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VERTEBRATE: INDIVIDUAL OR COLONY?

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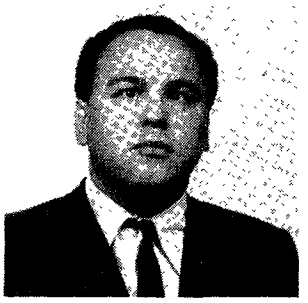

Abstract: *Serious problems about the finer details of the complicated topology of the internal deuterostomic structure raise the question if the vertebrates are secondary or tertiary animals, meaning the number of steps in which they were built up from living constituents. This question is discussed in the paper.*

1. INTRODUCTION

None too successful individuals or groups often look for successful aliens as kinsfolk or ancestors. However, in *Regnum Animalia* we *Vertebratae* are the most successful ones (according to our common opinion) and still our own ancestors and kinsfolk are not very popular objects of study; other *Deuterostomatae* are rather neglected as compared to such popular *Protostomatae* as *Annelidae*, *Insectae* or *Cephalopodae*. Before continuing this Introduction, Figure 1 shows a very schematic *deuterostomid* half of an evolutionary tree, and Figure 2 gives pictures of characteristic members of the *deuterostomid phyla*, after Ábrahám (1964), Dudich (1967), and Géczy (1979).

The *Deuterostoma* family album starts with *Sagitta hexaptera* for *Chaetognata*. The picture does not show yet anything resembling a *chorda dorsalis*, and it is difficult to see if the neural network is ancestral to a spinal cord. In any case it starts from the neighbourhood of the mouth, but it is natural to get a neural center at the apex.

Our second kin is not recent. It is *Stylophora*, mentioned earlier (Bérczi, Lukács, and Molnár, 1993) for its expressed lack of a bilateral symmetry. Recent discussions suggest that it was not an *Echinodermata* proper but rather something between positions *3* and *4*. In this case the opening at the apex is a mouth, the opposite one is the anus, the tail may have contained a *chorda dorsalis*, and the thickened part beside the anus housed a brain.

