

ON SYMMETRY AND TOPOLOGY OF ORGANISMS IN MACROEVOLUTION

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Abstract: *An evolutionary tree of animal symmetries and topologies is reconstructed. The tree is purely hypothetical, based on the hierarchy of geometrical symmetries and homotopies. Some correlation is guessed with the real evolutionary tree.*

1. INTRODUCTION

The global characterization and classification of the organisms in terms of their symmetry and topology are plausible and useful properties. This paper deals with the description of the symmetries and topologies of the organisms in macroevolution. The macroevolution consists of speciation and the formation of higher organisation levels, including phyla. This paper consists of three parts.

In the first part some problems of the origin, maintenance, and transition of symmetries and topologies in evolution are outlined. Afterwards, a deductive framework based on a paper by Lukács (1993b) for the embedding of the symmetries of organisms in evolution is presented. The logic of this approach is the gradual degradation of symmetries starting from an $E(3)$ symmetry. The third part is an analysis of the variation of the animal topologies.

2. THE PROBLEM OF ORIGIN, MAINTENANCE AND TRANSITION OF SYMMETRIES AND TOPOLOGIES OF ORGANISMS IN MACROEVOLUTION

It can be observed that there exists a hierarchy of symmetries at different levels of organisation. The jumps represent the global changes of the units of biological organisation. The examples include the hierarchy of ancient, sometimes retained, symmetry breaking mechanisms and the corresponding variation of symmetries or asymmetries of macroevolutional relevance. The origin of life may have involved the emergence and stabilisation of different classes of macromolecules (Avetisov *et al.*, 1991). The cellular handedness (Frankel, 1990) embodies in the anisotropy of intracellular structures, such as, e.g., the mouth organs of ciliates. The clonal cellular reproduction of certain cylindrical ciliates is also associated with conserved, topologically invariant patterns. This clearly shows that symmetry and topology can be closely related in the biological organisation.

The topological and symmetry transformations of the organisms in evolution stem from the changes of developmental dynamics. However, as Brown and Wolpert (1990, p. 1) state "The development of handed asymmetry is a deep and neglected problem. Deep because it involves a type of spatial ordering of quite special nature for which there are just no models, and neglected for, probably, just the same reasons." The handed asymmetry means consistent left/right differences.

The generation of symmetries and topology in development are also neglected fields. We know, for instance, that right and left sides are not distinguished in the development of fruit flies.

A consistent topological classification of developmental transformations may result in a rational basis for the intelligibility of generic morphological transformations in development and evolution. A similar endeavour failed in the context of catastrophe theory, neglecting real organisms and concrete mechanisms.

It is interesting to observe that in population biology a substantial amount of information has already accumulated on biological asymmetry. For instance, the fluctuating asymmetry characterising the left/right asymmetry of the two sides of organisms in isogenic or in natural populations can be regarded as a measure of developmental noise and environmental stress.

The implications of the ignorance of the generative mechanisms of symmetries and topologies of developing organisms belonging to different phyla are that in this paper we shall consider only the descriptive aspects of symmetries and topologies, mainly in animals.

We note that the evolutionary lineages also show some asymmetry (Gould *et al.*, 1987). This overall phylogenetic asymmetry cannot be explained simply in terms of biased birth-death processes. Instead we (Szathmáry *et al.*, 1990) illustrated the symmetry generating effects of different combinations of ecological factors. A more satisfactory explanation of evolutionary origin, maintenance and transition should involve genetic, developmental and ecological mechanisms and their interactions. From this enormous problem some emphasize internal factors and self-organisation in organisms, others do mainly directional and stabilizing selection.

Although it is well known that nature has preferred symmetries, such as spirals, emerging at many organisational levels, their repetitions and connections between levels are unknown.

These problems are hopelessly intractable at present. Therefore we simplify the problems to mathematical description in the next two Sections of this paper.

3. THE EVOLUTIONARY TREE OF ANIMAL SYMMETRIES

In a classical work Sir Thomas Browne (1646) denied the existence of a two-headed snake of the ancient Romans called *Amphisbaena*, telling that there is no species without bottom, top, front, back, left and right (Borges, 1967). Then the two-headed *Amphisbaena* cannot exist since "for the senses being placed at both extrems, doth make both ends anterior, which is impossible". This statement is quite conform with our everyday experience, but does not seem correct. From archaeological data, study of recent primitive animals and contemplations one can guess that the degree of animal symmetries is decreasing in evolution, due to increasing specialisation and complexity. To give only a partial reasoning, remember that all *Metazoa* start from a single cell, so its all cells should be equivalent, therefore the body symmetric. If not, some mechanism breaking this symmetry is needed.

