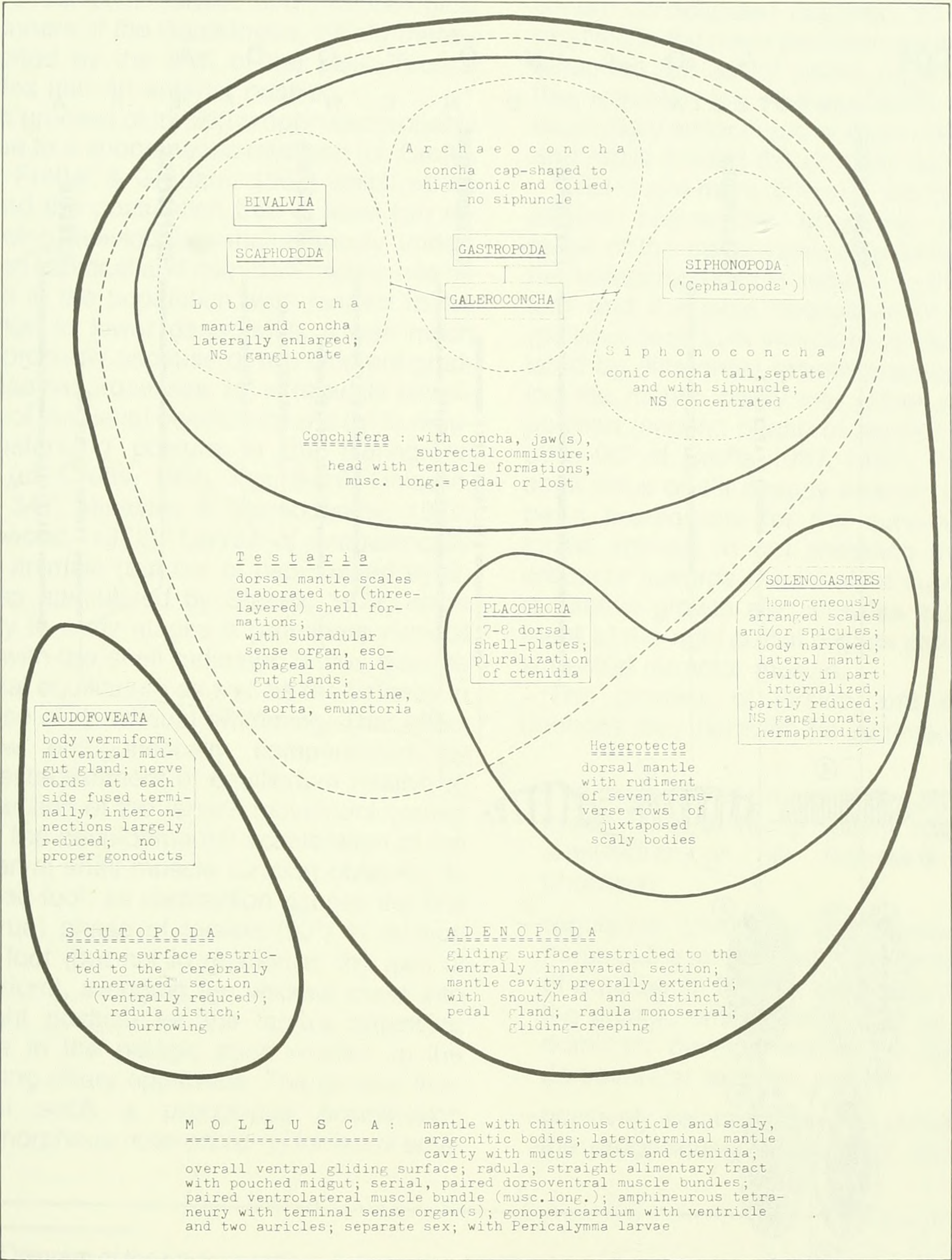


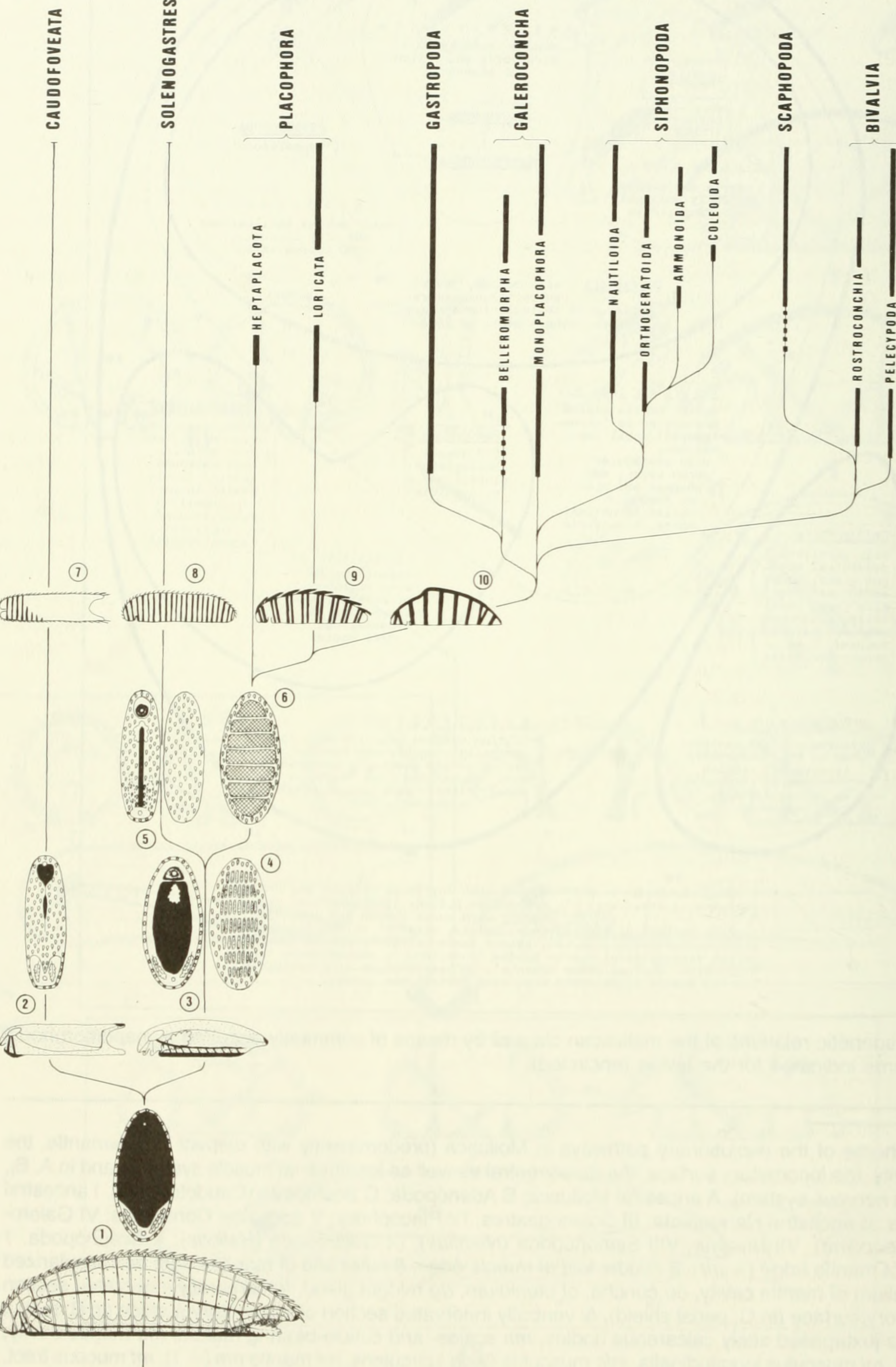
FIG. 4. Anagenetic relations of the molluscan classes by means of commonly-acquired (synapomorphous) main features indicated for the levels (encircled).

