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# A PHYLOGENETIC FRAMEWORK OF THE ENTEROCOELA (METAMERIA: COELOMATA)

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## ABSTRACT

The zoological treatise by Hyman represents the culmination of a century-old effort to produce broad morphological syntheses and intuitive phylogenetic trees. We do not entirely accept the present trend to value molecular phylogeny and numerical cladistics at the expense of a more intuitive Hennigian approach of phylogenetic reconstruction. Our main intention here has been to point out some simple and rather neglected ways of doing phylogenetics. We propose a scenario-like narrative of character transformations, from the tubicolous annelids to the vertebrates. The tubicolous annelid taxon Oweniidae is considered the sister group of the Enterocoela. Our main conclusions are that: (1) Chaetognatha represents the sister group of the Vertebrata, within a taxon Bioculata, **nov**.; (2) tunicates are closer to the Bioculata than the cephalochordates, forming with the Bioculata the taxon Cephalata, **nov**.; (3) calcichordates with echinoderm-like skeletons may belong strictly to the stem lineage of the Eupharyngotremata, **nov**.; (4) "Hemichordata" is a polyphyletic taxon, with enteropneusts, rather than echinoderms, being more closely related to the chordates; (5) "Pterobranchia" is paraphyletic, rhabdopleurids being more basal than cephalodiscids; (6) "Lophophorata" is also paraphyletic, with Phoronida being excluded from the Deuterostomata, whereas Ectoprocta is the more apical sister group of the Pharyngocoela, **nov**.; (7) the latter two groups are placed within the Coloniata, **nov**.; (8) Pogonophora, including the Vestimentifera, is the sister group of the Radialia and both groups belong to the Enterocoela.

**Keywords**: Hennigian systematics, phylogenetic principles, additive transformation series, deuterostome concept, vertebrate origins.

**Descritores**: Sistemática Hennigiana, princípios filogenéticos, séries de transformação aditivas, conceito dos deuterostomados, origem dos vertebrados.

## EULOGY AND PRESENTATION

The nineteenth century tradition of summarizing empirical and interpretative knowledge into great zoological treatises has culminated in the works of Libbie Henrietta HYMAN (1940, 1951a, b, 1955, 1959, 1967). Although unfortunately never completed, such a single-authored effort to synthesize the primary descriptive literature into a richly illustrated compendium, containing both valuable descriptions of higher taxa and authoritative phylogenetic interpretations, has never been achieved again.

We note that Hyman's treatises also represent a tribute to an intuitive phylogenetic tradition, which started with HAECKEL (1874) and reached its apex in the 1950s with the phylogenetic trees of HYMAN (1951a), CUÉNOT (1952), HADZI (1953), JÄGERSTEN (1955), HANSON (1958), MARCUS (1958) and REMANE (1958, 1959). This tradition has certainly furthered phylogenetic knowledge, and has helped to eliminate several non-monophyletic groups from taxonomy. However, with the perceptive work of HENNIG (1966), it has become clear to a growing number of researchers that many widely used taxa are based on plesiomorphic homologies, being invalid in a phylogenetic context. We consequently consider the incorporation of Hennigian principles not only a necessary refinement, but also the only explicit and logical approach for the further development of a century-old tradition in evolutionary systematics.

During the last decade we are witnessing a preponderance of sophisticated molecular techniques applied to phylogenetic reconstructions and a proliferation of phylogenetic inference packages for an ever faster manipulation of basic data. Molecular phylogeny and numerical cladistics are now prestigious research programs which will obviously be with us for a long time and will continue to revolutionize and to grow more and more rapidly. Notwithstanding these salutary and permanent trends in systematics, we do not share the conviction that these approaches alone are the most logical avenues for the obtainment in the near future of a dependable, phylogeny-based, general-reference system for biology (CHRISTOFFERSEN, 1994).

The users of a molecular approach may sometimes convey the idea that conventional morphology is outdated and has already exhausted its potential for the production of reliable phylogenies. Some may then go on to choose an appropriate molecule (rRNA or mtDNA, for example), select from scratch a few model biological specimens for analysis (including, for example, a blue-green alga [or Cyanobacteria] for "Prokaryota", or an earthworm for "Annelida"), choose one or a few among over a hundred available molecular methods (HUELSENBECK and HILLIS, 1993), and then produce a phylogeny of life, which may not necessarily be the most reliable reconstruction.

Numerical cladists, on the other hand, are empiricists that believe it is possible to start analysis with an objective data matrix that is as close as possible to empirical observations. With the choice of a preferred method (parsimony, maximum likelihood, neighbor-joining, etc.), an algorithm permits the production of a final cladogram. However, characters are predictions rather than observations (BUCKUP, 1991). In other words, observations alone are not sufficient in phylogenetic analysis. For example, recognition of a distinct trochophore larva usually results in the acceptance of a taxon Trochozoa. Yet, when several types of echinoderm larvae are interpreted as modified trochophores, the former taxon becomes invalid in a phylogenetic context. If the two types of larvae, and similarly many other apparently quite distinct morphologies forming transformation series, are coded as independent characters, the correct phylogenetic conclusion will not be obtained, either with or without a numerical analysis. Of course, once an acceptable interpretation is reached, characters may be coded as additive series. The point we are making is that objective, but incorrect phylogenies are sometimes produced before an acceptable working hypothesis is obtained.

We suggest that incorrect data matrices - which remain incorrect because the researcher is unaware that certain distinct characters belong to a single transformation series - are particularly prone to this type of error. Except for the most trivial cases of present/absent characters, or of numerical sequences of similar character states, a transformation series must be built in the brain, not by computers, and then tested by congruence with the remaining hypothetical character transformations. Significantly, in our example, examination of thousands of specimens of protostomians and deuterostomians may simply corroborate the supposed reality of the Trochozoa, Spiralia, or Protostomia, as long as the correct interpretations and the critical observations are not made.

Phylogeny needs transformational theory to provide unity and contiguity where observation and pattern may only capture distinctness and typological groupings. The phylogeneticist who does not recognize the importance of hypothesizing extended additive transformation series right from the beginning of a phylogenetic analysis is not operating under sound phylogenetic principles. "*The cognitive processes involved in step by step hypothesis testing of a manual method may provide the researcher with a more omnispective view regarding the relative merits of each individual character and may supply the means for the most discerning cladistic inferences*" (CHRISTOFFERSEN, 1987: 349). We recommend that computer-analyses should be preferably conducted after an exhaustive manual analysis. "*Perhaps the most discerning cladistic inferences for large data sets will be obtained if both traditional Hennigian and computer-generated cladograms are critically compared*" (CHRISTOFFERSEN, 1989: 267). For a detailed discussion of the differences between a more empirical cladistic taxonomy, and a more interpretative phylogenetic systematics, see CHRISTOFFERSEN (in press).

In our philosophy of science, empirical observations cannot be separated from theoretical insights. These must provide a global perspective and function as a starting point for dealing with more specific and partial points of view. BUNGE (1989) states that undoubtedly basic science enriches knowledge for its own sake, but its aim is ultimately to discover general laws that may explain reality in its totality. He believes that a greater expertise in system's theory would help to integrate a large number of partial and divergent points of view. Within the historical sciences, we feel that the Hennigian approach furnishes the means to deal coherently with an enormous data base on biological diversity and a realistic perspective towards the attainment of a holistic biological system. Thus we prefer the manual method of phylogenetic reconstruction (WILEY, 1981), in which interpretation and observation are viewed as complementary processes during all stages of a phylogenetic analysis. We feel strongly that only with insightful interpretation foremost, seconded by relevant critical observation, will we be able to decide crucial phylogenetic issues in a meaningful way.

The above characterizations of reductionist molecular approaches and empirical quantitative methods are not aimed at producing strawmen for an easy rebuttal of such promising modern techniques. Rather, we intend to focus our personal research program into a clearer perspective. We also advocate the apparently unrecognized potential of the available descriptive data for the obtainment of broad phylogenies. Our theoretical starting points are that: (1) only the explicit principles developed by Hennig are fully adequate for the reconstruction of hierarchic relationships among taxa; (2) broad synthetic phylogenies have precedence over more analytical approaches within narrow groups; (3) the manual phylogenetic method permits more perceptive transformation series to be proposed for widely divergent groups; and (4) consistent reinterpretation of existent descriptive data has priority over the obtainment of new data.

## INTRODUCTION

In this paper we follow a new scheme for discussing what is ordinarily known as the origin of the vertebrates, or the phylogeny of the deuterostomes.

### THE CONCEPT OF THE DEUTEROSTOMATA AND THE INSTABILITY OF EXISTENT CLASSIFICATIONS

The taxon Deuterostomata, since its conceptualization by GROBBEN (1908), is characterized basically by the secondary origin of the mouth and by the position of the anus, originating near or from the larval blastopore. HYMAN (1940, 1951a), ZIMMER (1973), and SCHAEFFER (1987) added to this concept the presence of (1) an enterocoelic coelom, (2) radial cleavage, and (3) a dipleurula larva. This redefinition has caused a certain instability in the placement of several minor phyla, which have some, but not all, of these diagnostic characters.

In addition to the chordates, echinoderms, and hemichordates, the following minor groups have previously been included in the Deuterostomata: Chaetognatha (HYMAN, 1959), "Lophophorata" (ZIMMER, 1973), and Pogonophora (IVANOV, 1988). By retaining the original concept of the Deuterostomata, it has been necessary to remove the Phoronida and Pogonophora to more basal positions within the enterocoelic-radialian lineage.

### THE MONOPHYLY OF THE ENTEROCOELA AND ITS DERIVATION FROM METAMERIC COELOMATES

The Pogonophora, which in our conceptual framework includes the Vestimentifera (SOUTHWARD, 1988), contains several transitional steps that permit us to derive the enterocoelic coelomates from schizocoelic tubicolous annelids. More specifically, we consider the Oweniidae Rioja, 1917 to be the sister group of the Enterocoela. *Owenia* and Pogonophora have a multisegmented opisthosoma behind the gonad containing somite (LIVANOV and PORFIRIEVA, 1965: 168). We interpret this opisthosoma as a synapomorphy of Oweniidae and Enterocoela. The implication is that deuterostome, radialian, and enterocoelic conditions are all derived in relation to the protostome, spiralian, and schizocoelic conditions. This interpretation refutes the archicoelomate theory of the origin of enterocoelic pouches from the gastric pockets of Cnidaria (SEDGWICK, 1884; REMANE, 1963). Our interpretation also implies that the "Protostomia", "Spiralia", "Trochozoa", and "Schizocoela" are non-monophyletic taxa within the Coelomata. These insights are a direct consequence of our overall scenario, in which Deuterostomata, Radialia, Enterocoela, Metameria, Coelomata, Bilateria and Metazoa form successively broader groups. In this particular reconstruction Deuterostomata thus becomes far removed from the Cnidaria.