The problem seems simple because some biomolecules do have chirality (Glück, 1993), plus there is the gravity singling out the vertical direction. However, primi

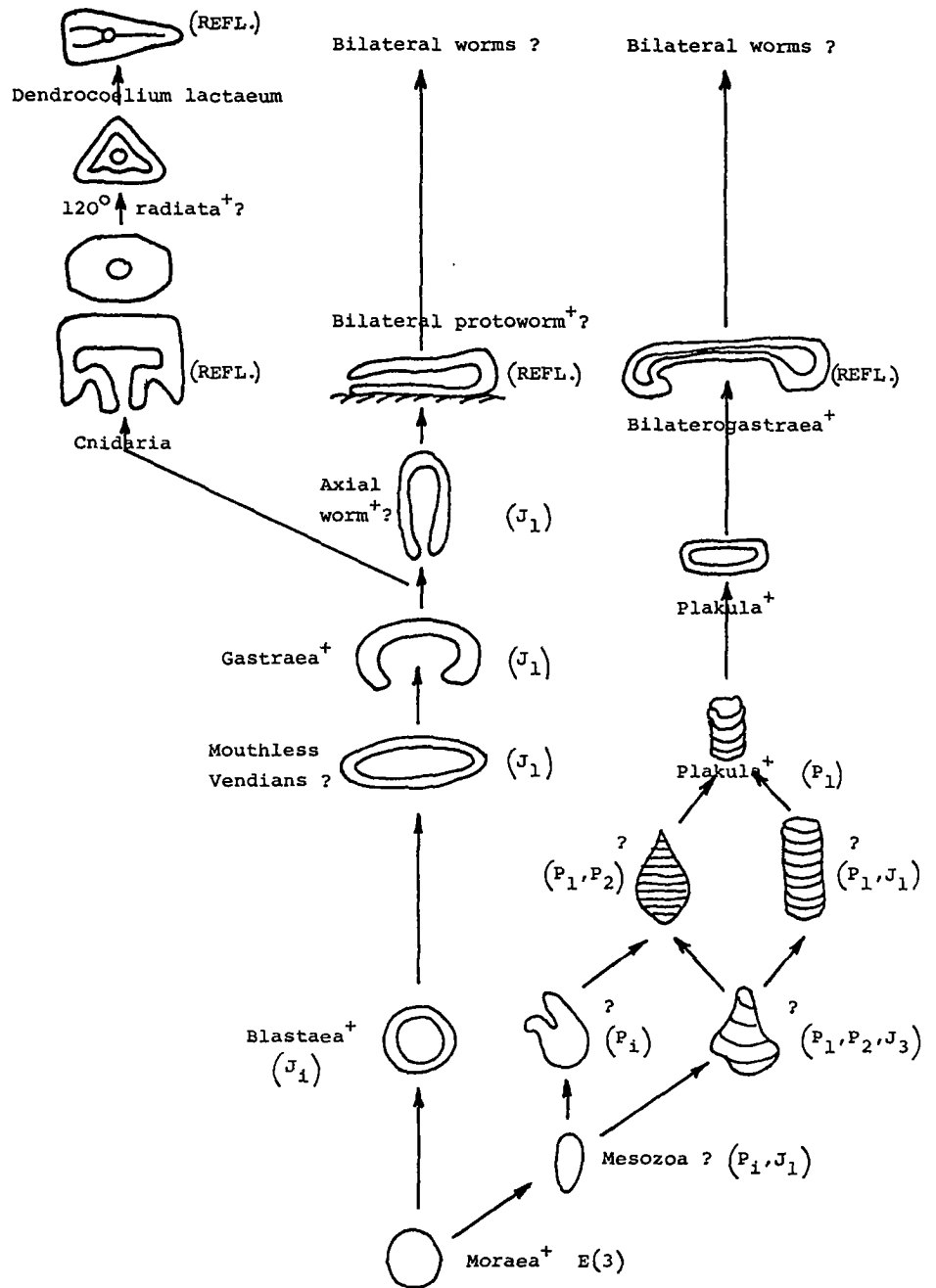


Figure 1

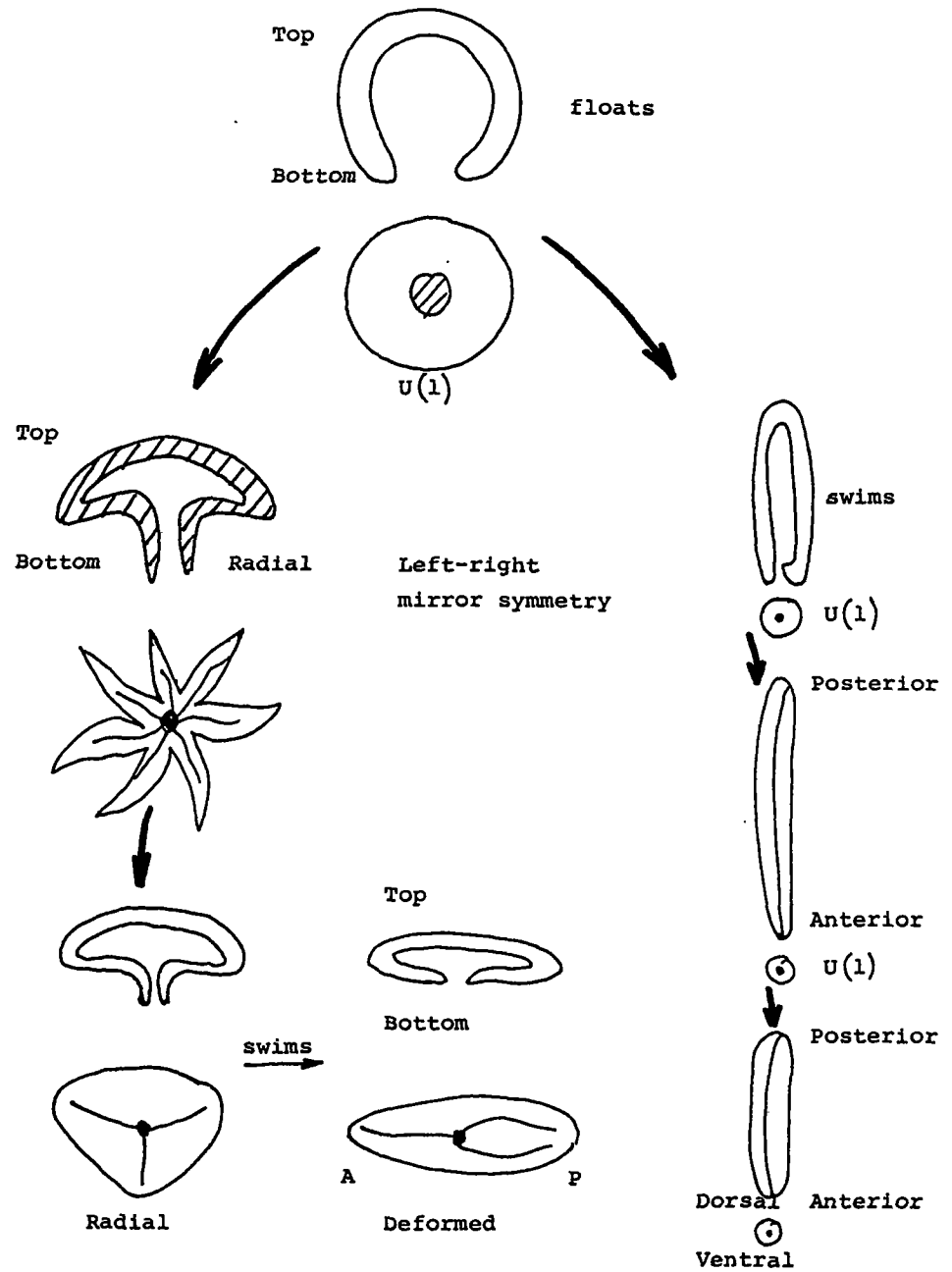


Figure 2

tive animals consist of predominantly water, so they are both globally and locally weightless in sea-water. So they do not feel too much of the vertical. As for the chirality of molecules, it *generally* would not lead to asymmetry of the body. This will be demonstrated on a simple physical example.

Consider a system of small magnetic dipoles (spins). If their interactions are weak and there is no external field ordering them, the ground state is completely disordered. Even with an external field the ordering is only partial, depending on the ratio of the external field and noise (temperature) (Kittel, 1961; Lukács and Marti-nás, 1990). Without external field the only possibility to get a state of parallel spins is *ferromagnetism*, to which a strong interaction of special form is needed (Kittel, 1961). I.e., in the generic case without an external agent the system of chiral molecules will lack chirality. If not, then a spontaneous symmetry breaking is present, needing special mechanisms.

So our starting point will be full $E(3)$ symmetry, and we draw an evolutionary tree of decreasing symmetry (and complicating topology). Since these changes may happen only in discrete steps, they belong to *macroevolution*, between the