FIG. 3. Scheme of the evolutionary pathways in Mollusca (predominantly with respect to the mantle, the mantle cavity, the locomotory surface, the dorsoventral as well as longitudinal muscle systems, and in A, B₁, C the main nervous system). A ancestral Mollusca; B Adenopoda; C Scutopoda (Caudofoveata). I ancestral Adenopoda; II ancestral Heterotecta; III Solenogastres; IV Placophora; V ancestral Conchifera; VI Galeroconcha (*Neopilina*); VII Bivalvia; VIII Siphonopoda (*Nautilus*); IX Gastropoda (*Halotis*); X Scaphopoda. 1 inner fold of mantle edge (= *mr*), 2 middle fold of mantle edge, 3 outer fold of mantle edge; *ce* cuticularized cilia-epithelium of mantle cavity, *co* concha, *ct* ctenidium, *dg* midgut gland, *fc* cerebrally innervated section of locomotory surface (in C: pedal shield), *fv* ventrally innervated section of locomotory surface (in B: foot), *i* intestine, *js* juxtaposed scaly calcareous bodies, *ma* scales- and cuticle-bearing mantle, *mc* mantle cavity, *mg* midgut, *ml* musculus longitudinalis, *m/c* musculus (long.) circularis, *mr* mantle rim (= 1), *mt* mucous tract, *p* periostracal groove, *pg* pedal gland, *re* rectum, *sg* sole glands, *so* terminal sense organ, *sp* shell plate.

SCUTOPODA

A D E N O P O D A

HETEROTECTA C O N C H I F E R A



were direct phylogenetic and morphological forerunners of the Gastropoda, initially merely separated by the shift of the pallio-visceral complex into an anterior position.

This process of torsion proper was probably not due to a spontaneous mutation (cf. Crofts, 1955; Fretter & Graham, 1962) which would demand the postulation that at least two reproducing individuals simultaneously underwent an identical and dominant mutation to be spread in the population; with respect to the condition in lower gastropods, it was much more probably because of two different gradual adaptive processes, (a) to regulate stabilization of the larval equilibrium and (b) to regulate balancing posture in the plantigrade stage (cf. Crofts, 1955: figs. 9–10; Ghiselin, 1966: 347; Minichev & Starobogatov, 1972; Underwood, 1972). Larvae of exogastrically coiled animals (but not of cap-shaped tryblidiids as speculated by Stasek, 1972) show already in early stages a prominent visceral mass with the shell rudiment; it thus disturbs the axial equilibrium as well as the balance in the case of directional swimming. That effect is now ontogenetically compensated by the reestablishment of equilibrium relative to the direction of the larva's movement carried out by the developmental acceleration of the right larval shell muscle running obliquely to the head-foot: its contraction causes the first (and true) phase of torsion (90°) in relation to the foot (but not in relation to the axis of equilibrium), swinging the visceral mass into the right position for the larva's balancing posture in the pelagic zone relative to the propelling ciliary apparatus. The genetic fixation of such a precocious acceleration (tachymorphous heterochrony) for larval equilibrium

consolidated torsion of 90° ; it directly resulted in the mere development of the (post-torsional) left set of pallial organs including the retractor (cf. Fretter, 1969), since the respiratory water currents enter (left-) frontally and leave toward the (frontal) right.

That quasi-monotocardian condition is not altered before the beginning plantigrade stage of the metamorphosing larva, in which the balancing posture relative to the substratum and the axial divergence of about 90° (palliovisceral bulk versus body axis) is regulated by differential growth processes—shifting the mantle cavity into rather an anterior position (second phase of approximately another 90° ; cf. Crofts, 1937, 1955). The mantle/shell sinus or slit already existing appears to be a prerequisite for the survival of such tortosed animals in not shedding their waste products towards the inhalant currents. The regulative growth also includes the development of the right pallial organs and right dorsoventral retractor muscle.

The process of torsion and its consequences may herewith be summarized as:

- The pretorsional presence of a planispirally coiled visceral hump with a midposterior shell-sinus or slit (compare *Bellerophon*);
- regulative shifting of the heavy visceral mass of the larvae towards an arrangement of equilibrium for their balancing posture in the pelagic environment, and the adaptive dominant development of the right larval, dorsoventral retractor muscle;
- positively selective, genetic stabilization of the precociously accelerated development

FIG. 5. Diagram of the phylogenetic radiation of the Mollusca (black bars indicate fossil records; time-scale in millions of years, logarithmic). (1) Hypothetical archi-mollusc (main organization, and ventral view) with overall ventral gliding surface (black), postero-lateral mantle cavity, scale-bearing mantle, straight midgut pouched laterally, serial dorsoventral muscle bundles, gonopericardial system, and main nervous system with terminal sense organ(s). (2) Evolutionary branch of burrowing Scutopoda (lateral and ventral) with cerebrally-innervated section of locomotory surface (= pedal shield, black) and reduction of its ventrally-innervated section. (3) Evolutionary branch of gliding-creeping Adenopoda (lateral and ventral) with ventrally-innervated section of locomotory surface (= foot, black) including the pedal gland, with rudiment of head, and with peripedal-preoral mantle cavity. (4) Level of primitive Heterotecta (dorsal view), dorsal mantle with seven transverse rows of juxtaposed scaly bodies. (5) Level of Solenogastres (ventral and dorsal) with narrowed body and foot, mantle cavity reduced to preoral sensory pit (atrial sense organ) and to internal tubes (spawning ducts); adult mantle cover altered again to homogeneous arrangement of scales. (6) Level of early Placophora (= Heptaplacota; dorsal view) with consolidation of juxtaposed scaly bodies to seven shell plates. (7) Regressive dorsoventral musculature in Caudofoveata. (8) Serial arrangement of dorsoventral musculature in Solenogastres; compare (1). (9) Serial arrangement of dorsoventral musculature in recent Placophora, concentrated according to the eight shell plates ($8 \times 2 = 16$). (10) Primitive Conchifera with further concentration of the placophoran dorsoventral musculature (9) according to the homogeneous concha (see *Neopilina*).

- of that right larval retractor: establishment of the first phase of torsion (90°);
- the predominant development of the pretorsional right (or: the retarded development of the pretorsional left) pallial organs due to respiratory currents (quasi-monotocardian stage);
- regulation of the divergent axial and balance conditions between the visceral hump and the head-foot respective to plantigrade movement by differential growth processes in metamorphosing animals: second phase of torsion⁶ of approximately another 90° ; this regulation includes and is combined with
- the development of the second (posttorsional right) set of pallial organs including the retractor muscle, the mantle/shell sinus/slit enabling the now paired inhalant respiratory current to be directed symmetrically from the latero-frontal areas towards the antero-medio-dorsal area.

Starting from such a possible torsion process of two different adaptive phases which fully corresponds to the developmental patterns, Recent gastropods appear to belong to different lines having achieved pallial asymmetry independently (water currents, ctenidia, etc.):

- 1) The most conservative stock—also with respect to shell structure (cf. MacClintock, 1967)—possesses paired pallial organs (Zeugobranchia) and paired dorsoventral retractor bundles in the adults: Scissurellidae, Fissurellidae, Haliotidae;
- 2) The predominance of the posttorsional right retractor muscle and helicoid coiling result in the loss of the left retractor muscle: Pleurotomariidae;
- 3) The hypertrophy of the right retractor muscle and helicoid coiling leads to the suppression of the left retractor as well as to the right set of pallial organs: Trochacea;
- 4) The reason for the change in water currents and the abandonment of the right set of pallial organs remains enigmatic (cf. Yonge, 1947: 493, Golikov & Starobogatov, 1975: 190 f), since both retractor muscles are obviously retained and are united posteriorly (cf. Smith, 1935: 122 & fig. 25 with Crofts, 1955: 730 & fig. 19; but compare also Dodd, 1957): Patellacea;
- 5) The hypertrophy of the (posttorsional) right

excretory-genital duct causes the pronounced asymmetry with the loss of the right set of pallial organs: Neritacea (paired retractor muscles retained);

- 6) The asymmetry of the pallial organs is due to a paedomorphous retention of the larval asymmetry (first phase of torsion, 90°) prior to regulation in the plantigrade stage. Owing to a long-lasting, planktotrophic larval life, the development of the right pallial organs as well as of the right retractor was more and more retarded; the period of formative potency to regulate the symmetry of the pallial organs was missed and the potency finally lost, so that the larval 'quasi-monotocardian' condition was preserved also in the post-metamorphic stage: Monotocardia, Pulmonata, Gymnomorpha, Opisthobranchia. The second phase of torsion during the early plantigrade stage thus merely comprises the differential growth to regulate the condition of balance and axes, but not the symmetrization of the pallial organs; occasional atavistic conditions may occur (e.g. paired retractor muscles in *Rissoella*, *Lamellaria*, *Trivia*, *Velutina*, or the larvae of *Acteon*; cf. Fretter & Graham, 1962; Bebbington & Thompson, 1968).

