REDUPLICATION IN EVOLUTION

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INTRODUCTION

IN 1894 William Bateson published his classic work *Materials for the Study of Variation*, in which he stressed the fundamentally important concept that the existence of patterns, defined as exhibiting symmetry with respect to certain points and axes, is a central fact of morphology. He distinguished 'Minor Symmetries,' formed by patterns completed in the several organs or parts, and 'Major Symmetries' which are compounded of minor symmetries. He proposed the term 'Merism' to include the phenomenon of 'Repetition of Parts' in organisms, "generally occurring in such a way as to form a Symmetry or Pattern"; and he noted that this phenomenon "comes near to being a universal character of the bodies of living things."

He then continued to distinguish two main kinds of variations, namely, 'Meristic Variations' and 'Substantive Variations.' As an example of meristic variation he cited the fact that the flower of a *Narcissus* is commonly divided into six parts but through meristic variation it may be divided into seven parts or into only four. As an example of a substantive variation he cites the occurrence of two distinct colors in different species of *Narcissus*.

Bateson, however, considered variability only in its present manifestations. Owing to his reaction against phylogenetic speculation, the chronological or phylogenetic aspect of variability was practically banned by him, especially in his famous Address before the British Association for the Advancement of Science at Toronto in 1914. In the present paper, on the contrary, certain phases of variability, hereinafter named *polyisomerism* and *anisomerism*, are considered from the phylogenetic viewpoint, in which the available facts of geology, palæontology and zoology are, so far as possible, constantly integrated.

REDUPLICATION AND INEQUALIZATION IN INVERTEBRATES

Trilobites, Crustaceans, Arthropods

The researches of palæontologists, especially those of Walcott, Beecher, Raymond and Leif Störmer (1933) have shown that some of the Cambrian trilobites, including *Triarthrus* (Fig. 1A) were remarkably generalized animals that were apparently near to the direct ancestors of the eurypterids, king crabs (*Limulus*), scorpions and spiders. In another direction they were related to the ancestors of the Crustacea. The thorax of normal trilobites consists of numerous segments, each of which bears on either side a jointed and usually biramous appendage; each of these paired appendages includes a basal piece or coxopodite from which branch outward two main divisions, an exopodite and an endopodite. The endopodites were used for crawling and consisted usually of six joints. The jointed exopodites were biramous distally, the posterior branch bearing a row of closely appressed gill-blades (Leif Störmer). In any individual trilobite the parts of one thoracic segment are severally comparable with those of other segments. The limbs of crustaceans, according to Leif Störmer, lack the gill-blades of the primitive exopodite, which are preserved in the

more primitive arthropods (e.g., *Limulus*). Thus the common trilobite-crustacean stock is probably Pre-Cambrian in origin.