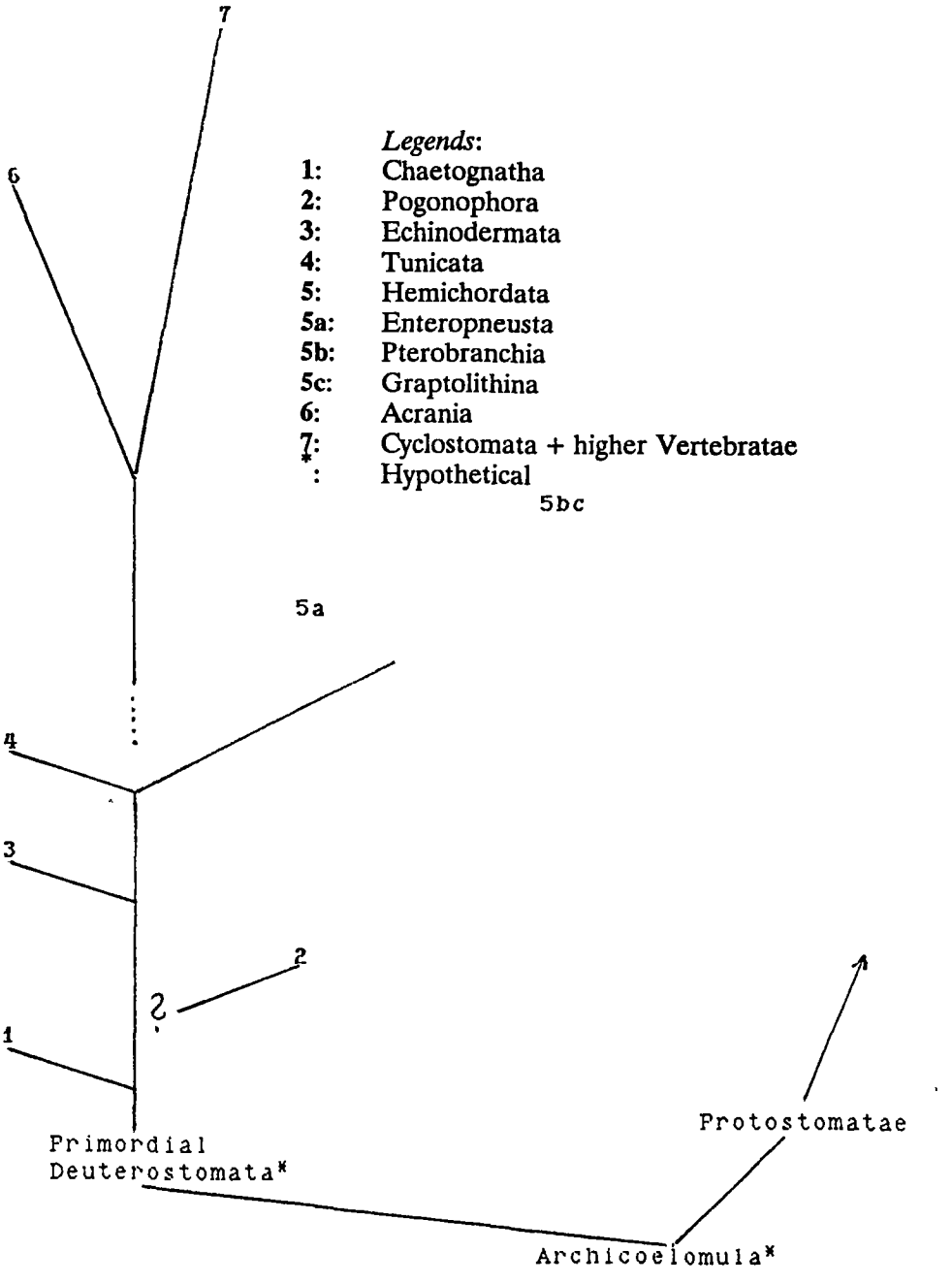

Figure 1: A schematic deuterostomic half of the evolutionary tree.
For representatives of the phyla see the opposite page.