Among these lines with differently caused asymmetry, in accordance with other characters (cf. Yonge, 1947; Cox, 1960a) the groups (1) and (2) form one branch, as do the more advanced Trochacea (3); all three lines, however, are characterized by the predominance of the (posttorsional) right retractor muscle, and they retain the right excretory organ. The latter character is also maintained in the Patellacea (4) which, however, have a special organization, combining certain conservative traits with advanced ones, unlike other archaeogastropods (cf. Golikov & Starobogatov, 1975): Thus the odontophore and the complexity of the radula musculature may be a conservative character (cf. Graham, 1964: 326; 1973: 343), as the ctenidium appears to be; in contrast, the rudimental coiling of the shell without sinus or slit together with other characters point to an advanced level, at least adaptively removed from the common origin as far as the Trochacea are concerned, but with special properties.—On the other hand, the Neritacea (5) as well as all other

⁶It must be pointed out that neither this second phase nor the 'detorsion' in Opisthobranchia and Gymnomorpha are true rotation processes, but are due to regulative growth processes (cf. also Brace, 1977).

(monophyletic ?) gastropods (6) show the left excretory organ retained; in the Monotocardia, etc., the loss of the right set, however, obviously is due to an inhibitory discontinuation during development (abandonment of the regulative symmetrization in the pallial organs), whereas in the Neritacea a special condition of the reproductive system shows quite different evolutionary pathways.

Additionally, both the Neritacea and Patelacea are characterized by a conservative morphology of their ctenidium: In contrast to Yonge (1947: 495 ff) we cannot regard these organs as derived from a condition almost identical to that in zeugobranch gastropods. The merely basal attachment of the ctenidium, its lack of skeletal rods, as well as its short and stoutish lamellae, these characters rather prove a primitive, i.e. conservatively retained condition when compared with the ctenidia in Caudofoveata, Placophora, and also *Neopilina*; the same holds good even for the Valvatacea. Thus, also in this respect, both groups appear to be early offshoots from the common gastropod stock, not yet having undergone in their ctenidia those alternations typical for the main lines (the skeletal rods, for example, are supports for mechanical needs, being analogous not only to those in Siphonopoda = Cephalopoda but also in Bivalvia).

Summing up the evolutionary pathways within early gastropods (cf. also Cox, 1960a; Golikov & Starobogatov, 1975), there appear to exist two main lines (1–3) and (6), as well as two early side-branches (4) and (5). In accordance with Yonge (1947) and Golikov & Starobogatov (1975), respectively, both the latter groups have to be admitted a more separate status⁷ within the Archaeogastropoda. Hence, the order Archaeogastropoda would be classified adequately in three suborders, viz. the Vetigastropoda (nov.), the Docoglossa = Patellina, and the Neritopsina; the new taxon Vetigastropoda (no former term available) is defined by the dominant presence of the (posttorsional) right dorsoventral retractor muscle as well as the right excretory organ and by bilamellate ctenidia with skeletal rods, and it includes the Macluritoidea, Pleurotomarioidea, Cocculinoidea, Trochoidea, and Murchisonioidea (?) (cf. Cox, 1960; Cox & Knight, 1960). Despite the emphasis of

Golikov & Starobogatov (1975), the other gastropods (line 6 above)—even if possibly polyphyletic—might better be classified in Caenogastropoda (including Mesogastropoda and Neogastropoda), Pulmonata, Gymnomorpha, and Opisthobranchia.

As is generally accepted and repeatedly evidenced by developmental patterns, the groups of Opisthobranchia underwent convergent, gradual so-called detorsion, thus secondarily regaining euthyneury in different degrees by regulative differential growth (cf. Brace, 1977). This is, however, not the case in the still “prosobranch” Pulmonata, the so-called euthyneury of which results from the extreme concentration of the nervous system. Hence, the Euthyneura are not a monophyletic group (cf. also Minichev, 1972) and the pair of taxa Streptoneura/Euthyneura should be dropped. Within the Pulmonata, in contrast to earlier opinion (cf. Boettger, 1954), there are three orders to be recognized (Archaeopulmonata, Basommatophora, Stylommato-phora). As accurately elaborated by Morton (1955) and Van Mol (1967), the Ellobiidae and Otinidae have to be separated as a special group, the basic Archaeopulmonata; that classification has already been accepted in the textbook by Götting (1974).

The Opisthobranchia, the monophyly of which—rooted in early, sediment-ploughing cephalaspideans (cf. Brace, 1977)—is becoming more and more weakened (cf. Robertson, 1974), are variously classified in five to nine or even more orders (cf. Morton, 1963, etc.); an arrangement in seven orders stands—according to recent knowledge—critical estimation: 1) The Pyramidellimorpha. 2) The Cephalaspidea, divided into the main group Bullomorpha and into the Thecosomata as suborders (cf. Boettger, 1954); herein the Philinoglossoidea and Acochlidoidea simply constitute two differently evolved bullo-morphan family groups (but no separate suborders or even orders; cf. Salvini-Plawen, 1973b). 3) The Anaspidea, divided into Aplysiomorpha and Gymnosomata (suborders). 4) The Saccoglossa (Sacoglossa emend., Ascoglossa, Monostichoglossa). 5) The Notaspidea. 6) The Nudibranchia, con-

⁷The separation of the Neritacea as an order distinct from the Archaeogastropoda appears not to be justified (as done by Yonge, 1947; Morton & Yonge, 1964; Franc, 1968), nor is the arrangement of the Patelacea as Cyclobranchia in contrast to Scutobranchia and Pectinibranchia (as done by Golikov & Starobogatov, 1975). Moreover, there is no organizational justification to hypertrophize the taxonomic rank of more or less constant family groups (as do Cox & Knight, 1960 or Golikov & Starobogatov, 1975).

fined to the suborders Dendronotina, Arminina, and Aeolidiina. 7) The Anthobranchia (= Doridacea) which are comparative-anatomically well-separated from the former group(s) (cf. Ghiselin, 1965; Minichev, 1970; Brace, 1977: 51 f).

The systematically greatly contested, shell-less Onchidiacea and Soleolifera (Veronicellacea) doubtlessly constitute a natural relationship (cf. H. Hoffmann, 1925; Van Mol, 1967). The more conservative Onchidiidae still retain a modified pallial cavity (the "cloaca"), and the so-called lung-cavity clearly represents an additional, new formation, not derivable from tissues of the pallial cavity (cf. Fretter, 1943, also H. Hoffmann, 1925: 324–326). Other characters ostensibly identical to those in Pulmonata (eye-tentacles, lamellate excretory organ, innervation of the penis, etc.) likewise have been demonstrated to be analogous (cf. Plate, 1893; Boettger, 1952; Morton, 1955; Van Mol, 1967; Salvini-Plawen, 1970a; Minichev, 1975; Starobogatov, 1976). Whereas some features (procerebrum and cerebral glands, paired albumen gland) point to a close root with the Archaeopulmonata (or simply to an identical environment of origin?), the nervous system combined with the mutual position of the mantle cavity and the likewise detorted female genital opening clearly demonstrate a pre-pulmonate offshot; further characters, i.e. the so-called detorsion, vacuolated cells (so-called larval kidneys), and so-called anal kidneys, in their turn evidence a distinct relation with (Prosobranchia and) primitive Opisthobranchia. Accordingly, the group cannot be included as an order (variously named Ditremata, Teletremata, Systelommatophora, or Gymnophila; cf. Salvini-Plawen, 1970a) into one of the existing subclasses; it serves to represent an evolutionary line (subclass) per se separate from the Opisthobranchia as well as from Pulmonata (cf. Stringer, 1963, Morton, 1963; Salvini-Plawen, 1970a; Minichev, 1975). With the inclusion of the formerly enigmatic Rhodopacea, Salvini-Plawen, (1970a) proposed the term Gymnomorpha for the proper unit of the three reclassified groups (the—later—term Opisthopneumona chosen by Minichev, 1975, is a misnomer, since neither the Rhodopidae, nor the Rathousiidae or several Onchidiidae are opisthopneumonous). In accordance with Minichev (1975), the three groups within the Gymnomorpha may tentatively be classified as orders.

BIVALVIA

A most confusing situation is found within the bivalves as concerns the supraspecific classification. The many different systems which were formerly and/or are actually in use strikingly demonstrate the precarious systematic situation. The lasting uncertainty of relationships between family groups is once more indicated by the over-estimation of certain characters (cf. Nevesskaya et al., 1971; Pojeta, 1971, and others) which in no way correspond to actual comparative-anatomical differences when compared with other molluscan groups. Most of these discrepancies are due to there being knowledge of only one or a few special characters, and that little effort has been made to judge pathways from the point of view of functionally synorganized alteration; more recent investigation (cf. Yonge, 1953, 1962; Stanley, 1972) have demonstrated the high degree of convergences and the need for thorough comparative analysis.