changes of fundamental biochemistry generating new *regna* (Cavalier-Smith, 1987) and the changes of general corporeal construction generating new phyla (Fedonkin, 1986). Since the old *Regnum Romanum* consisted of mere 3 tribes, it is hard to find a proper term for the intermediate units between regnum and phyla, but, as we shall see, the steps of the symmetry (and topology) tree roughly correspond to such 'superphyla' as *Radiata*, *Oligomer* and *Metamer Protostomata*, etc.

Figure 1 is the hypothetical tree according to the mathematics of symmetries (Lukács, 1993b); for transparency the spiral and helical possibilities ignored here. The symbols for the symmetries are as in the said paper; the names are the possible representatives. '+' denotes reconstructed forms and '?' uncertain correspondences. Some explanations follow.

Plakula and *Bilaterogastraea* belong to non-Haeckelian hypothetical lines (Jagerstein, 1972); we definitely do *not* want here to estimate the probabilities of hypothetical histories.

Some *Vendians* (*Ediacarans*) are said mouthless or gutless (Seilacher, 1989). If so, then they correspond to Haeckel's *Blastaea*. From the fossils oblateness cannot be judged; here we assume them oblate.

Symmetry considerations permit alternative ways to reach 'the generic *Platyhelminthes*' stage (a bilateral worm without anus). For our knowledge, polyphylecy of *Platyhelminthes* is neither proven nor excluded. For simplicity we discuss only the left and central lineages.