Regarding fossils, we accept the concept of the "†Calcichordata" as a stem group leading to the chordate lineage (JEFFERIES, 1991), and the placement of the †Conodonta among the jawless craniates (ALDRIDGE et al., 1986). The †Graptolithina have recently been compared to *Cephalodiscus* (DILLY, 1993). However, these colonial fossils typically also share a black stolon with the rhabdopleurids. Consequently, we wonder if graptolithids represent a monophyletic group or should rather be viewed at least in part as a stem group belonging to the main line (Coloniata, Pharyngocoela, and Pharyngotremata) leading to the chordates.

## BRIEF SURVEY OF CLASSIFICATIONS AND PHYLOGENIES OF THE ENTEROCOELA

PARKER (1982) provides general information on, as well as a taxonomic synopsis of, major groups of living organisms down to the family level. Recent manual phylogenetic approaches are JEFFERIES (1979, 1986, 1989, 1991), SCHAEFFER (1987), and AX (1989). Computer-assisted cladistic analyses of the Metazoa are provided by BRUSCA and BRUSCA (1990), SCHRAM (1991), and RUPPERT and BARNES (1994). Diverse evolutionary approaches are found in VANDEL (1961), DOUGHERTY (1963), CLARK (1964, 1979), DILLON (1965), SIEWING (1967), JÄGERSTEN (1972), JOLLIE (1973, 1982), EMIG (1982), SALVINI-PLAWEN (1982), NIELSEN (1985), BERGSTRÖM (1986), HOLLAND (1988), FIELD et al. (1988), and others. More general information is obtained in zoological treatises (e.g., HARMER and SHIPLEY, 1895, 1904; HYMAN, 1955, 1959; GRASSÉ, 1952, 1959a, b, 1966). Although many of these works contain conflicting views on phylogeny, the larger compilations are important sources of information, especially for bringing to the present evaluations of the relevance of work conducted in the nineteenth and beginning of the twentieth century. The treatises are especially useful in their schematic drawings and synthetic taxonomic treatments. A few representative phylogenies are presented in Fig. 1.

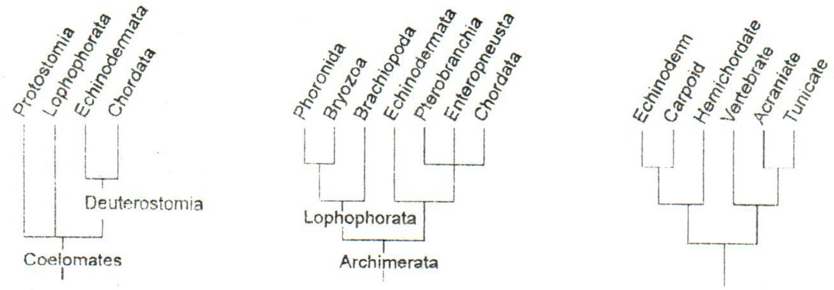
## OBJECTIVES

There are three major pitfalls affecting most of the previous approaches: (1) the prevailing myth of a protostome/deuterostome dichotomy; (2) the outstanding artificiality of the "Hemichordata" and "Lophophorata"; and (3) the attempts to diagnose taxa with characters belonging to incorrect levels of generality.

We remedy some of the above drawbacks by proposing a didactic summary of phylogenetic relationships among the major groups previously included in the Deuterostomata. A pedagogical format is applied for the discussion of the most conspicuous transformation series.

## MATERIAL AND METHODS

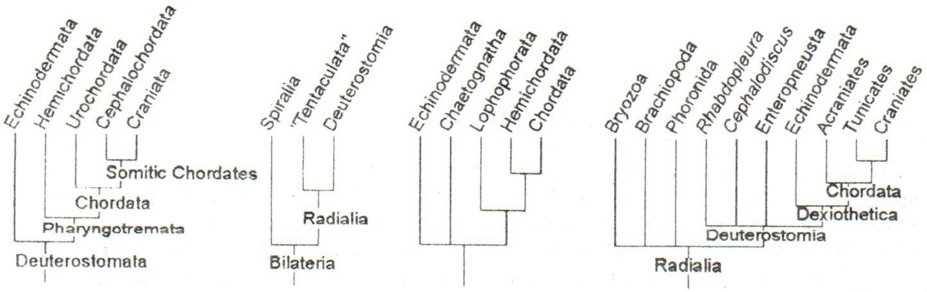
All descriptive information was obtained in the literature. In addition to the basic works cited in the introduction, we prepared many hundred pictorial tables with



(a) HYMAN (1951)

(b) EMIG (1982)

(c) JOLLIE (1982)

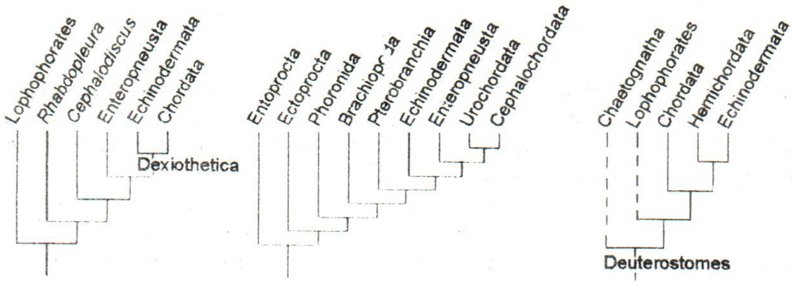


(d) SCHAEFFER (1987)

(e) AX (1989)

(f) BRUSCA and BRUSCA (1990)

(g) JEFFERIES (1991)



(h) CRIPPS (1991)

(i) SCHRAM (1991)

(j) RUPPERT and BARNES (1994)

FIGURE 1 – Some representative phylogenies of the Enterocoela.

illustrations from the primary literature. In these we could compare homologous structures throughout large clades.

The phylogenetic analysis was processed by hand, according to the principles for determining character generalities contained in HENNIG (1966), WILEY (1981), AX (1987), and AMORIM (1994). We used Metameria, Coelomata, and Bilateria as successively broader clades in order to follow character modifications through several subordinated levels. As the closest outgroups we used the tubicolous polychaetes, with the Oweneiidae as the immediate sister group. Rather than base all observations on a strictly defined set of outgroups (WATROUS and WHEELER, 1981; MADDISON et al., 1984; NIXON and CARPENTER, 1993), we preferred to change the extent of the outgroups themselves, according to the difficulties perceived for the correct interpretation of each individual character in the analysis. As another special case of outgroup comparison, we used the ontogenetic method of character polarization (FINK, 1982; NELSON, 1985; DE QUEIROZ, 1985; KRAUS, 1988; DE PINNA, 1994), in which ontogenetic transformations themselves were used as characters.

Characters have been organized into linear transformation series. Like the delimitation of individual characters, the choice of particular transformation series is arbitrary. The arrangement of the same character states into alternative transformation series would be acceptable. The important point is that all hypotheses of transformations should be maximally congruent among themselves. This approach emphasizes the importance of additive transformation series in phylogenetic analysis.

In our list of characters, all ramified transformation series have been subdivided into separate linear series. As a consequence of this manual procedure, we have also codified our secondary interpretations into the data matrix. Thus, secondary losses or very radical modifications of characters were first codified empirically as absences, followed between brackets by the character state that reflects our interpretation of its presence.

## RESULTS

Our results are summarized in a data matrix (Tab. 1), a cladogram (Fig. 2), and a phylogenetic system (Tab. 2). Only information intuitively perceived to make sense in a phylogenetic context has been included. Admittedly we may have been somewhat credulous in the incorporation of several classical ideas sometimes judged to be disreputable. Our justification is that this approach may provide further stimulus for thought. Ultimately, the information content and predictive power of particular sections in the phylogenetic tree stand or fall depending on the congruence of additional, credibly interpreted, data.

A separate list of apomorphies is provided for each taxon in the analysis (Appendix).

In the following list of character transformations, “0” indicates the plesiomorphic state of each transformation series, and lower case letters indicate successively apomorphic character states.

TABLE 1 – Morphological data matrix (0, plesiomorphies; a-d, successively apomorphic character states; -, non-applicable characters; *, reversals; ( ), character states interpreted *a posteriori*).

| | Ancestor | Pogonophora | Phoronida | Brachiopoda | Ectoprocta | Rhabdopleurida | Cephalodiscida | Echinodermata | Enteropneusta | Cephalochordata | Tunicata | Chaetognatha | Vertebrata |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 01. Coelom formation | 0 | a | b | b | b | b | b | b | b | b | b | b | b |
| 02. Coelom compartments | 0 | a | b | b | b | b | b | b | b | c | c | c | c |
| 03. Opistosoma | 0 | 0 | a | a | a | a | a | a | a | a | a | a | a |
| 04. Prosomal projection | 0 | 0 | a | a | a | a | a | 0(a) | 0(b) | 0(b) | 0(b) | 0(b) | 0(b) |
| 05. Metasomal projection | 0 | 0 | 0 | a | a | a | b | 0(b) | b | c | c | c | d |
| 06. Shape of cephalic shield | - | - | 0 | 0 | 0 | 0 | a | 0 | - | - | - | - | - |
| 07. Metasomal stalk | - | - | - | 0 | 0 | 0 | 0 | a | - | - | - | - | - |
| 08. Prosomal stem | 0 | 0 | 0 | 0 | 0 | 0 | 0 | a | 0 | 0 | 0 | 0 | 0 |
| 09. Digging prosomal proboscis | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | a | 0 | 0 | 0 | 0 |
| 10. Septum between trunk and tail | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | a | 0 |
| 11. Cleavage pattern | 0 | 0 | a | a | a | a | a | a | a | a | a | a | a |
| 12. Heart and pericardium | 0 | a | a | a | 0(b) | a | a | 0(b) | a | 0(b) | a | 0(b) | a |
| 13. Type of circulatory system | 0 | 0 | 0 | a | a | a | a | - | a | 0(b) | a | - | 0(b) |
| 14. Modif. of circulatory system | 0 | 0 | 0 | 0 | a | 0 | 0 | - | 0 | 0 | 0 | - | 0 |
| 15. Modif. of heart and pericardium | 0 | 0 | 0 | 0 | - | 0 | 0 | a | 0 | - | 0 | - | 0 |
| 16. Vascular system | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | a | 0 |
| 17. Posit. and develop. of the heart | 0 | 0 | 0 | 0 | - | 0 | 0 | - | 0 | - | a | -(a) | b |
| 18. Protective case | 0 | 0 | 0 | 0 | 0 | 0 | 0 | a | a | a | 0(a) | a | a |
| 19. Protective tunic | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | a | 0 | 0 |
| 20. Dispos. of gonads in metasoma | 0 | a | a | a | a | a | a | a | 0(b) | 0(b) | c | c | a(d) |
| 21. Right gonad | - | 0 | 0 | 0 | 0 | 0 | 0 | a | 0 | 0 | 0 | 0 | 0 |
| 22. Sex | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | a | a | 0(b) |
| 23 Paired male and female gonads | - | - | - | - | - | - | - | - | - | - | a | 0 | - |
| 24. Gut | 0 | a | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 25. Shape of digestive tract | 0 | 0 | a | a | a | a | a | a | 0(b) | 0(b) | 0(b) | 0(b) | 0(b) |
| 26. Torsion of digest. tube at metam. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | a | 0 | 0 |
| 27. Prosomal tentacles | 0 | 0 | a | a | a | a | a | a | a | a | a | a | a |
| 28 Lophophore | 0 | 0 | a | a | a | a | b | c | 0(d) | 0(d) | 0(d) | 0(d) | 0(d) |
| 29. Dispos. of arms of lophophore | - | - | 0 | 0 | 0 | a | 0 | 0 | - | - | - | - | - |
| 30. Hydrovascular system | 0 | 0 | 0 | 0 | 0 | 0 | 0 | a | 0 | 0 | 0 | 0 | 0 |
| 31. Respiratory organs | 0 | 0 | a | a | a | a | a | a | b | b | b | -(b) | c |
| 32. Feeding type | 0 | 0 | a | a | a | a | a | a | b | b | b | c | b |
| 33 Dorsal nerve chord | 0 | 0 | a | a | a | a | a | a | b | c | c | -(c) | c |
| 34. Mesosomal brain | - | - | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | a | b | c |
| 35. Nerve plates | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | a | a | a |
| 36. Dorsal nerve chord | - | - | - | - | - | - | - | - | 0 | 0 | 0 | a | 0 |