The adaptation of some tryblidiid predecessors of the Bivalvia to soft bottoms, correlated with the elaboration of inherited cerebrally-innervated labial organs (cf. Drew, 1901: 353, 373; Allen & Sanders, 1969; Lemche & Wingstrand, 1959: 23 f), simultaneously resulted in the narrowing of the foot and the lateral compression of the body. The reduction of the buccal mass clearly points to the probability that mucociliary feeding by the labial palps gradually replaced the original mode of feeding, since ctenidian filter-feeding per se would not seem suitable to replace radular feeding at that early level of evolution (although the latter is adequate for occasional transport of food; cf. Stasek, 1965). Thus, the ancestors of all Recent bivalves might have been provided with enlarged labial flaps (palps) singling out microorganisms and organic material from the currents entering from the anterior during ploughing in the sediment. That evolutionary level may be represented by the extinct Rostroconchia. The bent condition of the mid-dorsal mantle area finally led to the partition of the shell gland in an early ontogenetical stage (comp. Prodissoconch I) and resulted in the development of the two valves as well as in their subsequent functional equipment (adductors, hinge).

The evolutionary differentiation found in (Recent) bivalves is basically expressed by four developmental lines: two lines of the

Protobranchia s. l., the Lamellibranchia s. str., and the Septibranchia s. str. The protobranch groups retained the primitive state of bivalve organization with an anterior inhalent current, with pallial mucous tracts (hypobranchial gland), with predominant mucus-ciliary feeding by means of the labial flaps, with only a few orifices of the midgut glands, and with slightly modified ctenidia (cf. Yonge, 1939, 1959; Owen, 1959; Purchon, 1959). The ctenidiobranch and ctenodont Nuculacea retained further those primitive adult characters and larval features (Pericalymma-larva; cf. Salvini-Plawen, 1973a), but improved the labial flaps for deposit-feeding by adapting specialized palps with a tentacular appendage. On the other hand, the Solemyacea are adapted for filter-feeding of suspended material (cf. Yonge, 1953, 1959; Allen & Sanders, 1969) with respectively enlarged, foliate (plain-faced) ctenidia and with simplified labial palps.

The most successful line includes the lamellibranch bivalves (sensu Yonge, 1959, 1962; Purchon, 1959; Morton, 1963), characterized by the successive alteration of the ctenidia to filter-feeding. It may be presumed that the origin of those (monophyletic ?) groups occurred by invading the littoral (primary hard bottoms) characterized by variation of salinity (tidal zone): Both the paedomorphous retention of the byssus (cf. Yonge, 1962) and the development of protonephridia (not existing in all other molluscs except limnic gastropods; cf. Salvini-Plawen, 1969, 1972: 287 f & 353) positively support that probability (cf. also Stanley, 1972), as does the thorough adaptation from deposit- to filter-feeding itself. Rudimentarily present in ctenidiobranch bivalves (cf. Stasek, 1965), the enlargement of the gills by elongation of the axis and the laterally connected as well as ventrally-bent multiplied lamellae resulted in the filibranch level of organization; further specialization along that adaptive line finally led to the eulamellibranch condition. Especially that advanced level includes a high radiation of specialized groups which underwent two predominant, polyphyletic trends: the byssal attachment gave rise to different anisomyarian and monomyarian conditions in epifaunal forms, whereas the preference of (primary or secondary) infaunal habits resulted in the fusion of the mantle edges and the formation of siphons (cf. Yonge, 1953, 1962; Morton, 1963; Kauffman, 1969; Stanley, 1972); that radiation is also obvious

in the different types of hinge-dentition (cf. Newell, 1965; Nevesskaya et al., 1971), some of which likewise might be polyphyletic as, e.g. the taxodont type (cf. Pojeta & Runnegar, 1974).

A special situation is found in the septibranch condition. The investigations of Nakazima (1967), of Allen & Turner (1974), and of Bernard (1974) convincingly demonstrate that the Verticordiacea principally belong to the Anomalodesmata (= Desmodonta), the lamellibranch gills of which, however, are gradually replaced by their own lateral attachment-membranes increasingly forming a septum; as in the case of the ctenidia of other bivalves, that septum is also innervated by the visceral ganglion. In contrast to that condition, the septum in the Poromyacea and Cuspidariacea is innervated by the cerebral ganglion (cf. Bernard, 1974: 5, 18), which proves it not to be homologous with the verticordiacean septum. There are no vestiges of ctenidia in Cuspidariacea-Poromyacea and the origin of their septum is obscure. Purchon (1956, 1963; cf. also Nevesskaya et al., 1971) emphasized the unity of the septibranch stomach (including Verticordiacea: Gastrodeuteia) and its possible relationship to the Protobranchia (Gastroproteia). The analysis of the Verticordiidae demonstrates, however, that such characters of the alimentary canal are obviously in close correlation with the food (cf. Allen & Turner, 1974: 516 f), and their reliance on phylogenetic patterns is dubious. Hence, the structural relation of Cuspidariacea-Poromyacea to the Protobranchia with respect to the stomach becomes questionable, as it does so concerning most other (generally polyphyletic) characters; up to now there is no synorganized character confirming a closer relationship either to the protobranchs s. l. or to the lamellibranchs s. str.

In transferring the evolutionary pathways outlined above to a systematic arrangement, there is clear evidence that the bivalves should be subdivided into four major taxa, i.e. the two protobranch groups, the lamellibranchs s. str., and the septibranchs s. str.; this coincides with the paleontologic situation underlined by Newell (1969: 212 ff), that the Protobranchia s. l. are not a homogeneous group and can be united no longer within a single taxon. In contrast to the polyphyletic radiation within the lamellibranch line (s. str.), the gill structure reflects not only the levels of organization, but also major, synorganizationally monophyletic groups; hence the gills prove to

TABLE 2. Classification of the Bivalvia.

Classis BIVALVIA Linné, 1758	
I. Subclassis PELECYPODA Goldfusz, 1820	
1. Superordo Ctenidiobranchia nov. (= Palaeotaxodonta Korobkov, 1954)	
Ordo Nuculida Dall, 1889 (= Ctenodonta Dechaseaux, 1952, in Nevesskaya et al., 1971)	
2. Superordo Palaeobranchia Iredale, 1939 (= Cryptodonta Neumayr, 1883, in Newell, 1965)	
Ordo Solemyida Dall, 1889 (= Lipodonta Iredale, 1939)	
Ordo Praecardiida Newell, 1965	
3. Superordo Autobranchia Nevesskaya et al., 1971 (ex Autolamellibranchia Grobben, 1894)	
Ordo Pteriomorpha Beurlen, 1944 (= Filibranchia Pelseneer, 1889, plus Pseudolamellibranchia Pelseneer, 1889)	
Subordo Mytilina Rafinesque, 1815 (= Isofilibranchia Iredale, 1939)	
Subordo Arcina Stoliczka, 1871 (= Eutaxodonta Grobben, 1892 = Pseudectenodonta Dechaseaux, 1952 = Neotaxodonta Korobkov, 1954)	
Subordo Pteriina Newell, 1965	
Superfamilia Pterioidea Newell, 1965 (incl. Pinnoidea)	
Superfamilia Limoidea D'Orbigny, 1846	
Superfamilia Ostreoidea Ferussac, 1882	
Superfamilia Pectinoidea Adams & Adams, 1857	
Ordo Palaeoheterodonta Newell, 1965	
Subordo Lyrodesmatina Scarlato & Starobogatov, 1971	
Subordo Trigoniina Dall, 1889	
Subordo Unionina Stoliczka, 1871	
Ordo Heterodonta Neumayr, 1883	
Subordo Venerina Adams & Adams, 1856	
Subordo Myina Stoliczka, 1870 (= Adapedonta Cossmann & Peyrot, 1909)	
Ordo Anomalodesmata Dall, 1889	
Subordo Pholadomyina Newell, 1965 (incl. Verticordioidea Stoliczka)	
4. Superordo Septibranchia Pelseneer, 1888/1906	
Ordo Poromyida Ridewood, 1903	
Superfamilia Poromyoidea Dall, 1886	
Superfamilia Cuspidarioidea Dall, 1886	
II. Subclassis ROSTROCONCHIA Cox, 1960	
Ordo Ribeiriida Kobayashi, 1933	
Ordo Ischyriniida Pojeta & Runnegar, 1976	
Ordo Conocardiida Neumayr, 1891	

be the most adequate single character reflecting evolutionary pathways and may well serve as superordinal taxobases. The difficulties arise, however, with the classification within the possibly polyphyletic lamellibranch group (s. str.) since, according to the frequent convergences, an undisputed natural grouping has not yet convincingly been presented (cf. e.g. Cox, 1960b; Morton, 1963; Newell, 1965, 1969; Nevesskaya et al., 1971; Pojeta, 1971, 1975, and others). At the present state of our knowledge, the most adequate arrangement of its groups and of the hinged bivalves in

general appears to be the classification⁸ as summarized in Table 2.