The left story goes through *Radiata*. In gastrulation there is a single preferred point (the protostoma). So the original *Gastraea* must be axially symmetric. But then the animal is weak in orientation and motion. (no points of reference or nerve centres). So the evolution is expected finally to give up the last *continuous* symmetry and to remain with discrete rotation (or reflection) symmetry, arriving at a regular polygonal cross section. This is just the stage of recent *Radiata*. The protostoma is at the center of the ventral side (to eat from the benthos); guts and nerves run radially

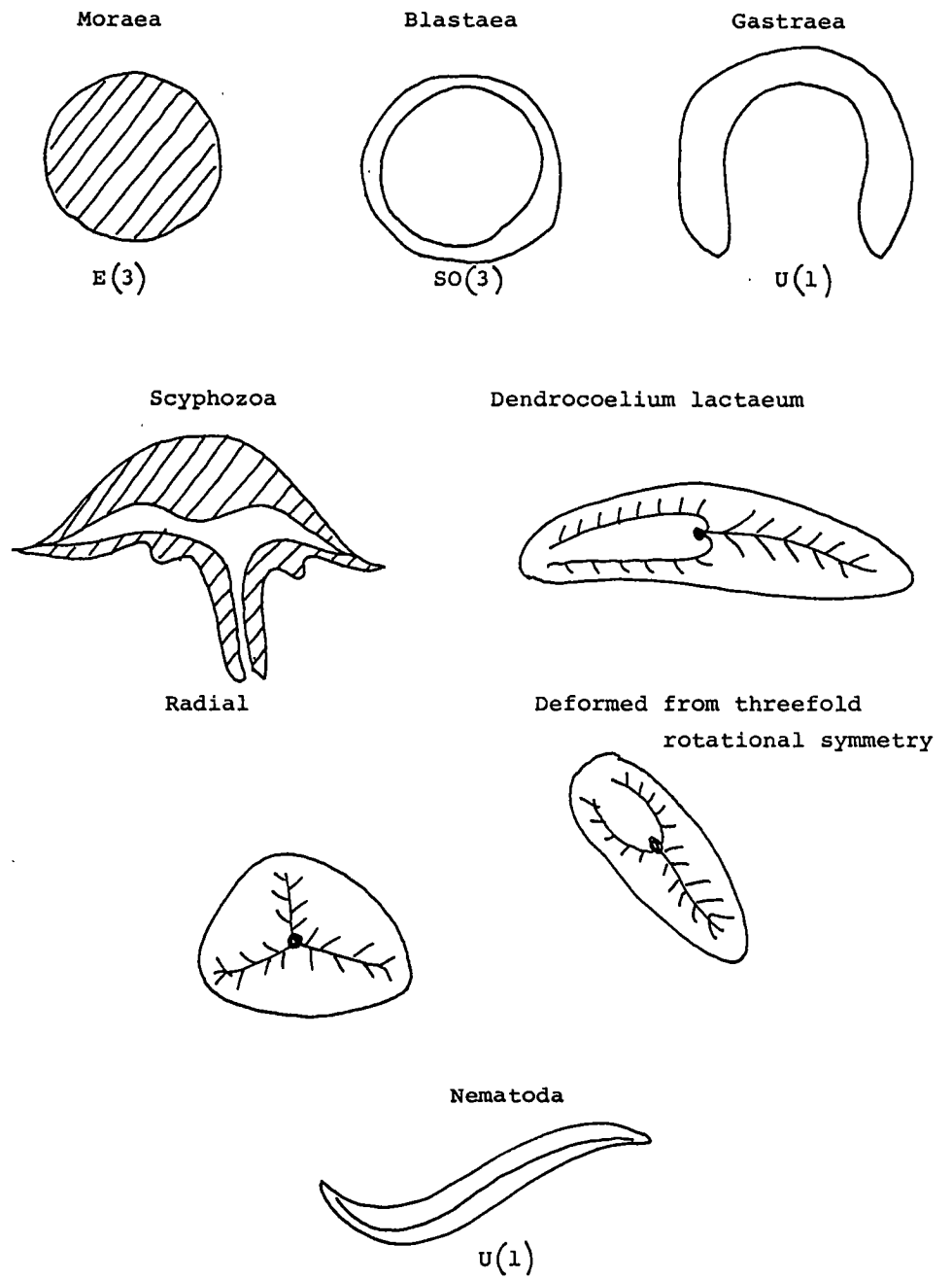
to the corners (organs of locomotion and sense located there). The less sides of the polygon, the higher needed information to build up the body, but the higher ability to orientate, move etc. One may visualize a *triangular Radiata* specialising to swim: it may become elongated to a randomly chosen corner resulting in something similar to recent *Dendrocoelum lactaeum*.

The central line is an alternative. The original axially symmetric *Gastrea* may become elongated. Then, with a 90° rotation it can specialise to swim, with eyes nerve centres etc. at the stomal end. This is a hypothetical 'axial protoworm', having an alternative future. Remaining at swimming it may end up in something classified among *Nemertoides* or *Nematoda*, but with primarily axially symmetric internal organs. On the other hand, migrating to the benthos, ventral and dorsal sides will be distinguished by the bottom and gravity. Again, we are at something Primitive bilateral worm.

Anyway, at the top of Figure 1, any lineage ends in an animal having distinguishable anterior (mouth, eye etc.) and posterior ends, ventral (legs) and dorsal (no leg) sides. But the left-right symmetry is still unbroken: the animal feels its own sides as unidentical but equivalent. It would not call them differently.