TABLE 1 – (continued).

| | Ancestor | Pogonophora | Phoronida | Brachiopoda | Ectoprocta | Rhabdopleurida | Cephalodiscida | Echinodermata | Enteropneusta | Cephalochordata | Tunicata | Chaetognatha | Vertebrata |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 37 Actinotroch larva | 0 | 0 | a | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 38. Larval stages | 0 | 0 | 0 | 0 | 0 | 0 | 0 | a | a | b | b | c | c |
| 39. Metatroch of larva | 0 | 0 | 0 | 0 | 0 | 0 | 0 | a | b | b | b | -(b) | b |
| 40. Bipinnaria larva | 0 | 0 | 0 | 0 | 0 | 0 | 0 | a | 0 | 0 | 0 | 0 | 0 |
| 41. Tornaria larva | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | a | 0 | 0 | 0 | 0 |
| 42. Fate of prototroch of larva | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | a | a | -(a) | b |
| 43. Endostyle | - | - | - | - | - | - | - | - | 0 | 0 | 0 | a | 0 |
| 44. Origin of mouth | 0 | 0 | 0 | a | a | a | a | a | a | a | a | a | a |
| 45. Valves | 0 | 0 | 0 | a | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 46. Colonies | 0 | 0 | 0 | 0 | a | a | b | 0(c) | 0(c) | 0(c) | 0(c) | 0(c) | 0(c) |
| 47. Pharyngeal evaginations | 0 | 0 | 0 | 0 | 0 | a | b | b | c | c | c | 0(d) | c |
| 48. Atrium | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | a | b | b | 0(c) | b |
| 49. Notochord | 0 | 0 | 0 | 0 | 0 | a | a | 0(a) | b | c | c | 0(d) | c |
| 50. Dorsal buccal diverticulum | - | - | - | - | - | 0 | 0 | a | 0 | 0 | 0 | - | 0 |
| 51. Glomerulus | 0 | 0 | 0 | 0 | 0 | a | a | 0(a) | a | 0(b) | 0(b) | 0(b) | 0(b) |
| 52. Axial gland | 0 | 0 | 0 | 0 | 0 | 0 | 0 | a | 0 | 0 | 0 | 0 | 0 |
| 53. Calcite skeleton | 0 | 0 | 0 | 0 | 0 | 0 | 0 | a | 0(b) | 0(b) | 0(b) | 0(b) | 0(b) |
| 54. Dexiothetism | 0 | 0 | 0 | 0 | 0 | 0 | 0 | a | b | b | c | 0(d) | 0(d) |
| 55. Position of mouth | 0 | 0 | 0 | 0 | 0 | 0 | 0 | a | 0 | 0 | 0 | 0 | 0 |
| 56. Cartilaginous rods | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | a | a | a | b | a |
| 57. Subneural gland | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | a | b | c | c | d |
| 58. Proboscis skeleton | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | a | 0 | 0 | 0 | 0 |
| 59. Cartilaginous endoskeleton | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | a |
| 60. Liver | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | a | a | a | b |
| 61. Buccal cirri | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | a | 0 | 0 | 0 |
| 62. Fin-folds | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | a | a | a | a |
| 63. Paired fin-folds | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | a |
| 64. Metamerism and striated fibers | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | a | a | 0(b) | a |
| 65. Differentiation of muscle blocks | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | a |
| 66. Eyes | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | a | b | c | d |
| 67. Multistratified epithelium | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | a | b |
| 68. Cephalic fold | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | a | 0 |
| 69. Sensory lateral line | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | a |
| 70. Induction of neural tube | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | a |
| 71. New hormone-producing organs | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | a |
| 72. Kidneys | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | a |

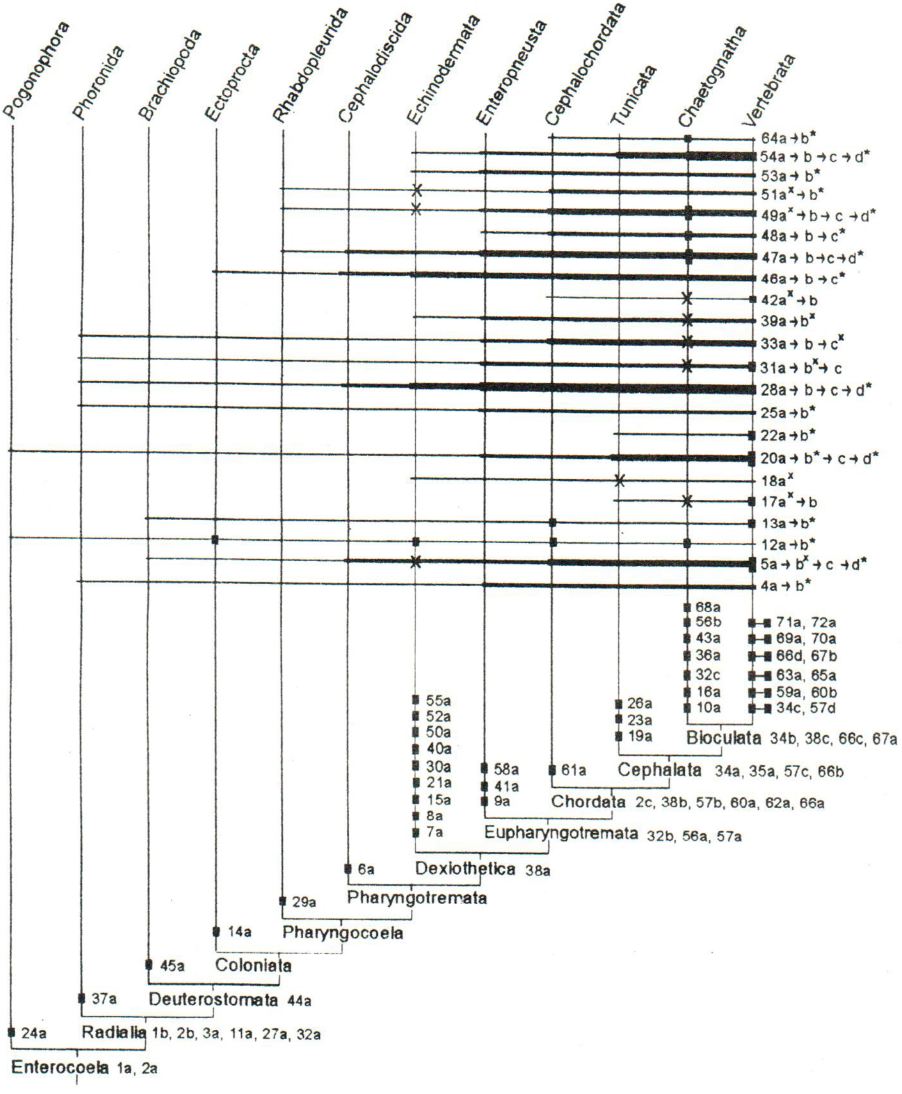


FIGURE 2 - Phylogeny of the higher taxa of Enterocoela, with 72 transformation series and 131 evolutionary steps. Reversals of a character (*) and reversals within a character ($^x$) are represented on the upper half of the phylogeny (the $^x$ reversals are also represented as independent apomorphies in the lower half of the phylogeny to avoid non-linear transformation series).

TABLE 2 – Non-categorized phylogenetic system of the Enterocoela.

- Enterocoela Huxley, 1875
  - Pogonophora Ivanov, 1949
  - Radialia Ax, 1989
    - Phoronida Wright, 1856
    - Deuterostomata Huxley, 1875
      - Brachiopoda Cuvier, 1802
      - **Coloniata, new**
        - Ectoprocta Nitsche, 1869
        - **Pharyngocoela, new**
          - Rhabdopleurida Schmiketsch, 1890
          - Pharyngotremata Schaeffer, 1987
            - Cephalodiscida Fowler, 1892
            - Dexiothetica Jefferies, 1979
              - Echinodermata Klein, 1734
              - **Eupharyngotremata, new**
                - Enteropneusta Huxley, 1875
                - Chordata Ehrenberg, 1836
                  - Cephalochordata Owen, 1846
                  - **Cephalata, new**
                    - Tunicata Lamarck, 1815
                    - **Bioculata, new**
                      - Chaetognatha Huxley, 1875
                      - Vertebrata Cuvier, 1817

## COELOM AND BODY REGIONS

1. Coelom formation: (0) schizocoelic; (a) anterior three pouches arise by enterocoely [**Enterocoela**]; (b) all vestiges of schizocoelic metamery are lost [**Radialia**].

In tubicolous annelids the body becomes subdivided into three distinct tagma: a tentaculate prostomium, a tube-secreting peristomium and an elongate gonad-containing trunk. In the Oweniidae a fourth tail region becomes distinct. We suggest that these four tagmas are homologous to the prosoma, mesosoma, metasoma, and opisthosoma of the Pogonophora.