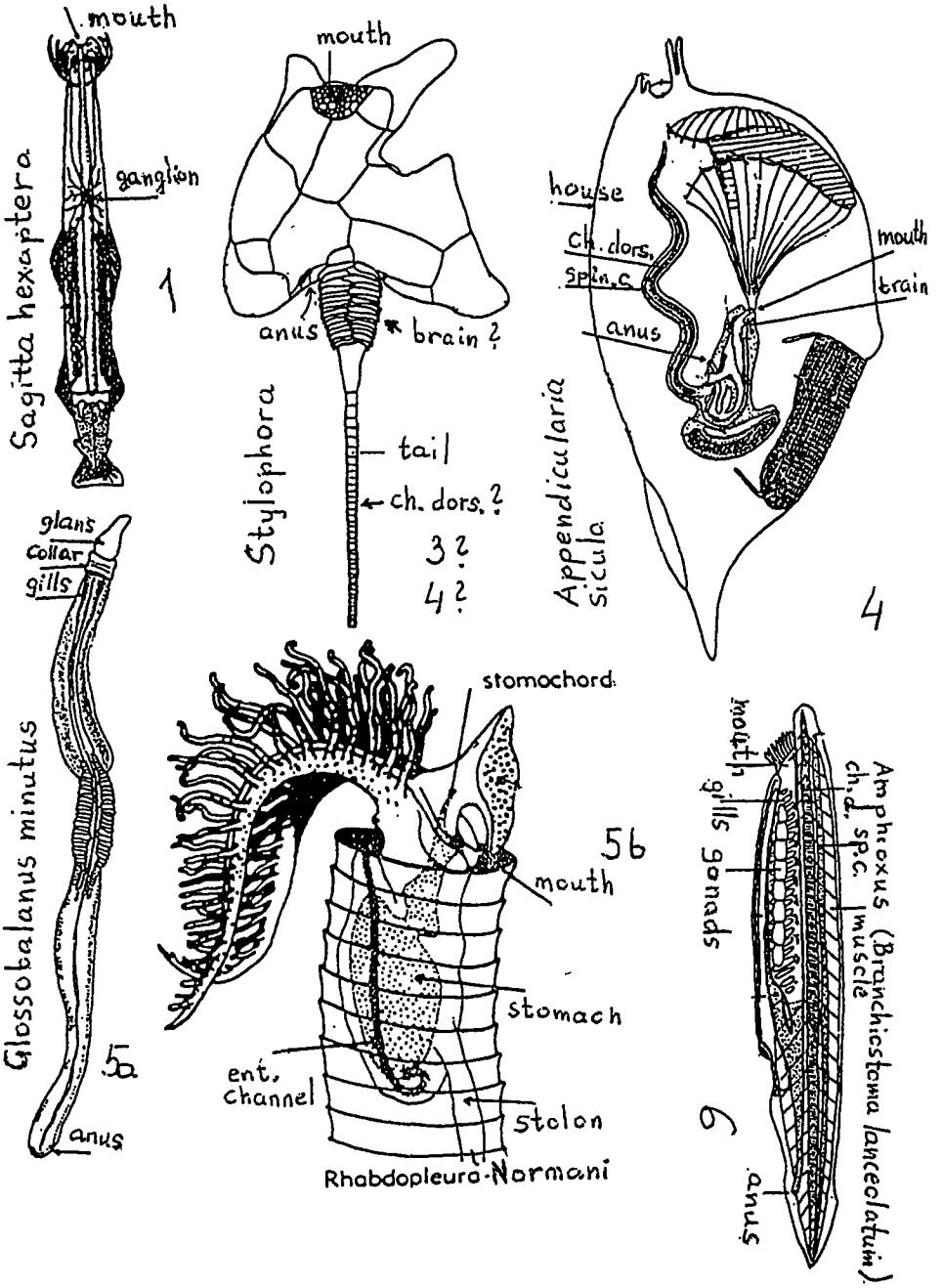

Figure 2: Some characteristic *Deuterostomata* as illustrations to the Figure 1. The positions are indicated via corresponding numbers.

The next picture shows *Appendicularia sicula*, belonging to *Tunicata*. There is a well developed *chorda dorsalis* in the tail, and in parallel on its dorsal side runs a neural fiber analogous to the spinal cord.

Glossobalanus minutus represents position *5a*. There is a so called notochord in the glands at the apical end, not seen here. It is sometimes regarded as the analogon of the *chorda dorsalis*. *Rhabdopleura Normani* stands for *5b*. These individuals form a colony connected via the stolon; in each member *two* channels start from the mouth, the enteral one (through the stomach to the anus) and the *stomochord* (which may be the analogue of the dorsal chord).

Finally *Amphioxus* (*Branchiostoma lanceolatum*) stands for *Vertebratae*. No need to bore the reader here with so familiar further kinsfolk as *Cyclostomata*, *Pisces*, etc., showing no important difference from us at all. *Amphioxus* will be discussed later in some details, so now observe only the segmented muscles, the many repeated gills, the homogeneous spinal cord and the lack of any mentionable head at the apical end. (The head will develop in later stages of evolution.)

Let us start with a problem in connection with the statement in another article (Bérczi, Lukács, and Molnár, 1993). It was demonstrated there, that deuterostomatae have a complicated topology, and this complicated structure *may* have permitted the possibility for higher complexity, effectivity or anything else behind our feeling of superiority. Thus far this is only a hypothesis, not discussed further. However one may ask about the *steps* leading to the more complicated topology, and then it turns out that at this point the picture is still partially obscure. This may indicate a fairly complicated evolution, with some very special steps.