Figure 2 gives some details to Figure 1, and Figure 3 sketches some stages of the preceding figures. Now let us start from the bilateral worm (the bottom of Fig. 4). It is better to generate a body bigger for not being eaten easily and more complicated for versatility. The central lineage is the *naïve* straightforward way followed by *Mollusca* but it is dispreferred by information theory. It is better to multiply itself in identical modules. The other four ways show such evolution. The leftmost one is colony forming, seen among *Bryozoa*, *Hemichordata* and *Tunicata*, maybe present in vertebrate evolution (Lukács, 1993c). The next is to grow the body in many direction (pseudo-symmetry of discrete rotation), seen among *Echinodermata*. The two cases on the right are to multiply the body lengthwise. This may lead to homologous metamerism, (discrete translation symmetry of *Annelida*), or the symmetry may be discrete spiral motion. For the last case the best candidate is *Ammonites* but there the symmetry is conform in the best case. (No definite measurements were performed to verify the conform scaling.)

All these lineages end in something *without* chirality. However now there are two orthogonal preferred directions, so, if the internal gradients are large enough, thermodynamic forces may order the chiral biomolecules and large-scale chirality may emerge. Still, substantial left-right asymmetries seldom appear in *Regnum Animalia* (if not by-products of spiralling up in snails etc.). A fairly asymmetric animal was *Stylophora* (for picture see Lukács, 1993c), but it seems to have been a *cul-de-sac* of evolution. *Vertebrate* bodies often exhibit *slight* asymmetry (mammal heart, avial oviducts etc.), but generally neither the outward appearance nor the functioning shows too much of this asymmetry. The mammal evolution led to *functional* left-right asymmetry (i.e., the emergence of notions of left and right) only several Mys ago in hominisation (Holba and Lukács, 1993).