Pojeta et al. (1972) elevated the former Conocardioidea (Bivalvia) to a separate class Rostroconchia Cox,⁹ characterized by a univalved protoconch and a bivalved concha without ligament, hinge teeth, and adductor muscles; subsequently (Runnegar & Pojeta, 1974) enlarged by the Ribeiroidea (formerly Crustacea-Conchostraca), that group in any case ranges very close to the Bivalvia, and may represent a more primitive evolutionary level of bivalve organization. We doubt, how-

⁸With respect to the largely uniform general organization of the Bivalvia, the four main groups of Pelecypoda should be ranked as superorders (but not as subclasses; cf. also Nevesskaya et al., 1971: 155).
⁹Authorship of Rostroconchia must be assigned to Cox (1960b), but not to Pojeta et al. (1972), since there is only elevation of rank without change of contents. Similarly, the term Caudofoveata remains assigned to Boettger (1955) and not to Salvini-Plawen (1967) who elevated the group to the status of an independent class.

Nautiloida sensu lato (cf. Ihering, 1881; H. Hoffmann, 1937; Flower, 1955; Lehmann, 1967b; Mangold-Wirz & Fioroni, 1970). Lehmann's proposition, therefore, merely holds good for his own Angustiradulata.

A subdivision of the class into only two taxa (as proposed by Lehmann) is neither morphologically nor phylogenetically satisfactory (cf. Donovan, 1964; Teichert, 1967; Mangold-Wirz & Fioroni, 1970). As stated by Flower (1955) and Teichert (1967), the primitive orthoconic groups and groups closely related to them differ considerably from the Nautiloida s. str. Likewise, orthoconic Endocerida (including Intejocerina), Actinocerida, and Discosorida, even if their organizations are more distinctive, cannot be regarded as representing ranks of subclasses since many of their features are repeated within other groups (cf. Teichert, 1967: 204), and since they appear merely to be smaller offshoots of the primitive Ellesmerocerida (cf. Flower, 1955; Donovan, 1964; Teichert, 1967). All these more or less closely related groups may consequently be united in one separate subclass, Orthoceroida (see Table 4).

MOLLUSCA

This presentation so far demonstrates that increase in knowledge implies alterations and even revisions of our understanding of phylogenetic pathways, and hence of systematic representation. This reflexion of permanent systematic flux also concerns the molluscs as a whole when emphasizing the evolutionary morphologically qualitative importance of organizations irrespective of quantitative contents (compare: Gastropoda with Scaphopoda, etc.).

Based upon an extensive study of the lower molluscs, Salvini-Plawen (1972) also did a comparative analysis of molluscan organization in general, especially with respect to phylogenetic pathways from the zoological (neontological) point of view; simultaneously, Stasek (1972) presented a study coming to similar conclusions in general outline, differing in detail, however, owing to his emphasis on the advanced groups only.

As summarized in Figs. 3–5, the evolutionary radiation within the Mollusca is not a weighted one, but dominates along the line of mantle(-foot)-differentiation culminating with the Siphonopoda (cephalopods); this condition also contributed to the under-estimation

of the lower molluscs. The earliest confirmable evolutionary branching already took place at the level of very primitive molluscan organization, still characterized by an overall ventral gliding surface, by a merely circum-posterior mantle cavity, and by an aculiferan mantle cover (chitinous cuticle with embedded aragonitic scaly bodies; cf. Degens et al., 1967: 640; Beedham & Trueman, 1968; Salvini-Plawen, 1969, 1972; Peters, 1972; Stasek, 1972; Carter & Aller, 1975; Trueman, 1976; Salvini-Plawen & Boss, 1980). The preference and subsequent adaptation of some populations to sediment-burrowing habits finally resulted in the Recent Caudofoveata, during their course of which the locomotory surface was restricted to its cerebrally-innervated section, i.e. the pedal shield. That evolutionary line of Scutopoda, including only the Caudofoveata, is contrasted phylogenetically to the Adenopoda: Selective pressure upon the improvement of food-uptake by the organisms while steadily gliding by means of cilia led to the individualization of a snout. The trend to release the oral region from its earlier locomotory function induced the extension of the postero-lateral mantle grooves towards the anterior to unite preorally. Additionally, the locomotory surface hence confined to the purely ventrally-innervated section, i.e. the foot, was subsequently supported in its function by the selection of an anterior accumulation of a distinct follicular gland. That pedal gland, innervated by the first nerves of the ventral/pedal system, proves itself to be a genetically well-established differentiation (cf. Salvini-Plawen, 1972: 304 ff). In its interdependent evolutionary synorganization with a peripedal-preoral mantle cavity it distinctly defines the phylogenetic branch of Adenopoda, including all (Recent as well as extinct) molluscan groups except the Caudofoveata.

Two adenopodan groups, the Solenogastres and Placophora, not only share the still primitive aculiferan mantle cover; they are also synapomorphously tied together by the rudiment of seven transverse rows of calcareous bodies in the larvae (see Fig. 2) which distinctly prove the monophyletic origin of both groups within the Adenopoda. Their later differentiation of the mantle cover demonstrates, however, the subsequent specific deviation: re-disintegration of the cover of spicules in the Solenogastres, and consolidation of the juxtaposed bodies to seven shell plates in early Placophora (Heptaplacota).

The ancestral, common character of transverse rows of middorsal scales in both Solenogastres and Placophora, as well as the subsequent tendency to consolidate these juxtaposed scaly elements to become homogeneous formations, is likewise obvious in the solenogastre *Nematomenia* (?) *protecta*: the scaly mantle cover of this species is characterized "by three peculiar shields at the dorsal side of the head, which are clearly formed by coalescence of several juxtaposed small scales; apparently about 10 small scales have been united by lateral fusion, so that the original separation is merely indicated by a number of indentations at the posterior rim. I always find three such shields, the anteriormost of which is located close to the anterior end of the animal and partly imbricates the immediately subsequent second shield. The third shield, on the other hand, is separated from the middle one by a small number of ordinary scales" (translated from Thiele, 1913: 39).

Placophora with eight (!) plates, however, must be considered ancestral to the Conchifera. Since these placophorans bend and roll up ventrally—effected by the primitive character of a longitudinal muscle bundle close to each mantle edge, likewise present in Solenogastres and even in Caudofoveata—not prior to the prevention of that bending (probably by living in an undisturbed environment) the centers of plate-formation concentrated and fused to create a single, homogeneous concha; Fig. 3 demonstrates the respective synorganized alterations (cf. Salvini-Plawen, 1972; Haas, 1972 *versus* Beedham & Trueman, 1967; Stasek & McWilliams, 1973). This fusion was followed by concentration of the dorsoventral (shell-pedal) muscle bundles from 16 to 8, and by further elaboration (jaws, statocysts, subrectal commissure). The recent tryblidiid *Neopilina* characteristically demonstrates a far-reaching 'connecting link'-configuration in combining characters of both Placophora and Conchifera (dorsoventral musculature, esophageal and digestive glands, slender intestine, subradular organ; cf. Boettger, 1959; Salvini-Plawen, 1972, and others).

In regard to the radiation within the Conchifera, unanimous opinion seems to exist from the zoological as well as from the paleontological point of view that the Bivalvia (including the Rostroconchia) and the Scaphopoda represent a somewhat closer relationship, mainly due to the developmental configura-

tion of the mantle-shell (cf. Salvini-Plawen, 1972: 312; Pojeta & Runnegar, 1976: 43; and others). On the other hand, the Tryblidiida, Bivalvia and Scaphopoda have retained the peripodal mantle cavity of the typical Adenopoda, and the merely single pair of ctenidia in Bivalvia may therefore serve additionally to indicate that these organs are secondarily pluralized in Placophora and *Neopilina*. In contrast, in Bellerophontida partim and in Gastropoda, as well as in Cephalopoda/Siphonopoda, the mantle cavity is confined to the (morphologically) posterior body in connexion with the increase of cephalization and the heightening of the shell. That condition clearly demonstrates that gastropods and siphonopods were derived from advanced, high-cyrtconic Galeroconcha in contrast to bivalves and scaphopods originating in more primitive, cap-shaped galeroconchs. The closer ancestral relationship of Cephalopoda/Siphonopoda and Bellerophontida-Gastropoda (cf. also Yochelson et al., 1973) might also be indicated by the possible homology of the eyes (cf. Salvini-Plawen & Mayr, 1977), presumably differentiated already in the more advanced galeroconchs. There is no substantiated reason, however, to join the three groups systematically into one supertaxon, and the reverse tendency by Mangold-Wirz & Fioroni (1970) and Fioroni (1974) to classify the siphonopods as separate from all other Conchifera is based merely upon present day differences; it disregards, however, the not-at-all extraordinary phylogenetic point of view, according to which there is continuous evolution and radiation (cf. Yochelson et al., 1973; Erben, 1964, 1966; Ristedt, 1968, and others).