In Oweniidae all coelomic spaces are distinctly schizocoelous, and the metasoma is clearly divided by internal dissepiments into a number of true metameres. In the Pogonophora, on the other hand, the coelomic spaces of the prosoma, mesosoma and metasoma arise by enterocoely. IVANOV (1963: 110, Fig. 77) illustrates how the pairs of mesocoels and metacoels become successively detached from the unpaired protocoel in *Siboglinum caulleryi*, following the typical enterocoelic pattern of coelom formation also seen in the enteropneust *Saccoglossus pusilus* (IVANOV, 1963: 110, Fig. 78). On the other hand, NØRREVANG (1970) observed that in the opisthosoma of *Siboglinum fiordicum* the coelomic spaces develop as paired splits in the mesoderm.

Pogonophora thus still retain a primarily schizocoelic pattern of metamere formation in the posterior part of the body, while a novel enterocoelic and tricoelomate pattern has become superimposed from fore to aft in the anterior region of the body.

In pogonophorans there are still indications that at least the outer body wall of the preceding tagma retain vestiges of a primitive metameric pattern: (1) the region of the mesosoma situated in front of the bridle sometimes appears ringed, in consequence of one to three secondary annular grooves (IVANOV, 1963: 14, Fig. 7); (2) the anterior region of the trunk contains lateral rows of metamerically arranged adhesive papillae, furnished with small cuticular plates. These are homologous to the parapodia and uncini of sedentary polychaetes (HARTMAN, 1954). They are used in both groups to cling to the inner surfaces of the tube, while the worm moves up and down inside it (IVANOV, 1963: 17); (3) the posterior region of the trunk is annulated, although these annuli are superficial, supposedly without affecting the nervous, muscular, and circulatory systems; (4) in late embryos the metasoma may be provided with more than one row of mobile setal bundles (IVANOV, 1963: 115, Fig. 81).

2. Coelomic compartments: (0) metameric, with multiple similar segments throughout the body; (a) metameric, with multiple similar segments restricted to the opisthosoma, as well as a single small protocoel, a pair of somewhat larger mesocoels, and a pair of large metacoels individualized by transversal septa in the anterior region [**Enterocoela**]; (b) oligomeric, with loss of the posterior schizocoelic metameres [**Radialia**]; (c) no distinct transversal septa dividing coelomic spaces in adult [**Chordata**].

3. Opisthosoma: (0) present; (a) absent [**Radialia**].

We interpreted the terminal digging or anchoring opisthosoma in Pogonophora as an unmodified relique of the annelid body organization. Besides containing pairs of coelomic cavities divided by internal septa, the metameres are clearly visible from the outside. Each metamere of the opisthosoma further contains bundles of retractile setae within distinct setal sacs, just like in annelids.

With the loss of the opisthosoma in the Radialia, all vestiges of a metameric body plan became lost. The radialians become exclusively enterocoelic and definitively tricoelomate. Externally, the body consists typically of a prosoma, mesosoma, and metasoma (MASTERMAN, 1898; EMIG, 1976).

4. Prosomal projection: (0) absent; (a) projected among the tentacles [**Radialia**]; (b) absent [**Eupharyngotremata**].

The prosomal projection (preoral lobe) is called an epistome in the lophophorates and a cephalic shield in the pterobranchs. We consider both these structures as homologous to the prosomal peduncle (stem) of the Echinodermata (see character 8a).

5. Metasomal projection: (0) undifferentiated; (a) a stalk, used to attach the organism to the substrate, differentiates from the posterior region of the trunk [**Deuterostomata**]; (b) the trunk stalk is no longer used for attachment [**Pharyngotremata**]; (c) the stalk becomes differentiated into a post-anal tail region for swimming [**Chordata**]; (d) the tail is used for active swimming by strong muscular blocks in adult [**Vertebrata**].

In *Cephalodiscus* the free stalk is the functional homologue of a tail, for it takes part in clinging and crawling movements as the animal creeps about among hydroids (EATON, 1970: 976) or up and down its colonial coenecium (DILLY, 1993). The metasomal stalk has been secondarily lost in the Echinodermata (see character 7a).

The free stalk region is retained as a vestigial structure in the young vermiform stages of some enteropneusts (HYMAN, 195: 136, Fig. 48a; EATON, 1970: 972, Fig. 3). In calcichordates, the free stalk pulls the body forward over the substrate.

6. Shape of cephalic shield: (0) oval, without lateral notches; (a) flat, with a more or less circular outline, indented laterally with a pair of notches (HYMAN, 1959: 157, Fig. 56c) [**Cephalodiscida**].

We interpreted the cephalic shield as homologous to the prosomal projection of the lophophorates and rhabdopleurids and to the echinoderm stem.

7. Metasomal stalk: (0) present; (a) absent [**Echinodermata**].

8. Prosomal stem: (0) absent; (a) present, used for attachment to the substrate [**Echinodermata**].

The crinoid stem is a new development, homologous to the cephalic shield (prosoma) of rhabdopleurids and cephalodiscids (EATON, 1970: 977).

9. Digging prosomal proboscis: (0) absent; (a) present [**Enteropneusta**].

The enteropneust proboscis, which is evidently homologous to the pre-oral lobe of the Radialia (i. e., the stem of Echinodermata, the cephalic shield of pterobranchs, and the epistome of lophophorates), has the entirely new function of digging into the substrate.

10. Septum between trunk and tail: (0) absent; (a) the trunk and post-anal tail become separated by a distinct septum (HYMAN, 1959: 39, Fig. 15a) [**Chaetognatha**].

## SEGMENTATION OF THE EGG

11. Cleavage pattern: (0) spiral; (a) radial (ZIMMER, 1973: 595) [**Radialia**].

Though biradial in the 16-cell stage and sometimes with an apparent spiral arrangement of the blastomeres, the typical radial arrays and the occurrence of 8-celled tiers during later stages dictate that cleavage in phoronids is radial and not spiral (EMIG, 1982: 16; ZIMMER, 1973: 595). Consequently, in our scenario the radial cleavage of the Radialia is independent from the radial cleavage also found in the Cnidaria.

CIRCULATORY SYSTEM

12. Heart and pericardium: (0) ventral vessel undifferentiated within the protocoel; (a) ventral vessel forming a pulsating heart and wall of protocoel modified into a pericardium [**Enterocoela**]; (b) heart and pericardium absent in ectoprocts (RYLAND, 1982) [**Ectoprocta**], echinoderms (HYMAN, 1955) [**Echinodermata**], cephalochordates (JOLLIE, 1973: 95) [**Cephalochordata**], and chaetognaths (HYMAN, 1969) [**Chaetognatha**].

13. Type of circulatory system: (0) closed, with well developed vessels; (a) open, vessels being reduced and opening into haemal spaces that do not contain vessel walls [**Deuterostomata**]; (b) secondarily closed [**Cephalochordata**, **Vertebrata**].

14. Modification of circulatory system: (0) circulatory system well developed ; (a) reduced to the funiculus of mesenchymal chords which still function in the transport of material between the colony members (CARLE and RUPPERT, 1983) [**Ectoprocta**].

15. Modification of heart and pericardium: (0) heart and pericardium present; (a) protocoel modified into the axocoel (axial sinus) and the heart vesicle originates the madreporic vesicle (dorsal sac) in the larvae (JEFFERIES, 1979) [**Echinodermata**].

These changes are associated with the modification of the left hydrocoel (mesocoel) into a hydrovascular system (see character 30a).

16. Vascular system: (0) present; (a) absent [**Chaetognatha**].

The circulatory system of Echinodermata is secondarily modified (see character 15a).

17. Position and development of the heart: (0) pre-pharyngeal, within the prosoma; (a) post-pharyngeal, in the region corresponding to the mesosoma [**Cephalata**]; (b) same position, becoming strongly muscularized (myocardium) and developing valves for a more efficient circulation [**Vertebrata**].

The change of position of the heart is evidently associated with the complete absence of a prosoma in the Bioculata. Whether the prosomal and mesosomal hearts are homologous or independent structures remains to be clarified.

Although the Chaetognatha do not have a typical heart and a vascular system (see characters 12a and 16a), we interpret these absences as secondary reductions associated with the small size of these organisms.

EXTERNAL ENCASEMENT

18. Protective case: (0) present; (a) absent [**Dexiothetica**].

We consider the external cases of all basal groups (tubes in annelids, pogonophorans and phoronids, valves in brachiopods, zoaria or zoecia in Ectoprocta, and coenecia in pterobranchs) as homologous structures. Because the tunicates are far removed from these basal groups, we interpret the protective tunic as an independent acquisition (see character 19a). Interestingly, this homoplasy seems to be correlated with an additional reversal in tunicates, the U-shaped digestive tube (see character 26a).

19. Protective tunic: (0) absent; (a) the body is enclosed in a protective tunic containing a material akin to cellulose [**Tunicata**].

## GONADS

20. Disposition of gonads in metasoma: (0) arranged metamerically; (a) restricted to a single pair [**Enterocoela**]; (b) arranged metamerically [**Eupharyngotremata**]; (c) restricted to two pairs [**Cephalata**]; (d) restricted to a single pair [**Vertebrata**].

21. Right gonad: (0) present; (a) absent (JEFFERIES, 1979) [**Echinodermata**].

22. Sex: (0) animals dioecious; (a) animals monoecious [**Cephalata**]; (b) animals dioecious [**Vertebrata**].

23. Paired male and female gonads: (0) present; (a) one male and one female gonad lost from one side of the body [**Tunicata**].

## DIGESTIVE TUBE

24. Gut: (0) digestive tube present; (a) the digestive tube is totally absent in the adult [**Pogonophora**].

The straight larval gut specializes into an internal tissue (trophosoma), which harbours symbiotic chemoautotrophic bacteria that provide all the nutritional needs of the adults.

25. Shape of digestive tract: (0) digestive tract straight; (a) alimentary canal becomes permanently U-shaped, with anus located near mouth [**Radialia**]; (b) the alimentary canal becomes linear, leading from an anterior mouth to a posterior anus [**Eupharyngotremata**].

We correlate the straight digestive tube of Eupharyngotremata with the loss of an attachment stage.

The alimentary canal becomes contorted again in Tunicata as a consequence of the torsion of the larval body axis at metamorphosis (see character 26a).

26. Torsion of digestive tube at metamorphosis: (0) absent; (a) present [**Tunicata**].

## TENTACLES OF MESOCOEL

27. Prosomal tentacles: (0) present; (a) absent [**Radialia**].

We interpret the prosomal tentacles of the Pogonophora as homologous to the annelid prostomial tentacles.

28. Lophophore: (0) absent; (a) presence of a pair of tentaculate arms on the mesosoma [**Radialia**]; (b) presence of five or more pairs of tentaculate arms disposed radially on the dorsal surface of the mesosoma (HYMAN, 1959: 157, Fig. 56b) [**Pharyngotremata**]; (c) the tentacles from the original right side of the body become lost [**Dexiothetica**]; (d) the mesocoel tentacles are lost [**Eupharyngotremata**].