**Figure 3**

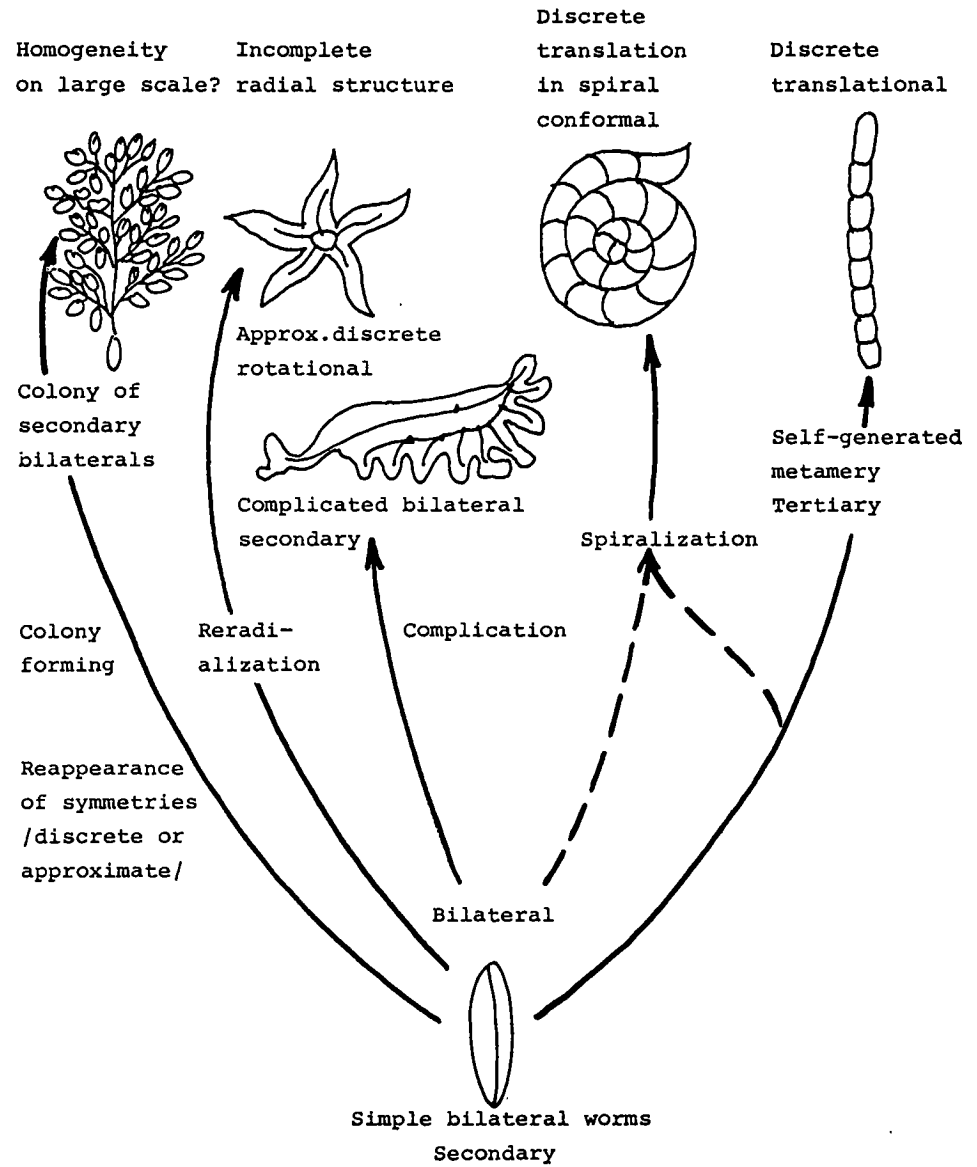


Figure 4

4. ON THE TOPOLOGY OF ANIMALS

Now let us turn from symmetry to topology. Again, the mathematics is given in Lukács (1993a). What we shall need is only a few inequivalent classes: a sphere; a sphere with a number of shafts driven through; and an empty sphere. That they are inequivalent, one can see by classifying possible closed curves in the bodies. In a sphere any closed curve can be continuously distorted into any other; in a sphere minus a shaft the closed curves belong to two disjoint classes (around and not around the shaft); with two shafts they give 4 classes (around *A*, around *B*, around both, not around any of them); with an *Y*-shaft again 4 classes exist, namely around the first, second and third legs and not around at all; finally an empty sphere divides the space into *three* domains: outside, inside and the body itself, while all the other configurations produce only *two* domains: outside and the body. Now let us start to climb on the evolutionary tree.

The *moruloid* stage of evolution (perhaps preserved in *Mesozoa*) is topologically a sphere. This radically changes in the *blastoid* stage, which is an empty closed shell. We do not know *recent* animals with this topology. However some *Ediacaran* fossils seem to lack mouth etc. (Seilacher, 1989; see Fig. 5). If this observation is correct then these animals (?) (Bérczi *et al.*, 1990) may have been in the blastoid stage.

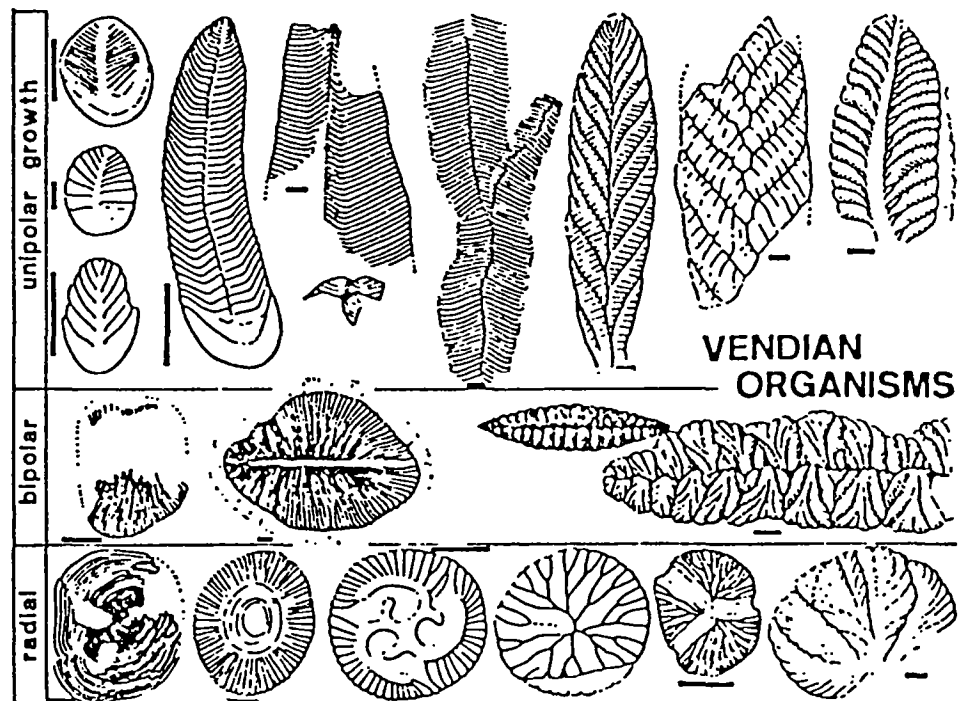


Figure 5: *Ediacaran Vendian* organisms after Seilacher and Gould.

Note that this topology is basically different to that seen in familiar animals. Such an animal can have *two* different environments in the same time: the sea-water outside and something other inside. There may be some exploitable possibilities in this fact (the presence of osmosis and other thermodynamic forces. Our knowledge on the way of life of *Ediacarans* is so limited that it is more prudent to pass this point; however we would have liked to emphasize a point worthwhile for interest.

In the *gastrulation* process the body returns to the previous topology of the sphere. The actual geometrical form may be arbitrarily complicated and sophisticated, still it is the same topology. In this topologic stage we can find *Cnidaria*, *Ctenophora*, and most *Platyhelminthes*, except for *Nemertodea*.

In *Nemertoides* appears first the second, anal opening. The enteral channel becomes a complete shaft driven through the body, so we have arrived at the topology of sphere minus a simple shaft. (Small openings of the secretion system as *proto-nephridia et al.* are neglected here for simplicity.) This structure remains in the whole *Protostomata* branch.

One of the most important developments about understanding phylogeny was the recognition of the two halves of the evolutionary tree above *Radiata*. On the protostomic side the protostoma of the gastruloid stage remains the mouth and the anal opening is new. On the deuterostomic side the mouth is new, and the protostoma either closes or becomes the anus. From cladistic viewpoint it is very important to divide the tree into *two*; however from topologic viewpoint the division is different.

The protostoma had double roles, which are later separately inherited by the two opposite openings. Thus a possible kind of deuterostomy is simply a flow direction *opposite* than for a *Protostomata*. This is an important difference, a signal of independent origin, but the same topology or global pattern.