Let us mention only one possible 'anomaly'. If one tries to visualize the possible steps to reverse the roles of mouth and anus, then the simplest reconstruction is the one mentioned in (Bérczi, Lukács, and Molnár, 1993): a primitive *Coelomata* had distorted itself into a U-shape, then the intestinal channel worked improperly at the turning point, so there developed a secondary channel with a new opening, and this new one has become a mouth instead of the opposite, for reasons of its own. The functionless half of the channel provided a possibility to house something new and useful: either the spinal or the dorsal chord. Then the branching point of the enteral and neural channels (or that of the first and the *chorda dorsalis*) is expected at the neighbourhood of the mouth.

It seems to be so for *Chaetognata* (intestinal and neural channels) and for *Hemichordata* (intestinal channel and stomochord). However, the embryonic development of *Amphioxus* (*Acrania*) suggests a different story. The very schematic picture is Figure 3 (after Hatschek and Ábrahám): compare this with the corresponding figure of (Bérczi, Lukács, and Molnár, 1993) and the difference is obvious. Now the bifurcation point is at the anal end of the mature organism. We do not have to accept Haeckel's biogenetic law to see the problem: cases of human *spina bifidia* conform with the structure observed *in Amphioxus*.

So something special may have happened on the *Vertebrata* branch of the evolution, between the recent *Amphioxus* (*Acrania*) and the common ancestor of *Acrania* and *Hemichordata* or *Tunicata* or both, anyway well in the *Precambrian*. We do not know this common ancestor from fossils, just as *any* ancestor of *Acrania* is

unknown, so there is still room for speculation. (We would rather avoid fruitless discussions about the *exact* location of *Acrania* on the evolutionary tree; the term *Vertebrata* will be used in a broad sense including *Acrania*. Anyway, *Amphioxus* has a well developed *chorda dorsalis*, and with enough imaginative power one can bridge the gap between *Acrania* and *Cyclostomata*.)

Here we want to discuss the possibility that one critical step creating 'anomalies' may have been a *unification*. More specially: in this paper we discuss some arguments for an evolutionary path leading from a colony of primitive *Deuterostomatae* (visualizable as analogous to *Enteropneusta*) to an integrated organism whose parts started thereafter to specialise. We are well aware that the idea is not new, was suggested a century ago by Hatschek (Kretzoi, 1964), but was opposed by such relevant people as Haeckel (1878) and Spencer (Collins, 1901). Still, there is no harm in rediscussing the possibility after a century.

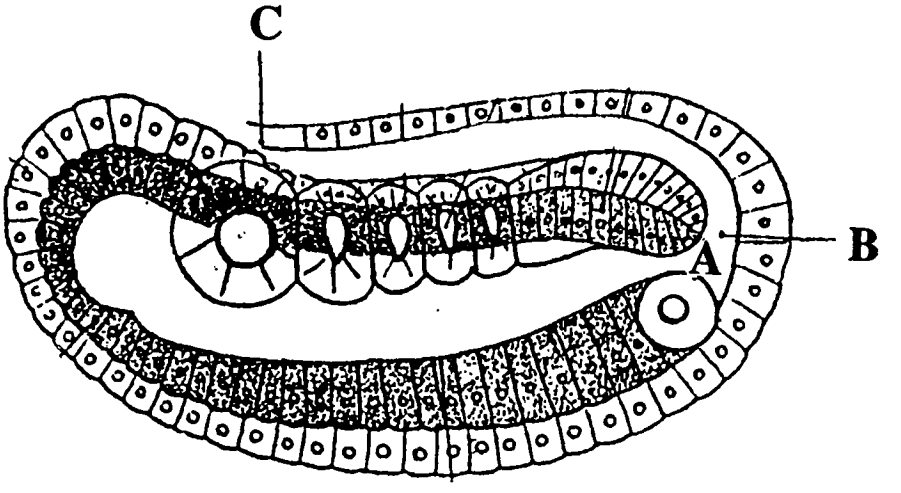

Figure 3: Amphioxus embryo in the stage of 5 stomites (after Ábrahám & Hatschek). Observe the developing U-shape of the "enteral channel". The dorsal branch will later house the spinal cord. Legends: *A*: protostoma; *B*: canalis neurentericus (the branching point); *C*; neuroporus (closing later). Consider the points disturbing any simple evolutionary scheme: *i*) the canalis neurentericus is at the protostoma, so will be at the anal end of the mature animal (if it is deuterostomic), compare this to *Rhabdopleura* on Figure 2; *ii*) the development process of the neural channel seen here cannot reflect phylogeny, because then for many generations the animals could not eat; *iii*) the dorsal branch of the channel here does not contain entoderm at all, so does not seem a part of the original enteral channel.

