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V. *Mollusca: Gastropoda*[1]

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During the past several years, Dr. J. Brookes Knight, with the junior authors, has been studying the morphology and systematics of the Paleozoic gastropods for the Treatise on Invertebrate Paleontology. Recently we have spent some months in an effort to integrate systematically our findings on Paleozoic genera with those of other workers on post-Paleozoic forms. From these studies we have constructed a classification that embodies ideas and principles taken from an examination of living and fossil gastropods. This classification, given in Figure 1, is still tentative, and its full meaning will not become evident until the families and genera in the superfamilies are given in the completed Treatise.

We have used the anatomy of the soft parts as the basis for constructing this classification. By coordinating information about the anatomy of living forms and their shell features, it has been possible to make an estimate of the probable soft anatomy of many fossil gastropods — at least in broad outline. Actually the shell can be brought to yield, with a reasonable degree of probability, much more anatomical information than has been generally thought. If applied with due consideration for the order in which animals appear in time, for ecological differences, and for similarities due to convergence, inferences based on this information lead to results in classification that seem more plausible than those constructed by using other methods. Of course, like all attempts at phylogenetic classification this one is hypothetical, and additional information or different interpretations may later alter it.

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From the time of Lamarck, the construction of phylogenies and classifications was chiefly the work of neontologists. They based most of their conclusions on studies of the comparative anatomy of a relatively few living species. Much of their interest