According to that analysis, one could certainly subdivide the Conchifera with respect to possible evolutionary pathways (see Fig. 4), and classify them, e.g. as Ventropoda or Archaeoconcha (Galeroconcha and Gastropoda), Siphonoconcha (Siphonopoda/Cephalopoda), and Loboconcha (Bivalvia and Scaphopoda); this grouping would be more adequate than a subdivision into Cyrtosoma and Diasoma as proposed by Runnegar & Pojeta (1974) which, in addition, relies on a partially imagined or even incorrect character (Tryblidiida; Scaphopoda). All these attempts are mere supposition, since they still appear to be more or less contestable speculations. The Conchifera are a phylogenetically as well as morphologically compact group ancestrally tied to the Galeroconcha, and subdivision of

them at our present state of knowledge is not justified.

In consideration of the widely substantiated, comparative-anatomical as well as evolutionary levels within the molluscan organization, only three essential evolutionary steps are conspicuous: (1) The restriction of the ventral locomotory surface to the ventrally-innervated section combined with beginning cephalization and the preoral extension of the mantle cavity; this evolutionary differentiation separates the Adenopoda from the Scutopoda. (2) The elaboration of a shelled mantle cover (Placophora) correlated with the beginning concentration of the dorsoventral musculature, and accompanied by the specific differentiation of the alimentary canal s. l. (esophageal and midgut glands, slender and winding intestine, subradular sense organ; differentiation of the pericardioducts as excretory organs ?); that evolutionary step within the Adenopoda separates the Placophora and Conchifera from the Solenogastres. (3) The establishment of a homogeneous concha, accompanied by the differentiation of the jaws, the statocysts, the subrectal commissure, and the cerebrally-innervated tentacle formations (preoral tentacles and velum in *Neopilina*, cephalic tentacles in Gastropoda, palps in Bivalvia, captacula in Scaphopoda, arms in Cephalopoda/Siphonopoda; cf. Lemche & Wingstrand, 1959; Allen & Sanders, 1969; Grobben, 1886; Gainey, 1972; and others); these synapomorphies separate the Conchifera.

An adequate classification would have to reflect the above steps (Fig. 4) systematically; this, however, would also result in an unjustified over-accentuation of the Solenogastres. In an endeavour not to hypertrophize the specialist's own group, it must be stated that the Solenogastres are quite distinct from the Caudofoveata (see Adenopoda versus Scutopoda), but within the Adenopoda they constitute merely an early side branch. The close relationship of the Placophora and Solenogastres, synapomorphously tied together by the rudiments of seven transverse rows of juxtaposed spicules (see Figs. 2–3), justifies including both groups under one taxon for which the appropriate term Heterotecta may be coined (defined as Adenopoda without concha and characterized by the developmental rudiment of seven transversely arranged rows of juxtaposed calcareous bodies at the middorsal mantle; these bodies have different fates). Such a classification also ap-

pears more adequate in regard to the morphological weight of the phylogenetically most successful Conchifera, as well as concerning the reasonable subdivision of the Adenopoda solely into two groups, i.e. to separate the Conchifera from the collectively more primitive Placophora and Solenogastres. Consequently, the systematic grouping of the Mollusca results as compiled in Fig. 5 and Table 3.

OTHER TAXA

The Scaphopoda do not need special discussion. Their somewhat close relationship to the Bivalvia has been mentioned above. Emerson (1962) as well as Palmer (1974a, b) have reclassified the group, Palmer (1974a) introducing two orders Dentaliida and Siphonodentaliida (compare footnotes 3 and 10).

There are several terms and taxa associated with the molluscs still to be discussed shortly. The familiar term Aplacophora (Ihering, 1876) has already been dealt with; it must be dropped due to the diphyletic origin of the Caudofoveata and Solenogastres.

The term Amphineura (Ihering, 1876) was originally created because of the seemingly similar nervous systems in Aplacophora and Placophora; more recently, many scientists tend to confine the term to the Placophora. Since neither the Solenogastres, nor the Caudofoveata still possess a truly amphineural nervous system (i.e. two separate pairs of medullary cords (= without ganglia formation) provided with irregular ventral as well as lateroventral interconnexions), this condition is still represented only in Placophora and—although already more specialized—also in *Neopilina*. Other configurations only reflect the general tetraneury typical of all Mollusca.

The term Aculifera (Hatschek, 1891) is more adequate when considering the aplacophoran and polyplacophoran groups—as originally introduced and as used by Salvini-Plawen (1968b, 1969, 1972); it has been misleadingly limited by Stasek (1972; and copied by Pojeta & Runnegar, 1976) to the aplacophoran groups. This taxon, however, shares with the 'Aplacophora' disregard of the evolutionary branching into Scutopoda and Adenopoda, thus including three different groups having conservatively retained the symplesiomorphous character of the mantle cover with cuticle and aragonitic bodies.

TABLE 3. Higher classification within molluscs.

	Subphylum	Infraphylum/Superclassis	Classis
current grouping (Götting, 1974; Lehmann, 1976)	Aculifera		{ Caudofoveata Solenogastres Placophora
	Conchifera		{ Monoplacophora Gastropoda Bivalvia Scaphopoda Cephalopoda
corrected version	Scutopoda		Caudofoveata
	Heterotecta		{ Solenogastres Placophora
	Conchifera		{ Galeroconcha Gastropoda Siphonopoda Bivalvia Scaphopoda
phylogenetically adequate classification	Scutopoda		Caudofoveata
	Adenopoda	{ Heterotecta	{ Solenogastres Placophora
		{ Conchifera	{ Galeroconcha Gastropoda Siphonopoda Bivalvia Scaphopoda

The enigmatic Late Cambrian *Matthevia* still remains one of the 'problematica' with molluscan affinities (cf. Yochelson, 1978). Yochelson (1966) reviewed recent records and erected a new class for the genus; on the other hand, Runnegar & Pojeta (1974) suggest that the two, co-occurring, somewhat unequal and massive shells with two tapering cavities each represent the conical valves of a primitive chiton. Disregarding the evidence for a very different evolution of the Placophora (see Figs. 3 & 5) than that speculated by Runnegar & Pojeta, it remains here to stress (1) that the placophoran plates "in no way resemble the hard pieces of *Matthevia*" (Yochelson, 1966: 8) even when compared with Chelodida, and (2) that the conical internal cavities of the shells separated by a strong septum are situated in succession but not in juxtaposition. If compared to Placophora, both the latter characters point to highly specialized features, the paired dorsoventral muscle bundles being then concentrated apically (in contrast to Tryblidiida and Placophora). The strange reconstruction of *Matthevia* by Yoch-

elson (1966), however, raises a question as to how such organisms should have been adaptively selected; in contrast to the opinion of Yochelson, the reconstructed condition is not streamlined (compare *Patella*, *Ancylus*, etc., which press their anterior shell margin to the bottom), and the animal cannot retract into the small cavities (which are, additionally, filled by "powerful muscles")—and the size of the organisms is purely speculative. Is it not possible that the soft parts of the body greatly exceed the shell(s) (analogously to Bivalvia-Pholadoidea or -Clavagelloidea)?

The Stenothecoida with their two symmetrical and unequal hingeless valves must be placed incertae sedis until more information can be offered in favour of a distinct relationship to another group (within or even outside of the molluscs; cf. also Yochelson, 1978). While Yochelson's reconstruction (1969) is not quite satisfactory as concerns a 'mollusk,' the interpretation of Runnegar & Pojeta (1974: 316) as "bivalved monoplacophorans, with the lower valve formed by the sole of the foot" appears to be pure speculation.

TABLE 4. Classification of the Mollusca proposed herein (+ = extinct).