The lophophore is a novel structure formed by a double ridge of the body wall, which has a crescentic shape and originally encircles the mouth, but not the anus. It contains a single row of tentacles with extensions of the mesocoel. The tentacles are used mainly for microphagous feeding by ciliary tracts and mucous production, and also promote gaseous exchanges with the circulating feeding currents of water. The lophophore derives from the postoral feeding metatroch (ciliary band) of the larva, which becomes tentaculate in the actinotroch of phoronids (SALVINI-PLAWEN, 1982: 78).

The loss of tentacles from the right side of the body in Dexiothetica is associated with the new habit of the semi-colonial zooids of leaving the coenecium and crawling over the mud on their right side (JEFFERIES, 1991).

In the Echinodermata the lophophore of the left side of the body becomes modified into the hydrovascular system (see character 30a).

29. Disposition of arms of lophophore: (0) horizontal, in the form of a horseshoe that embraces the mouth; (a) vertical and parallel to each other, projecting upwards in the proximal region and then curving backwards and downwards in the rear region when the zooid is extended from its tube (HYMAN, 1959: 181, Fig. 67c) [**Rhabdopleurida**].

30. Hydrovascular system: (0) absent; (a) tentacles from the original left mesocoel (hydrocoel) form the water vascular system [**Echinodermata**].

Given the similarities between the tentacles with coelomic extensions of the hydrovascular system and the lophophore (RUPPERT and BARNES, 1994: 989), we interpret these structures as homologous. In other words, the hydrovascular system is a modified lophophore.

The hydrovascular apparatus is still used in ciliary feeding, but in free-living echinoderms becomes the main system for locomotion.

## RESPIRATORY EXCHANGES

31. Respiratory organs: (0) the tentacular apparatus of the prosoma functions as the main gas-exchanging organ; (a) respiratory exchanges occur mainly on the mesosomal lophophore [**Radialia**]; (b) with the loss of a lophophore, respiration occurs on the walls of the branchial slits [**Eupharyngotremata**]; (c) as body size increases, the walls of the branchial slits become modified into respiratory gills [**Vertebrata**].

In Vertebrata, the walls of the branchial slits give rise to internal and external vascular folds or gills for respiration. The gills are another response to the active nature of the animal.

The gill slits are secondarily lost in the Chaetognatha (see character 47d).

## FEEDING

32. Feeding type: (0) microphagic, by tentacles of prosoma: (a) microphagic, by tentacles of lophophore [**Radialia**]; (b) microphagic, inside the pharynx [**Eupharyngotremata**]; (c) macrophagic, by grasping spines and teeth on the head [**Chaetognatha**].

The microphagic feeding is by mucous and ciliary movements, despite the changes from prosomal to mesosomal tentacles in the Radialia. Even with the entirely novel pharyngeal filtering mechanism appearing in the Eupharyngotremata, the feeding type still is by mucous and ciliary movements, now within the pharynx.

It is interesting that the adults of the Vertebrata are also macrophagic, actively swimming nektonic predators, and that the branchial slits loose their alimentary function to become exclusively respiratory. However, as the mucous ciliary feeding mechanism is still retained in the ammocoetes larvae of the Vertebrata, it becomes necessary to interpret the predatory habits of Chaetognatha and within Vertebrata as independent evolutionary events.

## NERVOUS SYSTEM

33. Dorsal nerve chord: (0) presence of a dorsal cerebral ganglion, circumpharyngeal connectives, and a ventral nerve chord; (a) nervous system is diffuse and intraepidermal [**Radialia**]; (b) a dorsal collar chord, which is occasionally hollow and has a neuropore, becomes differentiated from the epidermal plexus of the mesosoma (HYMAN, 1959: 200) [**Eupharyngotremata**]; (c) the dorsal nerve chord extends posteriorly to the tip of the tail region of the trunk [**Chordata**].

We consider the prosomal dorsal cerebral ganglion of Pogonophora to be homologous to the prostomial ganglion of annelids. In metameric animals the dorsal prostomial ganglion is derived from the apical plate of the larva.

In the Radialia, on the other hand, this apical plate degenerates at metamorphosis and the adult nervous system differentiates from the dermal nerve net of the larva (SALVINI-PLAWEN, 1982: 80).

In Eupharyngotremata, the dorsal nerve chord is derived from the larval ciliary bands of the metatroch. These new developments are functionally correlated with the creeping-burrowing habit and increase in body size.

The extension of the dorsal nerve chord into the tail region in Chordata is associated with the posterior metamerization of the muscular myotomes and the concomitant formation of a supporting notochord.

We interpret the absence of a dorsal nerve chord in Chaetognatha as a secondarily reduction (see character 36a).

34. Mesosomal brain: (0) the collar ganglion, when present , is an intraepidermal thickening of the nervous plexus, from which it is not definitely delimited (HYMAN, 1959: 161, Fig. 59a); (a) a cerebral vesicle, that is individuated from the epidermis and its basal membrane, is present in the larva [**Cephalata**]; (b) a dorsal cerebral ganglion is conspicuous in the mesosoma of the adult [**Bioculata**]; (c) the mesosomal ganglion becomes enlarged into a true brain, encased in a cranium [**Vertebrata**].

We suggest that the development of the dorsal cerebral ganglion in Bioculata is associated with the development of a pair of frontal eyes.

The improved cephalization found in the Vertebrata is correlated with improved predatory capabilities. Characteristic cranial nerves are formed to coordinate paired sensory structures (nasal, optic, otic) in the frontal region. With the acquisition of a true brain, all circumenteric connectives of the nervous system are lost and an increasingly motile free-living organism evolves.

35. Nerve plates: (0) nerve ends simple; (a) nerves that innervate the myotomes provided with motor end plates [**Cephalata**].

36. Dorsal nerve chord: (0) present; (a) absent [**Chaetognatha**].

The loss of the dorsal nerve chord is probably associated with the loss of the notochord. Although HYMAN (1959: 64) considers the central nervous system of Chaetognatha reminiscent of nematodes, we interpret the lateral ganglia in the head, the circumenteric mesenteries and the various longitudinal nerves (HYMAN, 1959: 18, Fig. 7c) as secondary acquisitions.

## LARVAE AND ENDOSTYLE

37. Actinotroch larva: (0) absent; (a) present [**Phoronida**].

The presence of an actinotroch larva is considered an autapomorphy for Phoronida, even though a larva is absent in one species (CARLE and RUPPERT, 1983: 190).

We follow HYMAN (1959: 271) in considering the actinotroch larva an altered trochophore.

38. Larval stages: (0) trochophore; (a) dipleurula-type larva [**Dexiothetica**]; (b) development abbreviated, with loss of larval stages that swim by ciliary bands [**Chordata**]; (c) loss of a characteristic larval stage, the young animals being miniatures of the adults [**Bioculata**].

The "larva" in the Chordata (essentially a miniature of the adult), although still having cilia in early developmental stages (JOLLIE, 1973: 88), now begins to swim by muscular undulations. Thus the previous pattern of ciliary locomotion in the larva is abandoned. Furthermore, a muscular post-anal tail, homologous to the calcichordate tail and to the stalk of the cephalodiscids, and still retained in some enteropneusts, provides a new mode of forward propulsion for the animal. In Chordata the tail action is reversed in relation to that of calcichordates, wherein the tail served to pull the animal over the substrate. We suggest that such a reversal may be correlated with the loss of the calcichordate skeleton already in the stem-line of the Eupharyngotremata. All these novelties are functionally correlated with a locomotor axial system (notochord, myotomes, and dorsal nerve chord ) in both larvae and adults.

39. Metatroch of larva: (0) forming a circle around the middle of the body; (a) becoming convoluted and forming perpendicular bands along the aboral side of the larva [**Dexiothetica**]; (b) ciliary bands invaginate to form a hollow neural tube with anterior and posterior neuropores [**Eupharyngotremata**].

The multipolar nerve cells which innervate the cilia in Eupharyngotremata probably originate a distinct category of neurons in the spinal chord (see LACALLI and WEST, 1993).

We interpreted the absence of a neural tube in Chaetognatha as a secondary loss, associated with the absence of its embryological inductor, the notochord (see character 36a).

40. Bipinnaria larva: (0) absent; (a) present, the posterior ciliary band (telotroch) having been lost [**Echinodermata**].

We derive the bipinnaria larva from the dipleurula. Other echinoderm larvae (brachiolaria, auricularia, and pluteus) are further derived, as inferred from the phylogeny of the Echinodermata (SMILEY, 1988: 71).

41. Tornaria larva: (0) absent; (a) present [**Enteropneusta**].

We derive the tornaria larva of Enteropneusta from a dipleurula-type larva.

42. Fate of prototroch of larva: (0) presence of a circumoral band of cilia; (a) the circumoral band of cilia migrates into the mouth and becomes converted into a midventral endostylar muco-ciliary organ with peripharyngeal bands inside the pharynx [**Chordata**]; (b) part of the endostyle of the ammocoetes larva becomes the thyroid endocrine gland at metamorphosis [**Vertebrata**].

In the Chordata, the endostyle contains peroxidase-producing cells (SCHAEFFER, 1987: 219).

In Chaetognatha, the endostyle has been secondarily lost (see character 43a), together with the loss of the gill slits.

43. Endostyle: (0) present; (a) absent [**Chaetognatha**].

The loss of the endostyle in Chaetognatha is associated with the loss of gill slits (see character 47d) in this taxon.

## BLASTOPORE

44. Origin of mouth: (0) The blastopore originates the mouth during ontogeny; (a) the mouth is a new aperture opposite to the blastopore [**Deuterostomata**].

In Deuterostomata the blastopore thus indicates the posterior pole of the larva, in the proximity of which the anus opens (ZIMMER, 1973).

SHELL

45. Valves: (0) shell absent; (a) mantle lobes of the body secrete a pair of valves [**Brachiopoda**].

COLONIALITY

46. Colonies: (0) animals free-living, or sometimes aggregated to each other, but not interconnected; (a) colonies of zooids become physically interconnected [**Coloniata**]; (b) animals semi-colonial, physical contact between zooids being lost [**Pharyngotremata**]; (c) animals free-living [**Dexiothetica**].

Within the Tunicata, coloniality is supposed to have arisen several times from solitary forms (RUPPERT and BARNES, 1994:879).