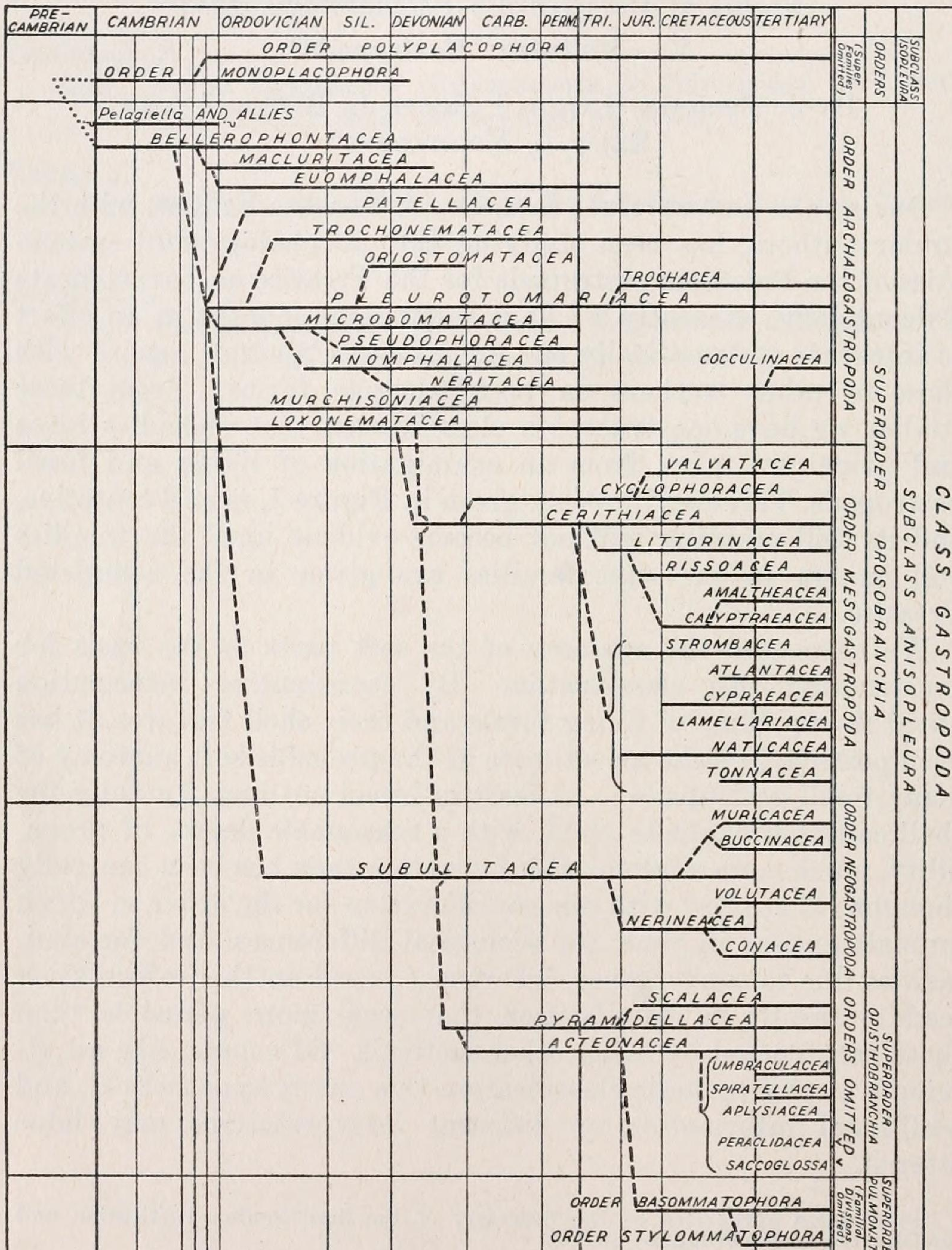

Fig. 1. Proposed phylogeny of the Gastropoda.

was concentrated in the attempt to discover missing links and to construct hypothetical ancestral types, all with little attention to or understanding of fossils.

Paleontologists, on the other hand, busy describing genera and species, were seldom concerned with supra-familial categories and were content to have their fossils placed in divisions erected for living species. Paleozoic gastropods suffered the most from this haphazard treatment because they differ most from the living forms. Mesozoic species were generally classified more rationally. Those of Cenozoic age, which differ little from those living today, were for the most part correctly classified but placed without roots into the past.

The great difference in Paleozoic gastropods as compared with living ones can be seen by observing the distribution of the major categories in time as shown in Figure 1. Note the concentration of Archaeogastropoda in the Paleozoic era and the Mesogastropoda and Neogastropoda together with the Opisthobranchia and Pulmonata in the late Mesozoic and Cenozoic eras.

It has only been within the past decade that sufficient information about the anatomy, embryology, and physiology of critical living species has been available. This information combined with previous observations — and above all with a deeper understanding of the more ancient fossils — has made possible the recognition of the probable ancestral groups of the major ordinal categories and some understanding of the evolution among them.

Let us turn to an example of what can be done by correlating the anatomy of the soft parts with conchology. Among the Monoplacophora, which range from early Cambrian to Devonian, is a group of cap-shaped shells, the Tryblidiidae. For many years they were considered to be primitive patellids, which they do resemble superficially in shape. In 1938, Wenz made the suggestion that those ancient forms were actually very primitive bilaterally symmetrical animals. He based this idea on the presence of symmetrically paired dorsal muscle scars as contrasted with the horseshoe-shaped muscle scar of the patellid shell. If Wenz was correct, as we believe he was, it follows that these primitive forms did not undergo torsion of the soft parts as do the patellids but were quite similar in internal organization to the chitons (Polyplacophora).

This was a revolutionary idea in gastropod systematics. It was arrived at by discounting superficial shell resemblances and concentrating on what might be learned from the record of the soft parts that was preserved in the shell. In this case it was merely the scars left by the pedal muscles, but it was enough to give a clue to the probable internal anatomy of monoplacophorans. The cap-shaped shell of *Patella* and patellid like forms has been achieved by many unrelated rock-clinging gastropods; it is most often an ecological adaptation and does not necessarily point to relationships. Unfortunately, except in cap-shaped shells, muscle scars are extremely difficult to observe, even in Recent gastropods.

Other features in the shell often correlate with specific features of the anatomy. One of the most important shell features that can be correlated with anatomical characters is the emargination or channel that marks the position of the anal tube. Since the ctenidia (primary gills) and other pallial organs have fairly definite relationships to the position of the anus, this may give information as to whether there was the primitive pair of gills or only a single gill. An anterior canal or notch accompanied by certain related features commonly indicates an inhalent siphon. A heterostrophic nucleus has been shown to characterize certain opisthobranchs inhabiting the present-day plankton. These examples indicate the type of inferential data that is important in the estimation of the anatomy of extinct gastropods.