2. POSSIBLE CLASSES FOR COMPOSITE ORGANISMS

All *Metazoa* have, of course, living parts, *similar* to some independent living organisms. E.g., *Parazoa* consist of some cells similar to recent *Flagellatae*. Then, going beyond the statement that something is composite, it is useful to describe the rela-

tions between the animal studied and its, at least virtually, living parts. Many classifications may be relevant; we discuss three in this section.

The first and oldest one is based on the existence of parts and subparts. Then an animal may be of (Collins, 1901)

1) **Primary**, having no separable parts. *Examples: Protozoa.*

2) **Secondary**, having separable primaries. *Examples: lower Metazoa, as Platyhelminthes; Mollusca.*

3) **Tertiary**, having separable secondaries. *Example: Annelida, whose segments more or less resemble individual lower worms.*

A further, **quartiary** step would be the integration of tertiaries into a single organism. *A candidate is an ant-hill of very integrated insects*, as was philosophically suggested by Marais for termites (n.d.). However in this classification one cannot decide if the organism is indeed a unit or not. But remember this example for further use.

Let us see our place in this classification. The classical authors (Haeckel, 1878; Collins, 1901) agree that we are secondaries. One may recapitulate the arguments following Spencer.

The *Vertebrata* (just as *Mollusca*) organism does not show any tendency to spontaneously separate into parts in any stage of ontogeny.

No homologous segments appear; the apparent segments are not original but come from adaptation (e.g., to undulating swimming); the vertebrate animal cannot be divided into segments containing *most of* the vital organs (as digestive, respiratory and reproductive ones for example). The *Vertebrata* is a secondary organism superficially segmented by external influences (while the segmented insects are true tertiaries).

Therefore the only secondary organisms showing large and complicated forms would be molluscs and vertebrates.

In this section we list, not judge, possibilities. So now let us go to the second possible classification, according to the degree of integration and autonomy. For details see (Lukács, 1993) and further citations therein. We use 3 degrees:

(*A*) **Confederation.** Mainly independent parts with interactions. *Examples: sponges* (separated cells survive, but for a different kind of life, until reestablishing the secondary organism); *an earthworm* (can be cut into two and parts may live for a while to regrow the lost parts).

(*B*) **Federation.** Identifiable separate parts, but with some vital functions located at the level of the whole organism. A separated part can survive for a while but with restricted functions; it cannot regrow the whole organism and cannot live its independent life. *Examples: an insect* (can survive decapitation for a short time, but cannot become a complete insect anymore); *an ant-hill of termites* (from which a termite can be separated for a short time but will die without reproduction etc.).

(*C*) **Unity.** No possibility for survival of the separate parts for any mentionable time. *Example: majority of higher animals* (whose amputated fingers do not survive at all).

Obviously we belong to Case (*C*): an amputated human limb cannot survive as an individual organism in any sense.

Now we introduce a third viewpoint into the classification, according to the *origins* of the parts. Several logical possibilities may exist but it is useful, and conforms with European traditions, to think in triads. So here we define two extremal cases and every other transitional one will be classified simply between them:

α) **Symbiosis** of originally independent animals.
β) **Transitional** cases.
γ) **Self-generation** of new segments.

It is difficult to give here examples because we should know the *prehistory* of the composite organism. However, for Case α) one can mention the *Eucariotes* of *endosimbionta* origin (Cavalier-Smith, 1987), while Case γ) is suggested by the *ontogeny* of the tapeworm or the *Pogonophora* (ancestry unknown). We will return to Case β) after having some suggestions to specify.