Phylum <i>MOLLUSCA</i> Cuvier, 1795	
Subphylum <i>SCUTOPODA</i> Salvini-Plawen, 1978	
Classis CAUDOFOVEATA Boettger, 1955	
Ordo Chaetodermatida Simroth, 1893	
Subphylum <i>ADENOPODA</i> Salvini-Plawen, 1971	
Infraphylum/Superclasssis HETEROTECTA nov.	
Classis SOLENOGASTRES Gegenbaur, 1878	
Superordo Aplotegmentaria Salvini-Plawen, 1978	
Ordo Pholidoskepia Salvini-Plawen, 1978	
Ordo Neomeniomorpha Pelseneer, 1906 (emend.)	
Superordo Pachytegmentaria Salvini-Plawen, 1978	
Ordo Sterrofustia Salvini-Plawen, 1978	
Ordo Cavibelonia Salvini-Plawen, 1978	
Classis PLACOPHORA Ihering, 1876	
+ Subclassis HEPTAPLACOTA nov.	
Ordo Septemchitonida Bergenhayn, 1955	
Subclassis LORICATA Schumacher, 1817	
+ Ordo Chelodida Bergenhayn, 1943	
+ Ordo Scanochitonida Starobogatov & Sirenko, 1975	
Ordo Lepidopleurida Thiele, 1910	
Ordo Chitonida Thiele, 1910	
Infraphylum/Superclasssis CONCHIFERA Gegenbaur, 1878	
Classis GALEROCONCHA nov.	
Ordo Tryblidiida Wenz, 1938 = Monoplacophora Odhner in Wenz, 1940	
+ Ordo Bellerophontida Ulrich & Scofield, 1897 = Belleromorpha Naef, 1911	
Classis GASTROPODA Cuvier, 1795	
Subclassis PROSOBRANCHIA Milne-Edwards, 1848	
Ordo Archaeogastropoda Thiele, 1925	
Subordo Vetigastropoda nov.	
Subordo Docoglossa Troschel, 1866	
Subordo Neritopsina Cox, 1960	
Ordo Caenogastropoda Cox, 1960	
Subordo Mesogastropoda Thiele, 1925	
Subordo Neogastropoda Thiele, 1929	
Subclassis PULMONATA Cuvier, 1817	
Ordo Archaeopulmonata Morton, 1955	
Ordo Basommatophora Keferstein, 1864	
Ordo Stylommatophora Schmidt, 1855	
Subclassis GYMNOMORPHA Salvini-Plawen, 1970	
Ordo Onchidiida Rafinesque, 1815	
Ordo Soleolifera Simroth, 1908 = Veronicellida Gray, 1840	
Ordo Rhodopida Fischer, 1883	
Subclassis OPISTHOBRANCHIA Milne-Edwards, 1848	
Ordo Pyramidellimorpha Fretter, 1979	
Ordo Cephalaspidea Fischer, 1883	
Ordo Anaspidea Fischer, 1883	
Ordo Saccoglossa Ihering, 1876 (= Ascoglossa Bergh, 1879)	
Ordo Notaspidea Fischer, 1883	
Ordo Nudibranchia Ducrotay-Blainville, 1814	
Ordo Anthobranchia Férussac, 1819	
Classis BIVALVIA Linné, 1758	
Subclassis PELECYPODA Goldfusz, 1820	
Superordo Ctenidiobranchia nov.	
Ordo Nuculida Dall, 1889	
Superordo Palaeobranchia Iredale, 1939	
Ordo Solemyida Dall, 1889	
+ Ordo Praecardiida Newell, 1965	
Superordo Autobranchia Nevesskaya et al., 1971	
Ordo Pteriomorpha Beurlen, 1944	
Ordo Palaeoheterodonta Newell, 1965	

TABLE 4 (Continued).

Ordo Heterodonta Neumayr, 1883
Ordo Anomalodesmata Dall, 1889
Superordo Septibranchia Pelseneer, 1888/1906
Ordo Poromyida Ridewood, 1903
+ Subclassis ROSTROCONCHIA Cox, 1960
Ordo Ribeiriida Kobayashi, 1933
Ordo Ischyriniida Pojeta & Runnegar, 1976
Ordo Conocardiida Neumayr, 1891
Classis SCAPHOPODA Bronn, 1862
Ordo Dentaliida Palmer, 1974
Ordo Siphonodentaliida Palmer, 1974
Classis SIPHONOPODA Lankester, 1877 = CEPHALOPODA Schneider, 1784
+ Subclassis ORTHOCERATOIDA Kuhn, 1940
Ordo Ellesmerocerida Flower, 1950
Ordo Orthocerida Kuhn, 1940
Ordo Ascocerida Kuhn, 1949
Ordo Discosorida Flower, 1950
Ordo Endocerida Teichert, 1933
Ordo Actinocerida Teichert, 1933
Subclassis NAUTILOIDA Lamarck, 1812
+ Ordo Oncocerida Flower, 1950
Ordo Nautilida Agassiz, 1847
+ Ordo Tarphycerida Flower, 1950
+ Subclassis AMMONOIDA Lamarck, 1812
Ordo Bactritida Shimanskij, 1951
Ordo Goniaticida Hyatt, 1884
Ordo Ammonitida Agassiz, 1847
Subclassis COLEOIDA Bather, 1888
+ Ordo Aulacocerida Jeletzky, 1965
+ Ordo Belemnitida Zittel, 1885
Ordo Sepiida Naef, 1916
+ Ordo Phragmoteuthida Jeletzky, 1964
Ordo Teuthida Naef, 1916
Ordo Vampyromorpha Grimpe, 1917
Ordo Octobranchia Boettger, 1952 (pro Octopoda Leach, 1817)

The following taxa are considered to include Mollusca dubiosa: Hyolitha, Tentaculita, Agmata and Jinonicellina. There is need of much more information whether the Hyolitha (cf. Marek & Yochelson, 1964, 1976; Runnegar et al., 1975; Yochelson, 1978), the Tentaculita (cf. Blind, 1969; Runnegar et al., 1975), the Agmata (*Volborthella*, *Salterella*; cf. Yochelson, 1977b; Glaessner, 1976), and the Jinonicellina (cf. Runnegar, 1977; Yochelson, 1977a; Pokorny, 1978) are actually of molluscan organization or rather belong to other shelled organisms (compare, e.g., Glaessner, 1976 for the 'Agmata'). With respect to the hyoliths, we doubt the interpretation given by Runnegar et al. (1975) concerning the position of the muscle bundles, the insertions of which are preserved on both the operculum and cone; such strong bundles indicate the need for strenuous performance and correspondingly the need for rigid structures of insertion, but not connective tissue. Moreover, and in addition to the critique by Marek & Yochelson (1976), in firmly shelled organisms (and in contrast to deformable tube-

dwelling bodies like sipunculids or some polychaetes) pressure upon the body fluid can easily be exercised by circular musculature; only the retraction of the body needs compact musculature. Since muscle bundles from the dorsal to the ventral side of the shell itself serve no purpose whatsoever, the bundles might have inserted either at a compact organ (i.e. radula bolster, cartilage-like structures, and other) or rather—and more likely—at the operculum with its five pairs of muscle scars (cf. Yochelson, 1974; compare also the rudists = Hippuritoidea).

FINAL DISCUSSION AND PROPOSAL

The Mollusca constitute one of the best defined groups within the animal kingdom and are distinguished by several synorganized characters original to the phylum, viz. the dorsal integument secreting chitinous cuticle and/or calcareous formations = the aplacophoran/polyplacophoran/conchiferan mantle; a respiratory mantle cavity with ctenidia,

mucous tracts and body outlets; the ventral body surface serving for locomotion by means of cilia and mucous glands as well as partly of dorsoventral musculature; the gono-pericardial complex and an open circulatory system; a series of paired dorsoventral muscle bundles and—primitively—a pair of longitudinal muscle bundles along the margin causing the animal to roll up; the radula; and the tetraneury associated with a pallial sense organ (terminal sense organ, osphradia).

Owing to the fact that most molluscs produce fossilizable hard structures, we fortunately are able to study a great deal of molluscan phylogeny by means of these shell formations within different levels and groups. That condition, however, largely suppresses the importance and morphologically equivalent significance of other groups of molluscs of which no fossils have been handed down. Supported by the overwhelming quantitative dominance of the shell- (especially concha-) bearing molluscs, that discrepancy as concerns the comparative importance of different molluscan groups has become nearly inexcusable. In consideration of phylogenetic reconstruction and the endeavour to trace evolutionary pathways, two essential reflexions should always be taken into account: (1) Any adaptive alteration of a character is tied at any time to anatomical and functional interdependence on syn-organization; (2) a close, monophyletic relationship, i.e. the common descendant from an ancestral organization, is only substantiated by new character(s) acquired in common (syn-apomorphies), whereas the common retention of conservative characters (syn-plesiomorphies) merely demonstrate a more general relationship within a superior frame. Thus, many speculations and (mis-)interpretations, about *Neopilina* for example, could have been avoided under these premises, as well as the revival of the taxon 'Aplacophora' (cf. Scheltema, 1978).