If we then reconstruct the soft anatomy of our early gastropods inferentially, we can discuss their probable evolution in terms of three principal adjustments: flexibility in the Isopleura and increased motility and enhanced sanitation in the Anisopleura.

To return to the monoplacophoran, we have inferred that it had the anatomy of a bilaterally symmetrical organism, much like that of the chiton. The major evolutionary advance within the Isopleura was the replacement of the single monoplacophoran shell by a series of eight transverse plates. This gave the animal greater flexibility and permitted it to cling closer to the irregular surfaces of the rocks. So successful was this adjustment to its narrow environment that the chitons, appearing for the first time in the late Cambrian, survive today with very little change and virtually no adaptive radiation.

It may be appropriate to say at this point that most zoologists who are unfamiliar with the fossil record and who may not be aware of the existence of the Monoplacophora regard the chitons as a separate class reflecting characters of the ancestors of the gastropods, if not all mollusks. As paleontologists we prefer to be guided by the fossil record and suggest the Monoplacophora for the ancestral role. Whether the Isopleura be regarded as a subclass or a separate class from the Anisopleura is relatively unimportant; if the current separation is maintained, we feel that the Monoplacophora should be included with the chitons (see Figure 1).

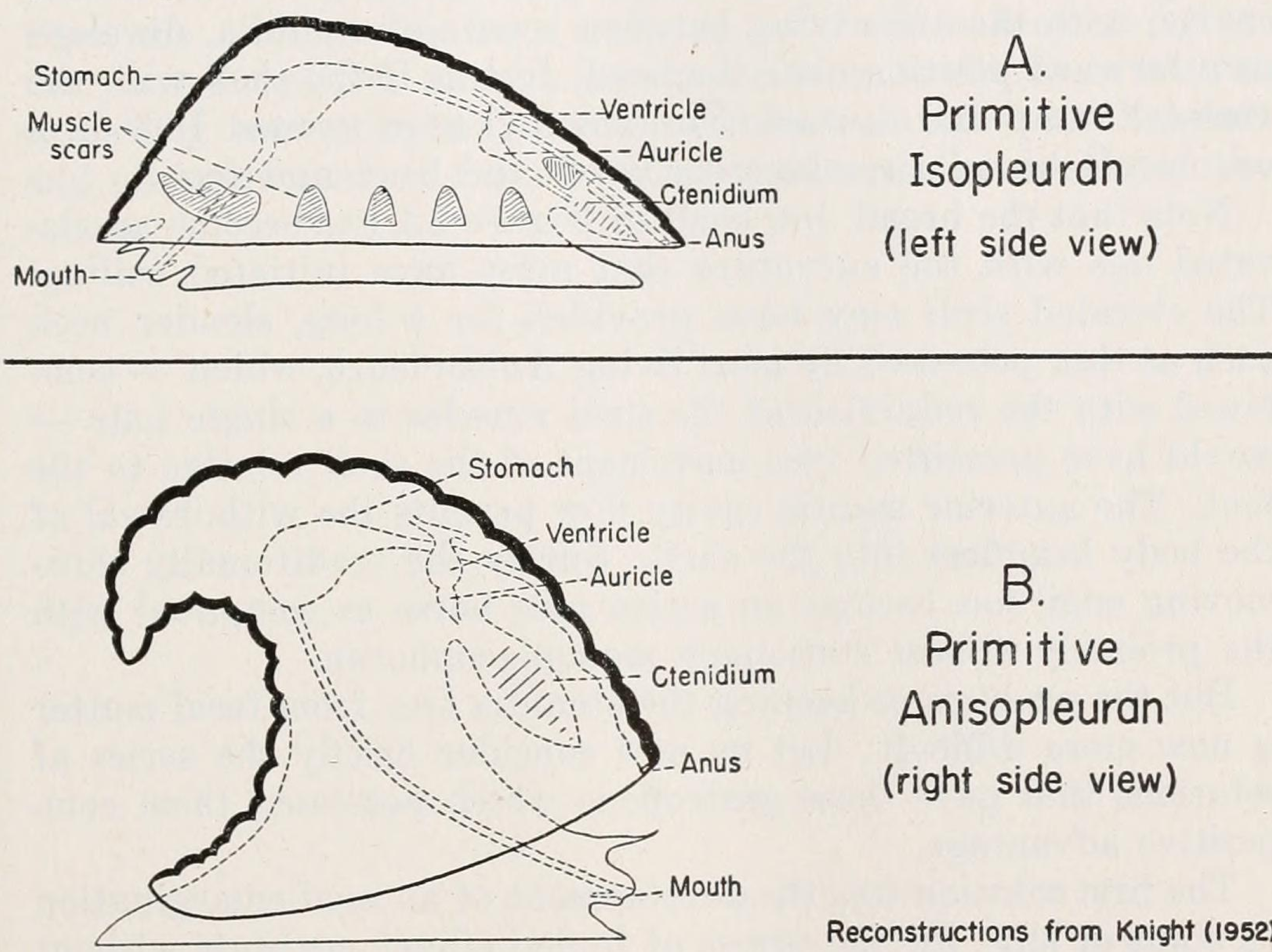

Fig. 2. Schematic reconstructions of two gastropods.

The introduction of the phenomenon of torsion gave rise to the Anisopleura with greatly increased motility and a newly important problem of sanitation. Figure 2A represents the left side of a primitive monoplacophoran restored with an organization similar to that of a chiton, shown with the shell transparent. Note that the anus lies in a posterior mantle cavity between a pair of ctenidia. As in the chiton, the posterior position of the anus obviates the need of any elaborate provisions for sanitation. Note also that the broad, low shell with its equally broad, low foot and its rather complex muscle attachment, permit little movement of the shell and probably allowed only very sluggish progression.

Figure 2B represents a restoration of a gastropod-like mollusk of the early Cambrian that is thought to be a primitive bellerophont, an advanced, relatively tall monoplacophoran, so to speak, that has undergone torsion. This is a view of the right side and is also drawn as being transparent. As is well known, torsion takes place in an early stage of the trochophore larva. This torsion occurs in such a way that the primitively posterior mantle cavity, with the anus lying between a pair of ctenidia, develops in a forward position over the head, just as if the shell with the visceral hump and contained organs had been twisted 180° in a counterclockwise direction relative to the head and foot.