However on the deuterostomic side one can (?) observe a different, more complicated history, and this is the way leading to us. Based on the embryogenesis of *Amphioxus*, on observations of recent lower vermins, and on common sense a last improbable story is reconstructed, which, following Kretzoi (1964), goes in the steps schematically shown on Figure 6.

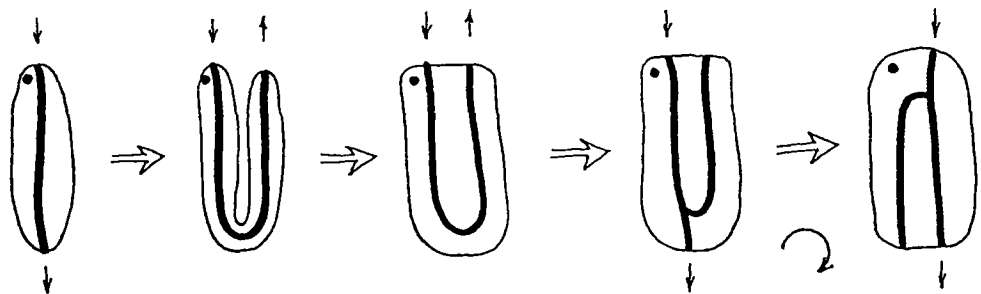


Figure 6: A scheme of deuterostomisation after Kretzoi.

- 1) The starting point is a 'sphere minus a simple shaft'.
- 2) The vermin takes U-shape (for any reason). Then the mouth and anus get close to each other, which is not optimal in the light of the Le Chatelier-Brown Law; nevertheless it is not uncommon (see *Phoronidea*, *Entoprocta* and *Echinodermata*).
- 3) The animal reintegrates, preserving the U-shape of the channel. *Until this point the topology is unchanged.*

Both the neighbouring positions of the opening and the U-shape of the channel have disadvantages. (For the latter: the flow in the channel is difficult at the turning point.) It is profitable to get a new opening near the turning point. However, because of the original flow pattern, *without serious reasons the new opening would be an anus*, so still protostomy. To get deuterostomy the animal must have changed its orientation too in this stage.

- 5) The final result is a sphere minus an Y-shaft; a new topologic class.

At this point one branch ceases to be operative, and can be utilized for a new function. From recent higher deuterostomic animals one may guess that the superfluous branch was going to house either the developing neural system (spinal cord) or the developing endoskeleton (*chorda dorsalis*).

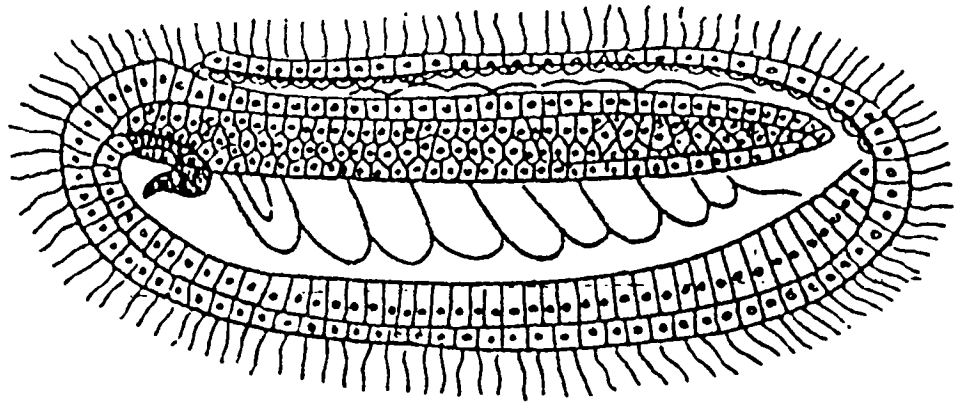


Figure 7: The larval stage of nine somites of *Amphioxus*.
Observe the second channel but without entoderm.

Unfortunately, the above story is not *fully* supported by the embryology of the *Amphioxus*. While there one can see the U-shaped channel, in one branch the entoderm is absent. Such a structure is very strange for an enteral system, but in the

same time useful for the easy development of the neural fibers of ectodermal origin. Now, in addition in the ontogeny of *Amphioxus* the dorsal channel is produced via the overgrowing ventral lip of the protostoma. If this were the recapitulation of the phylogeny, then the corresponding many generations would have had great difficulties in eating, so being unfit for survival. This suggests that here Haeckel's Biogenetic 'Law' cannot be directly used. So here we stop and return to the problem in a later paper (Lukács, 1993c).

Our conclusion here is that (some) *Deuterostomatae* have developed a topology different from and more complicated than that of *Protostomatae*. The change of topology cannot be made without a serious correlated rearrangement of the body, so it may be a rare event. On the other hand, a more complicated topology gives more possibilities to build up a versatile body. Is this more complicated topology (and so enhanced potentiality) behind our evolutionary success?

5. CONCLUSIONS

The above overview has demonstrated that Sir Thomas Browne was incorrect when assuming 3-axis asymmetry for *all* animals. Even for recent ones: what is anterior for an octagonal *Cnidaria*? What is more surprising: what defines the right forepaw of a cat?