PHARYNGEAL SLITS

47. Pharyngeal evaginations: (0) absent; (a) inner surface of pharyngeal wall with one pair of deep dorsolateral grooves which do not break through to the exterior (HYMAN,1959: 185, Fig. 70a) [**Pharyngocoela**]; (b) the single pair of branchial grooves open laterally on the metasomal trunk, just behind the posterior border of the collar [**Pharyngotremata**]; (c) multiple branchial slits pierce both sides of the pharynx [**Eupharyngotremata**]; (d) absent [**Chaetognatha**].

In Rhabdopleurida the pharyngeal grooves are surrounded by vacuolated cells (HYMAN, 1959: 185, Fig. 70a). This indicates the similarities in the origin of branchial slits and the notochord.

Although most echinoderms have lost the right branchial slit, this pore is still retained in stem-group cinctans (JEFFERIES, 1991).

With the loss of the feeding lophophore, an internal pharyngeal collecting system is developed in the Eupharyngotremata. Feeding is performed by mucous and ciliary filtering within the pharynx. The pharynx becomes gradually enlarged and pierced by multiple pharyngeal slits. The ciliated branchial slits result from evaginations of the endoderm that fuse with the ectoderm.

The series of fossil cornutes sequenced by JEFFERIES (1979) indicate that the multiple gill slits began first only on the left side and much later developed on the right side. This asymmetry in branchial slit development is still indicated in the ontogeny of the Cephalochordata.

In both Enteropneusta and Cephalochordata, the branchial slits begin ontogenetically as oval slits, become elongate on the dorsal surface of the pharynx, and the apertures becomes U-shaped with the downgrowth of hollow tongue bars, containing a coelomic cavity. The septa between successive pharyngeal slits may be bound to adjacent septa by cross connections termed synapticules. An arcade of trifid skeletal supports, and branches of these rods into the synapticules, are formed as a collagenous thickening of the basement membrane of the pharyngeal epithelium (HYMAN, 1959: 110, Fig. 37c, 38a, 39a).

The complete absence of gill slits in Chaetognatha is a response to a predatory life style. Together with the branchial slits, the endostyle, the dorsal nerve chord, the notochord, the myotomes, and their metameric nerves, are also lost.

Pharyngeal bars sometimes contain chitin. Chitin is a widespread structural polysaccharide found in metazoans, protozoans, and fungi. The synthetic pathways for its production is considered to have been lost in hemichordates, echinoderms and chordates. Graptolithids apparently also do not contain chitin (MILLER, 1991). However, the grasping spines of chaetognaths are composed of chitin (HYMAN, 1958). Chitin has also been uniquely reported in the pharyngeal bars of the cephalochordate *Branchiostoma floridae* and in the coenecia of some, but not all, species of *Rhabdopleura* (SANNASI and HERMANN, 1970).

Even though HYMAN (1959: 11) states that the grasping spines and teeth of chaetognaths are epidermal derivatives, it might not be too farfetched to imagine the grasping spines as homologous to the gill bars of enteropneusts and cephalochordates. Both structures are supposedly unique within the Pharyngotremata in having chitin. Furthermore, because the stomodaeum covers the inner walls of the pharynx and the branchial slits are formed by both endoderm and ectoderm, the endodermal nature of the visceral skeleton may not be a settled matter after all. Alternatively, the grasping spines of Chaetognatha could be of endodermal origin, despite being located on the outer surface of the mouth. The whole vestibule region in chaetognaths could be homologous to the pharynx of the craniates.

48. Atrium: (0) absent; (a) the branchial slits open collectively into branchial sacs [**Eupharyngotremata**]; (b) branchial sacs modified into a large pair of atria [**Chordata**]; (c) absent [**Chaetognatha**].

## NOTOCHORD AND BUCCAL DIVERTICULUM

49. Notochord: (0) absent; (a) anterior wall of buccal cavity evaginated into a dorsal, hollow diverticulum [**Pharyngocoela**]; (b) buccal diverticulum extended anteriorly within the protocoel [**Eupharyngotremata**]; (c) buccal diverticulum transformed into a rigid notochord [**Chordata**]; (d) loss of the notochord [**Chaetognatha**].

The buccal diverticulum in Pharyngocoela projects forward below the middorsal blood channel. As the boundary between ectoderm and endoderm has not been clearly established, the endodermal origin of this diverticulum is conjectural (HYMAN, 1959: 200).

A rodlike notochord extends along the length of the archenteron in the Chordata and is formed by an elevation of its roof. It has a sheath, vacuolated cells, a supporting function, and lies dorsal to the main blood vessel.

The buccal diverticulum (stomochord), the notochord, and the branchial grooves are all embryologically homologous. They are evaginations from the pharyngeal wall and are surrounded by vacuolated cells. The new function of the buccal diverticulum as a solid supporting structure can be associated with the formation of the axial muscular system of myotomes, and the loss of the calcichordate echinoderm-like skeleton. In the apt comparison of ROMER (1972), there occurs at this point a superposition of a locomotor system (notochord, segmental muscles and dorsal nervous system) on a visceral animal.

The buccal diverticulum has been lost in the Echinodermata (see character 50a).

The loss of the notochord in Chaetognatha is a possible response to a planktonic mode of existence.

50. Dorsal buccal diverticulum: (0) present; (a) absent [**Echinodermata**].

## GLOMERULUS AND AXIAL GLAND

51. Glomerulus: (0) absent; (a) the protonephridium derived from the blastocoel of the larva becomes associated with the protocoel and forms a vascular glomerulus, with an excretory function [**Pharyngocoela**]; (b) absent [**Chordata**].

We interpret the vascular glomerulus as having been modified into an axial gland in Echinodermata (see character 52a).

The loss of the vascular excretory organ in Chordata is correlated with the reduction of the prosoma.

52. Axial gland: (0) absent; (a) present [**Echinodermata**].

The axial gland is a modification of the glomerulus correlated with the loss of the circulatory system in the Echinodermata (see character 15a and remarks for character 16).

## MESODERMIC SKELETON

53. Calcite skeleton: (0) absent; (a) the mesoderm forms porous spicules or plates of calcite that may enclose the whole body [**Dexiothetica**]; (b) loss of the echinoderm-like calcite skeleton [**Eupharyngotremata**].

We diverge from JEFFERIES (1991) by suggesting that all the calcichordates could be interpreted as belonging to the stem-lineage of the Eupharyngotremata. A strict adherence to that author's reconstruction would demand acceptance of five independent losses of the calcitic skeleton (in Enteropneusta, Cephalochordata, Tunicata, Chaetognatha, and Vertebrata).

On the other hand, inclusion of the calcichordates within the Echinodermata would permit the hypothesis that the calcite skeleton appeared only once in Echinodermata, without its secondary loss. However, the gill slit scenario would become more complex (multiple slits in Dexiothetica, reduced to one pair in cynctans). Furthermore, the tail of the calcichordates, which is not homologous to the stem of the Echinodermata, would have to be lost independently.

## SYMMETRY

54. Dexiothetism: (0) body symmetrical; (a) right side of body reduced [**Dexiothetica**]; (b) a new plane of symmetry, perpendicular to that of Bilateria, is formed (JEFFERIES, 1979) [**Eupharyngotremata**]; (c) the pharynx is symmetrical, although the dorsal nervous system is still asymmetric [**Cephalata**]; (d) the animals are fully symmetrical [**Bioculata**].

The asymmetry trend culminates with the dexiothetism that occurred in the stem-lineage of the Dexiothetica. Dexiothetism implies that an animal resembling *Cephalodiscus* took to crawling right-side-downwards on the mud of the sea floor, pulling itself along by the stalk (JEFFERIES, 1991: 103, Fig. 6). The consequence is that the original sagittal plane of the Bilateria is lost, becoming horizontal in the stem line of the Dexiothetica.

The new plane of symmetry in Eupharyngotremata begins to be formed starting by the tail region (homologous to the stalk of *Cephalodiscus*) and advancing forward into the head. This trend may be followed through the cornute calcichordates according to the detailed reconstructions of JEFFERIES (1991). Several evidences of asymmetry, particularly in the pharynx, may be detected in the larval and young stages of Enteropneusta and Cephalochordata.

In the Bioculata the evolutinary trend which results in a new plane of symmetry perpendicular to that in the remaining Bilateria is virtually completed. Occasional vestiges of asymmetry have notwithstanding been reported in the lower chordates (GISLÉN, 1930).

## MOUTH AND SITE OF ATTACHMENT

55. Position of mouth: (0) subterminal, at anterior region of animal; (a) in centre of the upper (oral) surface [**Echinodermata**].

The new position of the mouth in the Echinodermata is a consequence of the larva which attaches by the prosoma and thus develops a new peduncle. The crinoid stem is thus not homologous to the metasomal peduncle of the Dexiothetica.

## VISCERAL SKELETON

56. Cartilaginous rods: (0) absent; (a) cartilaginous rods support the branchial slits [**Eupharyngotremata**]; (b) pharyngeal rods modified into buccal epithelial grasping spines and teeth for macrophagous feeding [**Chaetognatha**].

The pharyngeal rods are reported to contain chitin in Cephalochordata (SANNASI and HERMANN, 1970) and Chaetognatha (HYMAN, 1958). No experimental data is available on the presence of chitin in the branchial bars of Tunicata and Vertebrata. We suggest that at least the chitin-containing grasping spines and the vestibule in Chaetognatha are homologous to the pharyngeal bars and the pharynx of the Vertebrata, respectively.

## SUBNEURAL GLAND AND HYPOPHYSIS

57. Subneural gland: (0) absent; (a) presence of a pre-oral ciliary groove at base of proboscis, probably a sensory organ **[Eupharyngotremata]**; (b) ciliary groove modified into wheel organ **[Chordata]**; (c) the vibratile organ, homologous to the wheel organ, becomes associated with a subneural gland, which originates from the middle of the larval neural tube **[Cephalata]**; (d) the subneural gland becomes definitely fused with the previously sensory organ (hypothalamus + hypophysis), functioning as an endocrine gland (adenohypophysis or anterior pituitary) **[Vertebrata]**.

The sensory organ of Eupharyngotremata is probably modified from a simple epithelial ciliated chemosensory vesicle (VANDEL, 1961: 24).

The compound organ of Bioculata, as well as having an olfactory (chemosensory) function in connection with feeding, now also reacts to light (see VANDEL, 1961: 25).

The ciliary loop (*corona ciliata*) of chaetognaths is a peculiar sensory organ whose anterior end usually lies immediately behind the pore of the ganglionar and possibly glandular retrocerebral organ. This suggests to us a probable homology with the tunicate compound organ.

## CHONDROID SKELETON

58. Proboscis skeleton: (0) absent; (a) present **[Enteropneusta]**.

In Enteropneusta a proboscis skeleton, similar to cartilage of craniates, becomes associated with the stomochord in the prosoma.