Note that the broad, low shell in Figure 2A has become an elevated one with the curvature that must have initiated coiling. The elevated shell may have provided for a long, slender neck such as that possessed by most living Anisopleura, which — combined with the reduction of the shell muscles to a single pair — would have permitted free movement of the shell relative to the foot. The anterior mantle cavity now permits the withdrawal of the body headfirst into the shell. Surely the traditionally slow-moving snail has become an active race horse as compared with the probably almost stationary monoplacophoran.

But the problem of keeping the ctenidia free from fecal matter is now more difficult. Let us now consider briefly the series of solutions that gave those gastropods which possessed them competitive advantage.

The first solution was the development of an anal emargination (a sinus or slit) for the egress of fouled ciliary currents without contaminating the ctenidia that lay on each side. This solution was used by the bellerophonts and pleurotomarians. Next — after the introduction of asymmetrical coiling — came the suppression of the right-hand ctenidium and associated organs. As a result the ciliary currents entered the mantle cavity from the left anterior side and departed by the right posterior immediately after passing over the anus, which had migrated to that position after the loss of the right ctenidium. Such a development occurred several times within the archaeogastropods and led to the origin of other orders. Still further adaptations, also leading in part to the origin of new orders, were the gradual return of the anus to a posterior position in the adult of many opisthobranchs and — the last step — loss of the shell with almost full bilateral symmetry in the adult.

A final adjustment not discussed here is the adaptation for life on the land with conversion of the mantle cavity into a lung and the loss of ctenidia in the pulmonates.

In summary, this classification shows that while the living Isopleura have undergone very little change since late Cambrian time, the Anisopleura have radiated outward to become one of the most successful animal groups. Living snails have become extremely numerous and varied and have invaded all habitats and all environments from high mountains to the depths of the oceans.