Obviously the 3 classifications above (for composition, autonomy and origin) are not fully independent; not all the 27 combinations are possible, e.g., if something has no parts, then it must be a unity too. Again, one would expect higher autonomy for originally independent parts than for self-generated ones, but this is only an expectation and may depend on the history of the animal as well.

We close this section with Figure 4, which is a completed version of Figure 1. The conclusions from this figure will be postponed until the second section from this one.

3. ON AMPHIOXUS

The author is no expert of *Amphioxus*, and this section is no part of an *Amphioxus* monograph, only a list of some facts not quite consistent with Spencer's firm opinion (above) that no *Vertebratae* could be divided into homologous segments carrying most of the vital organs. But first we would like to emphasize that *Vertebratae* possess a 600 My evolution independently of any other *phylum* (say *Hemichordata* or *Tunicata*) and this time is quite enough to obliterate traces of autonomy by integration or those of homology by dissimilation, as seen, e.g., on *Metannelidae*. Also, our favourite *Amphioxus* is not an ancestor of other recent *Vertebratae*, up from *Cyclostomatae*: its origin is quite obscure, and we can only hope that it may be a 'living fossil'. Still, with sufficient imaginative power one can bridge the gap between *Acrania* and *Cyclostomata*. Now let us see some vital organs or functions of *Amphioxus*:

Respiration: Gills, with 80-100 openings.

Circulation: No heart; pulsating sections of an artery, as many thickenings as the number of gills.

Secretion: As many protonephridia as gills.

Reproduction: 22-25 pairs of gonads in segmental arrangement.

Sensors: A single olfactory cavity in forward position (possibly defunct). Sensitivity to chemical stimuli on the whole surface although enhanced at the apex. Optical sensitivity in diffuse cells of the spinal cord, segmentally arranged.

Neural system: Central part: spinal chord in segmental arrangement plus giant fibers connecting the segments. Dilatation at the apical end ('brain'). Dominantly gray matter for local functioning. Periphery: segmentally arranged neurons to muscles.

The above data definitely do *not* suggest a primordially unsegmented animal whose body became secondarily segmented for easier undulating motion. Such an adaptation might lead to segmented backbone muscles, but segmentally repeated eyes or gonads are not needed for easy swimming. Rather, the picture suggests a primordial homologous metamery, say between the homology of recent earthworms and insects, both always recognised unambiguously as good tertiary animals.

4. ON THE POSSIBLE ORIGIN OF METAMERY

Now let us return to Figure 4, which gives some suggestions. Lower *phyla* are generally oligomeric. The exception is *Pogonophora*. Then the first possible idea is that on the deuterostomic branch the tendency to grow multiple parts appeared independently, namely at the stage of *Pogonophora*, and this tendency is manifested in *Vertebratae*, but above *Acrania* in a rather obliterated way. To multiply the body is a very economic way (from an informatical viewpoint) to be larger and more versatile, and such a body is a useful starting point for later evolution, so if the tendency has appeared, it will probably be preserved by selection. In this case our position in the 3 by 3 classification is $3C\gamma$.

However in this way we run at least into two difficulties:

1) The tendency to self-generate segments seems absent in some higher units as *Echinodermata* and *Enteropneusta*.

2) In *Pogonophora* the metameric part is the *opisthosome* at the very end of the body. This part does not seem homologous to the segmented *middle* parts of *Vertebratae*, or to *any* part of them.