In consideration of the evolutionary pathways within the Mollusca, there are four essential steps of progressive differentiation (Scutopoda/Adenopoda, Solenogastres/Testaria, Placophora/Conchifera, and radiation of Conchifera); since the Caudofoveata and Solenogastres are only tied together by symplesiomorphies, and since the Solenogastres-Placophora, as well as the Placophora-Conchifera are each tied by synapomorphies, the phylogenetic lines are obvious (Figs. 3–5). Transposed to usable linear system (cf. also Mayr, 1974), these conditions

may be rendered by the final proposal as presented in Table 4.

SUMMARY

A reconsideration of systematic problems in the Mollusca raised by various recent studies results in the discussion of phylogenetic pathways and in the presentation of a correspondingly modified higher classification (as summarized in Fig. 5 and Table 4):

- 1) The original, common organization of Mollusca, characterized by an overall ventral gliding surface and a posterior-lateral mantle cavity, according to further way of life differentiated along two basic evolutionary lines: a) the burrowing Scutopoda with the locomotory surface restricted to the cerebrally-innervated section (Caudofoveata only); b) the continuing gliding-creeping Adenopoda with the locomotory surface confined to the ventrally-innervated section, with the differentiation of a rudimentary head, with a preorally extended mantle cavity, and with a distinct pedal gland (Solenogastres, Placophora, and Conchifera).
- 2) Within the Adenopoda, both the Solenogastres and Placophora are monophyletically (synapomorphously) interconnected by the rudimental mantle differentiation of seven middorsal, transversely arranged rows of juxtaposed calcareous bodies (cf. Fig. 2). Accordingly, the Septemchitonida are raised to a separate subclass Heptaplacota, and both Solenogastres and Placophora are classified together as Heterotecta, separated from the Conchifera.
- 3) Within that classification, the Caudofoveata constitute an isolated, early separated group (Scutopoda) interconnected to the Solenogastres and/or other molluscs merely by the conservative presence of ancestral (symplesiomorphous) characters. Placophora and Conchifera are interconnected by several synapomorphous characters; herein, the organization of *Neopilina* constitutes a connecting link.
- 4) No sufficient characters are obvious to serve for justified supraclasses within the Conchifera.
- 5) A reconsideration of the torsion process leads to the presumption that the two separate torsional phases reflect different evolutionary adaptations. Correlative to

that interpretation, the Bellerophontida (Belleromorpha) are considered to have been untorted organisms and are hence reclassified together with the Tryblidiida (Monoplacophora) within the new taxon Galeroconcha, and the pallial asymmetry of the higher gastropods other than Archaeogastropoda is regarded to be a paedomorphous character.

- 6) Onchidiacea, Soleolifera, and Rhodopacea are demonstrated to represent a separate line (subclass Gymnomorpha) distinct from both the Pulmonata as well as the Opisthobranchia. The Doridacea must be separated from the Nudibranchia as a separate order Anthobranchia.
- 7) The Rostroconchia are regarded as a subclass of the Bivalvia, and the hinged, pelecypod Bivalvia may phyletically be grouped in four lines according to way of life (feeding, differentiation of gills); the Poromyida must be classified as a separate group (Septibranchia).
- 8) The recent confirmation that the arms of cephalopods are cerebrally-innervated organs favours the term Siphonopoda for the class. The various early lines of fossil Siphonopoda (cephalopods) are classified within the taxon Orthoceroida and set apart from Nautiloida, Coleoida, and Ammonoida.
- 9) Other taxa, groups, and terms are briefly discussed, with special emphasis on the avoidance of hypertrophy of systematic categories which are not justified comparatively.

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ZUSAMMENFASSUNG

EINE NEU-BEURTEILUNG DES SYSTEMS DER
MOLLUSKEN (PHYLOGENIE UND GROSZ-GRUPPIERUNG)

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Eine Analyse verschiedener Unstimmigkeiten, welche durch in jüngerer Zeit durchgeführte Beiträge hinsichtlich phylogenetischer Zusammenhänge und systematischer Groszgruppierung entstanden, führt zur Darlegung neuerer Vorstellungen zum stammesgeschichtlichen Entwicklungsablauf innerhalb der Mollusken und zu einem entsprechend modifizierten System (vgl. Fig. 5 und Tabelle 4):

- 1) Die ursprüngliche, gemeinsame Molluskenorganisation, welche u.a. durch eine die gesamte Ventralfläche einnehmende Gleitsohle und einen posterio-lateralen Mantelraum gekennzeichnet war, spaltete sich entsprechend der Lebensweise in zwei Entwicklungslinien auf: a) in die grabenden Scutopoda mit Einschränkung des Lokomotionsorganes auf den cerebral innervierten Abschnitt (nur Caudofoveata), und b) in die weiterhin gleitend-kriechenden Adenopoda mit Einschränkung der Lokomotionsfläche auf den ventral innervierten Abschnitt, mit der beginnenden Differenzierung eines Kopfabschnittes, mit einem sich praeorad ausdehnenden Mantelraum, und mit der Ausbildung einer distinkten Fuszdrüse (Solenogastres, Placophora, Conchifera).
- 2) Innerhalb der Adenopoda sind die Solenogastres und Placophora durch die monophyletische (synapomorphe) Ausbildung von sieben Querreihen nebeneinanderliegender Kalkkörper in der Mantelmitte verbunden (vg. Fig. 2). Dementsprechend werden die Septemchitonida als eine eigene Unterklasse Heptaplacota abgetrennt, und Solenogastres wie Placophora werden zusammen als Heterotecta den Conchifera gegenübergestellt.
- 3) Innerhalb dieses Gesamtrahmens stellen die Caudofoveata daher eine isolierte Gruppe dar (Scutopoda), welche mit den Solenogastres und/oder anderen Mollusken nur durch konservativ erhaltene (symplesiomorphe) Merkmale verbunden sind. Placophora und Conchifera sind durch mehrere synapomorphe Merkmale verbunden; *Neopilina* stellt hierbei eine vermittelnde Brückenorganisation dar.
- 4) Innerhalb der Conchifera lassen sich bisher keine ausreichenden Verbindungen erkennen, welche die Errichtung von Überklassen rechtfertigen würden.
- 5) Eine Analyse der Torsionsvorgänge führt zu der Annahme, dass die ontogenetische Zweiphasigkeit auf zwei evolutiv verschiedene Anpassungsprozesse zurückzuführen sind. Entsprechend dieser Aufschlüsselung werden die Bellerophontida (Belleromorpha) als untortierte Organismen aufgefasst und zusammen mit den Tryblidiida (Monoplacophora) im Rahmen einer Klasse Galeroconcha neu eingereiht, wie auch die Asymmetrie des Mantelraumkomplexes bei den Schnecken mit Ausnahme der Archaeogastropoda als eine Paedomorphie interpretiert wird.
- 6) Onchidiacea, Soleolifera und Rhodopacea lassen sich als eine eigene, von Pulmonata wie Opisthobranchia unabhängige Entwicklungslinie feststellen (Unterklasse Gymnomorpha). Die Doridacea sind als eigene Ordnung Anthobranchia von den Nudibranchia abzutrennen.
- 7) Die Rostroconchia werden als eine Bivalvia-Unterklasse (und nicht als eigene Klasse) aufgefasst. Die mit Schlosz versehenen pelecypoden Bivalvia können entsprechend ihrer Lebensweise (Ernährung, Kiemendifferenzierung) in vier Entwicklungslinien gruppiert werden; die Poromyida sind hierbei als eigene Gruppe zu führen (Septibranchia).
- 8) Die in jüngerer Zeit bestätigten Befunde, dass die Fangarme der 'Cephalopoden' rein cerebral-innervierte Organe darstellen geben der Bezeichnung Siphonopoda für die Klasse den Vorzug. Die verschiedenen, frühen Entwicklungslinien fossiler Siphonopoden werden als eine Unterklasse Orthoceroida zusammengefasst und so den Nautiloida, Coleoida und Ammonoida gegenübergestellt.
- 9) Einige weitere Taxa und Gruppenbezeichnungen werden diskutiert, wie darauf hingewiesen wird, eine vergleichend nicht gerechtfertigte Hypertrophie systematischer Gruppen zu vermeiden.