59. Cartilaginous endoskeleton: (0) absent; (a) present **[Vertebrata]**.

In Vertebrata, the notochord induces the formation of cartilaginous endoskeleton, later replaced by endochondric ossification of the vertebral column and cranium. Proteic matter, as well as calcium, is incorporated into such bone tissue.

## HEPATIC CAECA

60. Liver: (0) hepatic caeca absent; (a) presence of a single pair of intestinal diverticulae **[Chordata]**; (b) presence of a complex endodermal organ, the liver **[Vertebrata]**.

SCHAEFFER (1987: 225) suggests that the homology between the intestinal diverticulum of amphioxus and the craniate liver still remains to be demonstrated. However, no character conflicts are present that would question this transformation series.

## BUCCAL TENTACLES

61. Buccal cirri: (0) absent; (a) surrounding the oral vestibule **[Cephalochordata]**.

We have been unable to find conclusive evidence of homology of the buccal cirri of cephalochordates with the mesocoelic tentacles of the basal groups of Radialia (see character 28).

## FINS

62. Fin-folds: (0) absent; (a) presence of median fin-ridges [**Chordata**].

Median fin-ridges are present in the ascidian tadpole larva and in the adult Larvacea. We interpret the fins as having been lost in some tunicate subgroups with specialized adult habits (sessile, colonial, etc.).

63. Paired fin-folds: (0) absent; (a) present, with strong skeletal supports [**Vertebrata**].

## MUSCULATURE

64. Metamerism and striated fibers: (0) absent; (a) muscles become metameric along whole length of trunk and contain striated fibers [**Chordata**]; (b) absent [**Chaetognatha**].

As a consequence of the metamerization of the muscles, the dorsal nerves which innervate them also become metameric.

Histologically the body wall muscle fibers in Chaetognatha somewhat resemble those of nematodes (HYMAN, 1959: 14), being the basis for the alignment of these two taxa. In our scenario we interpret the absence of myotomes, notochord, dorsal nerve chord and associated metameric nerves as correlated secondary reductions.

In the Tunicata the metamerism and the muscle blocks become less distinct as a consequence of specialized life habits. The musculature of the tail is not segmented in the larva.

65. Differentiation of muscle blocks: (0) not differentiated; (a) the mesoderm becomes dorsalized and differentiated into dermatomes and sclerotomes, in addition to myotomes [**Vertebrata**].

The mesoderm induces the formation of more complex endodermal organs (liver, pancreas, etc.) (SCHAEFFER, 1987: 219).

## VISION

66. Eyes: (0) absent; (a) presence of median unicellular cup-shaped photosensory cells (GRASSÉ, 1966: 990, Fig. 436) [**Chordata**]; (b) presence in tadpole larva of a median, compound cup-shaped ocellus (GRASSÉ, 1966: 679, Fig. 144) [**Cephalata**]; (c) a pair of eyes of the inverse type, consisting of five combined pigment-cup ocelli, occurs on the sides of the mesosomal head (HYMAN, 1859: 23) [**Bioculata**]; (d) eyes of a vesicular grade of organization become associated with the optic centers of the brain [**Vertebrata**].

## STRATIFIED EPITHELIUM

67. Multistratified epithelium: (0) absent; (a) present in the cephalic and collarete regions (VANDEL, 1961: 35; HYMAN, 1959: 8, Fig. 3c) [**Bioculata**]; (b) the entire epithelium becomes multistratified [**Vertebrata**].

Vertebrates are the only chordates to have a true skin, consisting of epidermis plus dermis.

### CEPHALIC HOOD

68. Cephalic fold: (0) absent; (a) presence of a fold of the body wall, containing a coelomic space, that can be drawn over the dorsal surfaces of the head like a hood to protect the grasping spines [**Chaetognatha**].

### LATERAL LINE

69. Sensory lateral line: (0) absent; (a) present [**Vertebrata**].

We find the hypothesis of the presence of a lateral line in mitrates (JEFFERIES, 1981: 114, Fig. 14c) interesting, but not entirely convincing. In our scenario, this hypothesis becomes weakened because of the absence of a lateral line in Tunicata and Chaetognatha.

### NEURAL INDUCTION

70. Induction of neural tube: (0) the neurogenic region is induced by the roof of the archenteron; (a) the neurogenic region is induced by mesentoderm at the moment of gastrulation (VANDEL, 1961: 23) [**Vertebrata**].

Neural induction includes the neural crest.

### ENDOCRINE ORGANS

71. New hormone-producing organs (parathyroids, adrenals, pineal, pancreas, metanephridia, gut, etc.) (SCHAEFFER, 1987: 225): (0) absent; (a) present [**Vertebrata**].

In the Vertebrata, the endocrine glands become elaborate, in association with the increased complexity of the autonomic nervous system. These glands are derived from the endoderm interacting with the mesoderm.

### EXCRETION AND OSMOREGULATION

72. Kidneys: (0) absent; (a) presence of a pair of complex osmoregulatory and excretory organs, the kidneys [**Vertebrata**].

## DISCUSSION

Our first novel idea, that the taxon Enterocoela is closely related to tubicolous annelids, has far-reaching implications. The "Annelida" become definitely non-monophyletic. Two important taxa are excluded from the descendants of the common ancestor of all annelids: the Enterocoela and the Arthropoda. This larger monophyletic group should be referred to as Metameria. Thus the "Annelida", like the classical non-monophyletic group "Reptilia", should be abandoned.

Our second important insight is that the Pogonophora retain transitional characters between tubicolous annelids and enterocoels, comparable to those of Onychophora between mandibulate annelids and arthropods. Previous opinions on the phylogenetic position of the Pogonophora have alternated between a deuterostome (IVANOV, 1963) and an annelid (SOUTHWARD, 1975) relationship. Our conclusion differs from both in that pogonophorans are not annelids after all, neither strictly deuterostomes. As summarized in our cladogram, the Pogonophora are the sister group of the Radialia.

The Lophophorata (or Tentaculata) have been accepted (e. g., EMIG, 1982, Fig. 1b) or rejected (e. g., SCHRAM, 1991, Fig 1i) as a monophyletic group. Under either interpretation, the group has been alternatively included (e. g., BRUSCA and BRUSCA, 1990, Fig. 1f) or excluded (e. g., JEFFERIES, 1991, Fig. 1g) from the Deuterostomata. Because we have established that the characters traditionally used to diagnose the Deuterostomata have very different generalities (enterocoely for Enterocoela, radial cleavage for Radialia, mouth originating secondarily for Deuterostomata, dipleurula-type larva for Dexiothetica, and dorsal nerve chord for Eupharyngotremata), we conclude that only the Phoronida among the lophophorates must be excluded from the Deuterostomata.

The new taxon Coloniata may represent the most vulnerable node in our phylogenetic tree. Character number 46 could be interpreted more parsimoniously by considering coloniality as a synapomorphy uniting Ectoprocta and the pterobranchs. However, in our analysis, there are four transformation series (characters 5b, 28b, 46b, and 47b) that unite Cephalodiscida with Dexiothetica. Only by coding these transformations as non-additive series would a numerical analysis be able to produce an alternative, more symmetrical tree, in which "Lophophorata" + "Pterobranchia" are the sister-group of the Dexiothetica within the Deuterostomata. In our manual analysis, we use the congruence among these four transformation series to justify the loss of coloniality as an apomorphy of the Dexiothetica. In this decision we have been preceded by CRIPPS (1991: 335, Fig. 2).

Our second new taxon, the Pharyngocoela, is based on only two apomorphies that contain reversals. Doubts could be raised as to whether the pair of metasomal pores in Cephalodiscida represent true gill slits. We consider the internal pharyngeal grooves surrounded by vacuolated cells in rhabdopleurids (character 47a) as strong empirical evidence for interpreting the gill slits as a valid synapomorphy uniting Rhabdopleurida and Pharyngotremata.

The old concept of the "Hemichordata" has been recently questioned in JEFFERIES (1991, Fig. 1g), CRIPPS (1991, Fig. 1h), and SCHRAM (1991, Fig. 1i). CRIPPS (loc. cit.) has finally dismembered the three taxa Rhabdopleurida, Cephalodiscida, and Enteropneusta. Both EERNISSE et al. (1992) and BACHELJAU et al. (1993) concluded that many details in the cladograms published by SCHRAM (op. cit.) are artifacts of his analyses. He has nevertheless anticipated us, in the perhaps surprising result that the Enteropneusta should be completely removed from the proximity of the pterobranchs.

JEFFERIES (1991) scheme was instrumental in our new concept of the Eupharyngotremata (including the "†Calcichordata"). Yet we have not accepted the finest details of his anatomical reconstructions. Even though these are far beyond the capabilities of most zoologists, we nevertheless doubt that "*the few ridges, grooves and pits can be interpreted in such detail*" (JOLLIE, 1982: 171). Consequently, we find it simpler to accept the gill slits as evidence for the non-echinoderm nature of the calcichordates, but to reject the tunicate and cephalochordate nature of some of the mitrates. In our scenario, all calcichordates belong to the stem-line of the Eupharyngotremata.

Our new taxon Cephalata is strongly corroborated in the phylogeny (eight apomorphies). It corresponds partially to the newly proposed taxon Olfactores (JEFFERIES, 1991: 116). However, our concept of the taxon Cephalata differs conspicuously from that of the Olfactores by the inclusion of the Chaetognatha.

Our most unexpected result refers to the position of the Chaetognatha. Evidently, chaetognaths are quite atypical chordates. Yet, they are not considerably more atypical than adult tunicates, for example. It is true that larval ascidians have a notochord, and adult tunicates have branchial slits. But it must not be forgotten that chaetognaths, like craniates, have entirely lost true larvae from their ontogeny, and, together with their specialized planktonic habits, the last rudiments of a notochord and associated structures (dorsal nerve chord and myotomes). On the other hand, chaetognaths share other exclusive structures with the craniates, as the pair of frontal eyes (on which character our new taxon Bioculata is based), a multistratified epithelium, and other less conspicuous traits. Finally, there is even fossil evidence suggesting that the protoconodont elements were homologous to the grasping spines of modern chaetognaths (SZANIAWSKI, 1982; BENGTSON, 1983). These homologies are no longer unexpected, considering the present placement of the †Conodonta among the jawless craniates (ALDRIDGE et al., 1986). We agree that each isolated piece of evidence is not unquestionable on its own. However, chaetognaths, to our knowledge, have never been definitely placed before in the zoological system (cf. JEFFERIES, 1986; BRUSCA and BRUSCA, 1990; SCHRAM, 1991). We have now placed them precisely within the Deuterostomata, for the first time, on the force of our total evidence.