Fortunately one does not have to be disturbed by the above difficulties because recent rRNA sequence analyses have classified *Pogonophora* among *Protostomatae* (Lake, 1990). Since in the lack of enteral channel the ventro-dorsal discrimination is ambiguous in this *phylum*, we may accept the result. Having removed *Pogonophora*, Figure 4 suggests the following pattern. Lowest *Deuterostomatae* are solitary and not metameric at the same time. First appears the tendency for forming colonies by cloning. Note that both for *Pterobranchia* and for *Tunicata* the slightly connected individuals are secondary unsegmented animals. The *phylum Hemichordata* may represent the transition: some classes have the tendency of colony-forming, some do not. Then going higher this tendency disappears, but 'in its place'

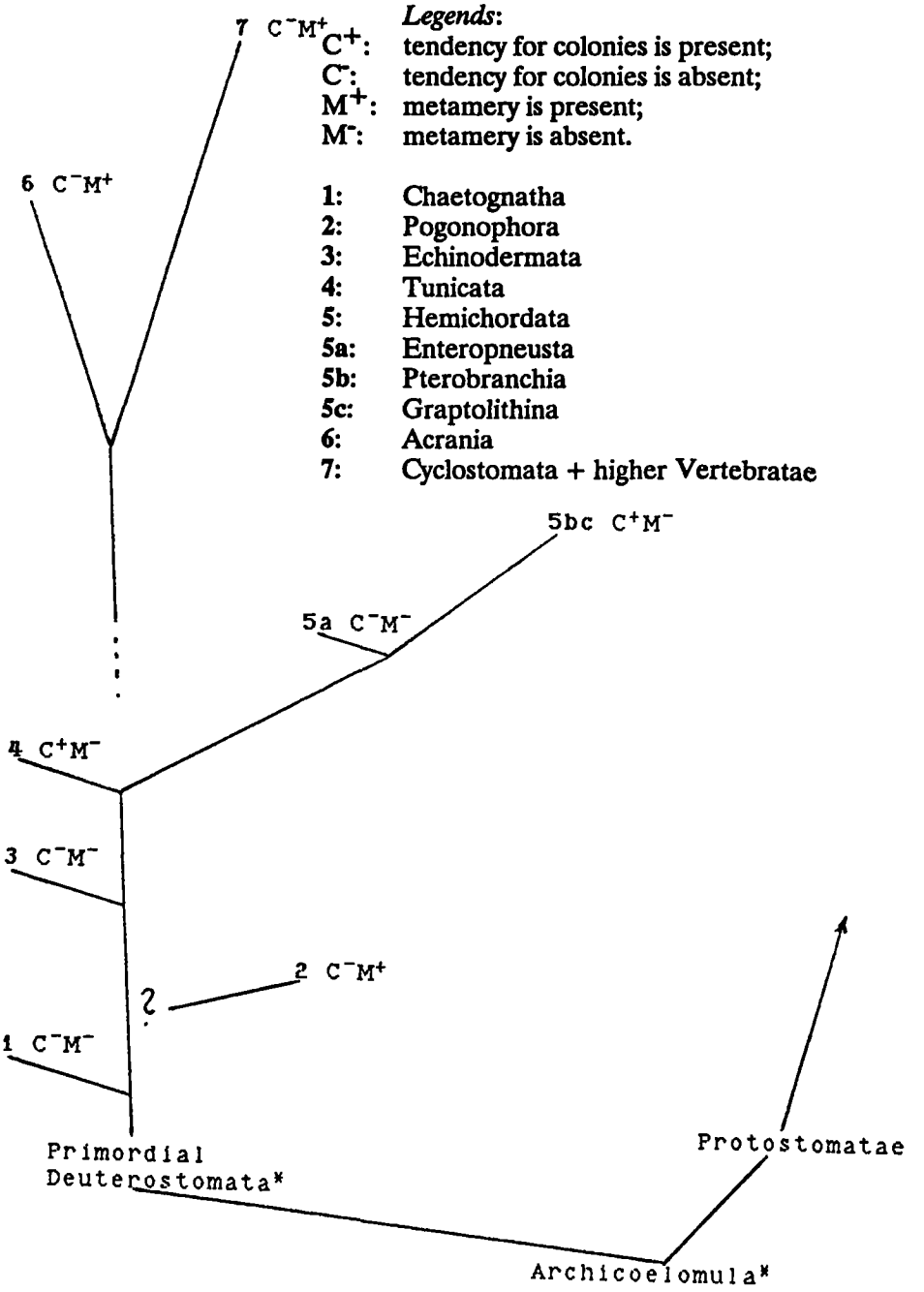

Figure 4: As Figure 1, but tendencies for colonies and metamery indicated.