A cat in herself without doubt has an anterior (head) – posterior (tail) distinction as well as a ventral (legs) – dorsal (no legs) one, but in the remaining direction body and function are (practically) mirror-symmetric i.e., equivalent. The *Katze in sich* will not feel her two forepaws left and right, although will feel them nonidentical. *We* introduce the notion of *her* left and right, extending the convention justified for us humans that left sides are behind each other if looking into the same direction.

With complete mirror-symmetry chirality would not appear and the individual would continuously confuse its left and right hands, having no way to identify them (sometimes observable partially in humans). On the other hand large differences again would destroy the ideas of left and right hands: in a virtual continuation of the line of *Stylophora* the resulting *paravertebrate* would have, say, a (right) hand and a (left) paw. Our notions correspond to *slight* asymmetry.

As seen our asymmetries are historical products. The anterior-posterior one (originally bottom-top) comes from gastrulation and appeared at or just after *Ediacaran*; the dorsal-ventral appeared between *Ediacaran* and *Cambrian* and the left-right sporadically many times in the past but this one is not a general characteristics of *Regnum Animalia* even now.

As for topology, the original stage must have been a sphere. The *empty* sphere is characteristic for *Ediacaran*, and absent among recent animals, although *Volvox* has this stage among *Metaphyta*. With gastrulation the original topology returned and became more complicated with shafts driven through. This change may have resulted in something resembling *Proto-* and *Deuterostomata*, but again the possible cases are more numerous as in the usual classification.

With further evolution the topology becomes too complex for complete classification. Still, look at the nice *cladistic* unit *Choanata* including *all* tetrapodes together with *their* *Crossopterigian* ancestors in contrast to other *Crossopterigians*. This distinction is based on the existence or nonexistence of a small and seemingly irrelevant extra opening on the head with a connection of the main internal channel.

REFERENCES

- Avetisov, V. A., Goldanskii, V. I., and Kuz'min, V. V. (1991) Non-equilibrium generation of optical reactivity in solid 1,1' Binaphthyl., *Physics Today*, July, 33.
- Barnes R. D. (1974) *Invertebrate Zoology*, Philadelphia: Saunders.
- Bérczi, Sz., Lukács, B., and Molnár, I. (1990) On phylogenesis, In: Lukács, B. *et al.*, eds., *Evolution: from Cosmogensis to Biogenesis*, Budapest: KFKI, 1990-50, p. 84.
- Borges, J. L. (1967) *El Libro de los Seres Imaginarios*, Buenos Aires: Kier S. A..
- Brown, N. A. and Wolpert, L. (1990) The development of handedness in left/right asymmetry, *Development*, 109, 1.
- Browne, Sir Thomas (1646) *Vulgar Errors*, London.
- Cavalier-Smith, T. (1987) The origin of cells: a symbiosis between genes, catalysts, and membranes, *CSHS, Quantitative Biology*, 52, 805-824.
- Frankel, J. (1990) Patterns in ciliate development, *Journal of Cellular Biology*, 97, 205.
- Fedonkin, M. A. (1986) The origin of metazoa, In: Hoffman, A. and Nitecki, M. H., eds., *Problematic Fossil Taxa*, Oxford: Oxford University Press.
- Glück, F. (1993) Chirality of organic molecules, *Symmetry: Culture and Science*, 4, 1, 83-92.
- Gould, S. J. (1989) *Wonderful Life*, New York: Norton.
- Gould, S. J., Gilinsky, N. L., and German, R. Z. (1987) Asymmetry in lineages and direction of evolutionary time, *Science*, 236, 1437.
- Holba, Á. and Lukács, B. (1993) Hominid cerebral lateralization as spontaneous symmetry breaking, *Symmetry: Culture and Science*, 4, 2, 161-169.
- Hyman, L. H. (1940-1967) *The Invertebrata*, vols. I-IV, New York: McGraw-Hill.
- Jagerstein, G. (1972) *The Evolution of Metazoan Life Cycle*, London: Academic Press.
- Kittel, Ch. (1961) *Introduction to Solid State Physics*, New York: John Wiley and Sons.
- Kretzoi, M. (1964) In: Tasnádi-Kubacska, A., ed., *Az élővilág fejlődéstörténete* [Evolutional History of Life, in Hungarian], Budapest: Gondolat.
- Lukács, B. (1993a) On geometric symmetries and topologies of forms, *Symmetry: Culture and Science*, 4, 1, 93-103.
- Lukács, B. (1993b) On the mathematics of symmetry breakings, *Symmetry: Culture and Science*, 4, 1, 5-11.
- Lukács, B. (1993c) Vertebrate: Individual or colony? *Symmetry: Culture and Science*, 4, 2, 139-149.
- Lukács, B. and Martinás, K. (1990) *Acta Physica Polonica*, 21B, 177.
- Neville, A. C. (1976) *Animal Asymmetry*, London: E. Arnold.
- Seilacher, A. (1989) Vendozoa: Organismic construction in the Proterozoic biosphere. *Lethaia*, 22, 229.

- Szathmáry, E., *et al.* (1990) The engagement of the Red Queen and King Midas in the phylogenerator model, *Coenoses* 5, 130.
- Thompson, D'Arcy W. (1917) *On Growth and Form*, Cambridge: Cambridge University Press.
- Wainwright, S. (1988) *Axis and Circumstance*, Cambridge: Harvard University Press.