The positioning of Chaetognatha has been difficult in the past because of its uniqueness. In our analysis, we have had to accept no less than 10 character reversals for this taxon. Nevertheless, chaetognaths share 14 synapomorphies with other Chordata, of which four are reversals, eight with other Cephalata (one reversal) and five with other Bioculata (one reversal). We note that character number 22 could be interpreted more parsimoniously by considering hermaphroditism a synapomorphy uniting Tunicata and Chaetognatha. Again, this alternative grouping would only become supported in a numerical analysis if a large part of our linear transformation series were to be coded as non-additive sequences.

This temporary and expedient pedagogical attempt at phylogeny reconstruction will undoubtedly expose us to the limitations in our factual knowledge. We expect that detailed comparative work on biological specimens, as well as much useful descriptive information that we have been unable to interpret satisfactorily here, will disclose further synapomorphies corroborating or falsifying our new phylogenetic insights.

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We hope this paper provides satisfactory answers to all the stimulating suggestions. We are certain our final product has become much better because of them. But we also expect to provoke further responses. Opinions on the acceptability or rejectability of several novel propositions will be our best reward.

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APPENDIX – List of apomorphies for each taxon in phylogeny (Fig. 2).

**Enterocoela**: (1a) Anterior three coelomic pouches arise by enterocoely. (2a) Coelomic compartments metameric, with multiple similar segments restricted to the opisthosoma, as well as a single small protocoel, a pair of somewhat larger mesocoels, and a pair of large metacoels individualized by transversal septa in the anterior region. (12a) Ventral vessel forming a pulsating heart and wall of protocoel modified into a pericardium. (20a) Gonads in metasoma restricted to a single pair.

**Pogonophora**: (24a) Digestive tube is totally absent in adult.

**Radialia**: (1b) All vestiges of schizocoelic metamery are lost. (2b) Coelomic compartment oligomeric, with loss of the posterior schizocoelic metameres. (3a) Opisthosoma absent. (4a) Prosomal projection among the tentacles. (11a) Cleavage pattern radial. (25a) Alimentary canal becomes permanently U-shaped, with anus located near mouth. (27a) Prosomal tentacles absent. (28a) Presence of a pair of tentaculated arms on the mesosoma. (31a) Respiratory exchanges occur mainly on the mesosomal lophophore. (32a) Feeding microphagic, by tentacles of lophophore. (33a) Nervous system is diffuse and intraepidermal.

**Phoronida**: (37a) Actinotroch larva present.

**Deuterostomata**: (5a) Metasomal stalk, used to attach the organism to the substrate, differentiates from the posterior region of the trunk. (13a) Circulatory system open, vessels being reduced and opening into haemal spaces that do not contain vessel walls. (44a) The mouth is a new aperture opposite to the blastopore.

**Brachiopoda**: (45a) Mantle lobes of the body secret a pair of valves.

**Coloniata**: (46a) Colonies of zooids become physically interconnected.

**Ectoprocta**: (12b) Heart and pericardium absent. (14a) Circulatory system reduced to the funiculus of mesenchymal chords which still function in the transport of material between the colony members.

**Pharyngocoela**: (47a) Inner surface of pharyngeal wall with one pair of deep dorsolateral grooves which do not break through to the exterior. (49a) Anterior wall of buccal cavity evaginated into a dorsal, hollow diverticulum. (51a) The protonephridium derived from the blastocoel of the larva becomes associated with the protocoel and forms a vascular glomerulus, with an excretory function.

**Rhabdopleurida**: (29a) Disposition of arms of lophophore vertical and parallel to each other, projecting upwards in the proximal region and then curving backwards and downwards in the rear region when the zooid is extended from its tube.

**Pharyngotremata**: (5b) The trunk stalk is no longer used for attachment. (28b) Presence of five or more pairs of tentaculated arms disposed radially on the dorsal surface of the mesosoma. (46b) Animals semi-colonial, physical contact between zooids being lost. (47b) The single pair of branchial grooves open laterally on the metasomal trunk, just behind the posterior border of the collar.

**Cephalodiscida**: (6a) Cephalic shield flat, with a more or less circular outline, indented laterally with a pair of notches.

**Dexiothetica**: (18a) Protective case absent. (28c) The lophophoral tentacles from the original right side of the body become lost. (38) Dipleurula-type larva. (39a) Metatroch of larva becoming convoluted and forming perpendicular bands along the aboral side of the larva. (46c) Animals free-living. (53a) The mesoderm forms porous spicules or plates of calcite that may enclose the whole body. (54a) Right side of body reduced (dexiothetism).

**Echinodermata**: (7a) Metasomal stalk absent. (8a) Prosomal stem present, used for attachment to the substrate. (12b) Heart and pericardium absent. (15a) Protocoel modified into the axocoel (axial sinus) and the heart vesicle originates the madreporic vesicle (dorsal sac) in the larvae. (21a) Right gonad absent. (30a) Tentacles from the original left mesocoel (hydrocoel) form the water vascular system. (40a) Bipinnaria larva present, the posterior ciliary band (telotroch) having been lost. (50a) Dorsal buccal diverticulum absent. (52a) Axial gland present. (55a) Position of mouth in centre of the upper (oral) surface.

**Eupharyngotremata**: (4a) Prosomal projection absent. (20b) Gonads in metasoma arranged metamerically. (25b) The alimentary canal becomes linear, leading from an anterior mouth to a posterior anus. (28d) The mesocoel tentacles are lost. (31b) With the loss of a lophophore, respiration occurs on the walls of the branchial slits. (32b) Feeding microphagic, inside the pharynx. (33b) A dorsal collar chord, which is occasionally hollow and has a neuropore, becomes differentiated from the epidermal plexus of the mesosoma. (39b) Ciliary bands of larva invaginate to form a hollow neural tube with anterior and posterior neuropores. (47c) Multiple branchial slits pierce both sides of the pharynx. (48a) The branchial slits open collectively into branchial sacs. (49b) Buccal diverticulum extended anteriorly within the protocoel. (53b) Loss of the echinoderm-like calcite skeleton. (54b) A new plane of symmetry, perpendicular to that of Bilateria, is formed. (56a) Cartilaginous rods support the branchial slits. (57a) Presence of a pre-oral ciliary groove at base of proboscis, probably a sensory organ.

**Enteropneusta**: (9a) Digging prosomal proboscis present. (41a) Tornaria larva present. (58a) Proboscis skeleton present.

**Chordata**: (2c). No distinct transversal septa dividing coelomic spaces in adult. (5c) The metasomal stalk becomes differentiated into a post-anal tail region for swimming. (33c) The dorsal nerve chord extends posteriorly to the tip of the tail region of the trunk. (38b) Development abbreviated, with loss of larval stages that swim by ciliary bands. (42a) The circumoral band of cilia in the larva migrates into the mouth and becomes converted into a midventral endostylar muco-ciliary organ with peripharyngeal bands inside the pharynx. (48b) Branchial sacs modified into a large pair of atria. (49c) Buccal diverticulum transformed into a rigid notochord. (51b) Glomerulus absent. (57b) Ciliary groove modified into wheel organ. (60a) Presence of a single pair of intestinal diverticulae. (62a) Presence of median fin-ridges. (64a) Muscles become metameric along whole length of trunk and contain striated fibers. (66a) Presence of median unicellular cup-shaped photosensory cells.

**Cephalochordata**: (12b) Heart and pericardium absent. (13b) Circulatory system secondarily closed. (61a) Buccal cirri surrounding the oral vestibule.

**Cephalata**: (17a) Heart post-pharyngeal, in the region corresponding to the mesosoma. (20c) Gonads in metasoma restricted to two pairs. (22a) Animals monoecious. (34a) A cerebral vesicle, that is individuated from the epidermis and its basal membrane, is present in the larva. (35a) Nerves that innervate the myotomes provided with motor end plates. (54c) The pharynx is symmetrical, although the dorsal nervous system is still asymmetric. (57c) The vibratile organ, homologous to the wheel organ, becomes associated with a subneural gland, which originates from the middle of the larval neural tube. (66b) Presence in tadpole larva of a median, compound, cup-shaped ocellus.

**Tunicata**: (19a) The body is enclosed in a protective tunic containing a material akin to cellulose. (23a) One male and one female gonad lost from one side of the body. (26a) Torsion of digestive tube at metamorphosis present.

**Bioculata**: (34b) A dorsal cerebral ganglion is conspicuous in the mesosoma of the adult. (38c) Loss of a characteristic larval stage, the young animals being miniatures of the adults. (54d) The animals are fully symmetrical. (66c) A pair of eyes of the inverse type, consisting of five combined pigment-cup ocelli, occurs on the sides of the mesosomal head. (67a) Multistratified epithelium present in the cephalic and collarete regions.

**Chaetognatha**: (10a) The trunk and post-anal tail become separated by a distinct septum. (12b) Heart and pericardium absent. (16a) Vascular system absent. (32c) Feeding macrophagic, by grasping spines and teeth on the head. (36a) Dorsal nerve chord absent. (43a) Endostyle absent. (47d) Pharyngeal slits secondarily absent. (48c) Atrium secondarily absent. (49d) Loss of the notochord. (56b) Pharyngeal rods modified into buccal epithelial grasping spines and teeth for macrophagous feeding. (64b) Muscle metamerism and striated fibers absent. (68a) Presence of a fold of the body wall, containing a coelomic space, that can be drawn over the dorsal surfaces of the head like a hood to protect the grasping spines.

**Vertebrata**: (5d) The metasomal tail is used for active swimming by strong muscular blocks in adult. (13b) Circulatory system secondarily closed. (17b) Heart post-pharyngeal, becoming strongly muscularized (myocardium) and developing valves for a more efficient circulation. (20d) Gonads in metasoma restricted to a single pair. (22b) Animals dioecious. (31c) As body size increases, the walls of the branchial slits become modified into respiratory gills. (34c) The mesosomal ganglion becomes enlarged into a true brain, encased in a cranium. (42b) Part of the endostyle of the ammocoetes larva becomes the thyroid endocrine gland at metamorphosis. (57d) The subneural gland becomes definitely fused with the previously sensory organ (hypothalamus + hypophysis), functioning as an endocrine gland (adenohypophysis or anterior pituitary). (59a) Cartilaginous endoskeleton present. (60b) Presence of a complex endodermal organ, the liver. (63a) Paired fin-folds present, with strong skeletal supports. (65a) The mesoderm becomes dorsalized and differentiated into dermatomes and sclerotomes, in addition to myotomes. (66d) Eyes of a vesicular grade of organization become associated with the optic centers of the brain. (67b) The entire epithelium becomes multistratified. (69a). Sensory lateral line present. (70a) The neurogenic region is induced by mesentoderm at the moment of gastrulation. (71a) New hormone-producing organs (parathyroids, adrenals, pineal, pancreas, metanephridia, gut, etc.) present. (72a) Presence of a pair of complex osmoregulatory and excretory organs, the kidneys.