metamery can be observed. This pattern gets a natural explanation *if* the segmented body is the inheritor of a colony, and the individual segments are inheritors of the individual members of the colony. Here it is worthwhile to note that in the Cambrian colonial *Graptolithinae* were quite common. While this time is slightly late for direct connection to ancestral *Vertebratae*, it is an indicator of a strong colony-forming tendency in the close neighbourhood of our ancestors.

We must confess that the present argumentation lacks constructive suggestions for the way of verifying or disproving the conjecture. *Amphioxus*' ancestors are not seen in fossils, and its embryogenesis does not seem to give a clear key (Bérczi, Lukács, and Molnár, 1993), which is not surprising after the adaptations of 600 Mys. Haeckel's Biogenetic Law cannot be taken at face value on this timescale. Still, we would like to recommend the above picture as a viewpoint when looking at ourselves. In what follows we do not question the picture but draw the logical conclusions.

5. CONCLUSIONS

If the *proto-vertebrates* were analogous to a colony of *Graptolithinae*, *Pterobranciae* or *Tunicatae*, with later integration and dissimilation, *then*

1) In the 3 by 3 classification *our* place is 3Cβ, where β stands for 'colony of semi-independent clones'. This is indeed a transitional case between 'symbiosis of aliens' and 'self-generation of new segments', since the symbiotic individuals are of common genetic origin (identical twins or clones), but they are not limbs or segments but *almost* independent individuals (connected only by stolons). The ancestral colony would be 3Aβ, the more integrated stage of the *proto-vertebrate* is maybe 3Bβ. The actual place of *Amphioxus* could be measured by the extent of its regenerative power.

2) The specific parts of the present vertebrate body are not homologous to those of *Chaetognata* and *Enteropneusta*. So any 'anomaly' may be expected when comparing the latter to *Amphioxus*.

3) The segmental arrangement of *Amphioxus*' gonads gets a natural explanation as a remainder of the original state. Indeed, in this case there is no serious genetic pressure to eliminate the multiple sources of reproduction, since the genetic information is the same in each cloned segment (except for the rare mozaicism).

4) Our classification 3Cβ generates disturbing philosophical ideas concerning ourselves. They will be given now at the end of the paper.

We *feel* ourselves indivisible units. However this feeling in itself has nothing with our origin or even with the constitution of our body. Our self-consciousness is generated simply by the *neocortex* of the brain, which is not repeated in the body. However, looking at *Amphioxus*, one sees that the *original vertebrate* central neural system is the spinal cord. This organ *is* segmented, and its apical part specializes *later* into a brain. The *Amphioxus* seems to have preserved the very first steps of this specialization with a 'brain' not qualitatively different from the posterior sections. Since a segment of the spinal cord possesses its own 'eyes' and chemical sensors,

and the intersegmental connections are not very strong, it is possible that the *Amphioxus* has a 'multiple personality' just as human society has: each segment can analyse data and command its own muscles independently, however with interaction and harmonisation between neighbouring personalities and with some 'leading' ones at the apex. It is possible, of course, that contemporary *Amphioxus* is already past this stage: maybe this point could be checked via teaching a particular segment by conditioned reflexes and then looking for answers in the neighbours.

Is it the case then that our original multiple personality is simply suppressed by the dominant mind(s) at the apex (now head), via the superabundant white matter conducting intersegmental commands, so that we cannot *feel* anymore the original multiple personality, and yet the specialisation has made the usurping apical segments so efficient that after some 600 Mys they can *find out* something about the original situation and can pay the obligatory respect to our own posterior, suppressed, atrophied, and finally neglected personalities?

ACKNOWLEDGEMENT

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