Trilobites, crustaceans, arthropods, as well as annelid worms, are metameric animals, in so far as they present an antero-posterior series of homologous segments of budding or subdivision of some parent substance or tissue. Polyisomeres are homologous or comparable parts, either in the same or in different segments or organs, e.g., the different individual gill-blades of a trilobite, either of a single segment or as between different segments.
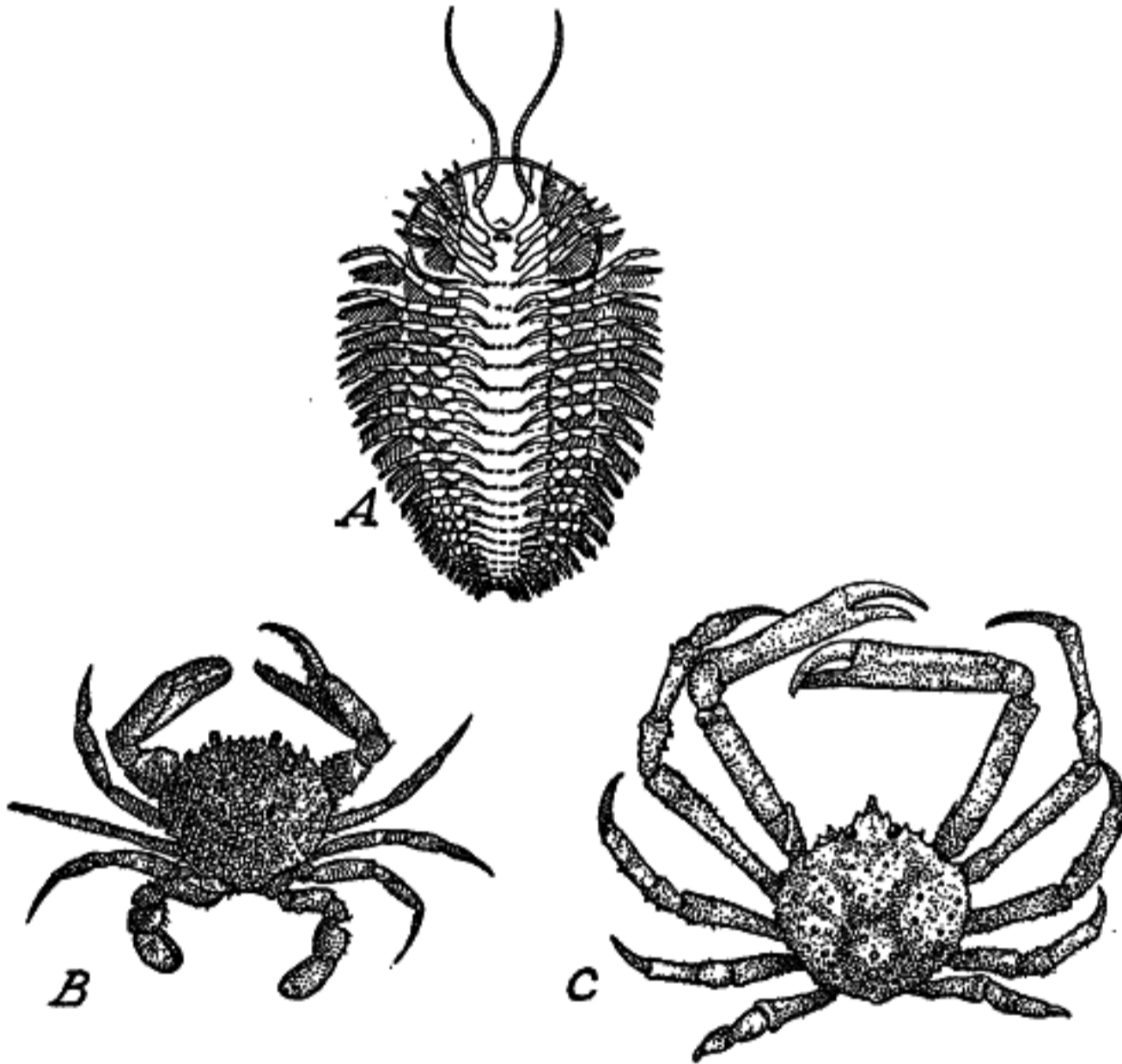

FIG. 1. POLYISOMERISM AND ITS OPPOSITE, ANISOMERISM, IN METAMERIC INVERTEBRATES

A. Primitive Cambrian trilobite, *Triarthrus beckii.* After Beecher. Under side, showing primitive longitudinal and transverse polyisomerism.

B. Modern crab (*Platyonichus ocellatus*). After A. G. Mayer. Dorsal side, showing high degree of anisomerism.

C. Spider crab (*Libinia dubia*). After A. G. Mayer. Dorsal side, showing secondary polyisomerism by convergence.

extending symmetrically on either side of the long axis of the body. Metamerism is, however, only a special case of poly-isomerism, or reduplication, which may be defined as the state in which many homologous parts are arranged along any primary or secondary axis, anteroposterior, transverse, vertical, spiral, etc. Poly-isomerism evidently results from a process

Thus we may have interorganic poly-isomerism or intraorganic polyisomerism.

If we now compare a modern lady-crab (*Platyonichus ocellatus*, Fig. 1B) with the primitive trilobite, we shall note that in the crab a number of the thoracic segments have fused with the head to form a cephalo-thorax, while the appendages have acquired a marked regional differen-

tiation, so that, for example, the powerful claws armed with sharp tooth-like projections on their "jaws" are quite different in general appearance from the walking legs and these again from the paddle-like appendages at the rear end. Here then is an example of true differentiation or *anisomerism*, which has grown out of a state of undifferentiation or primary *polyisomerism*.

Such local differentiation of homologous parts is due in part to heterogony, or differ-

ondary polyisomerism by convergence of a type which is extremely frequent throughout the animal and plant kingdoms.

There seems to be good evidence that the trilobite stock gave rise to the Silurian eurypterids and that some of these in turn produced the Silurian and later scorpions and spiders, while certain others are represented today in the king crab (*Limulus*), which is thus a 'living fossil' of the highest antiquity. In the higher arthropods the originally polyisomerous

A   B   C
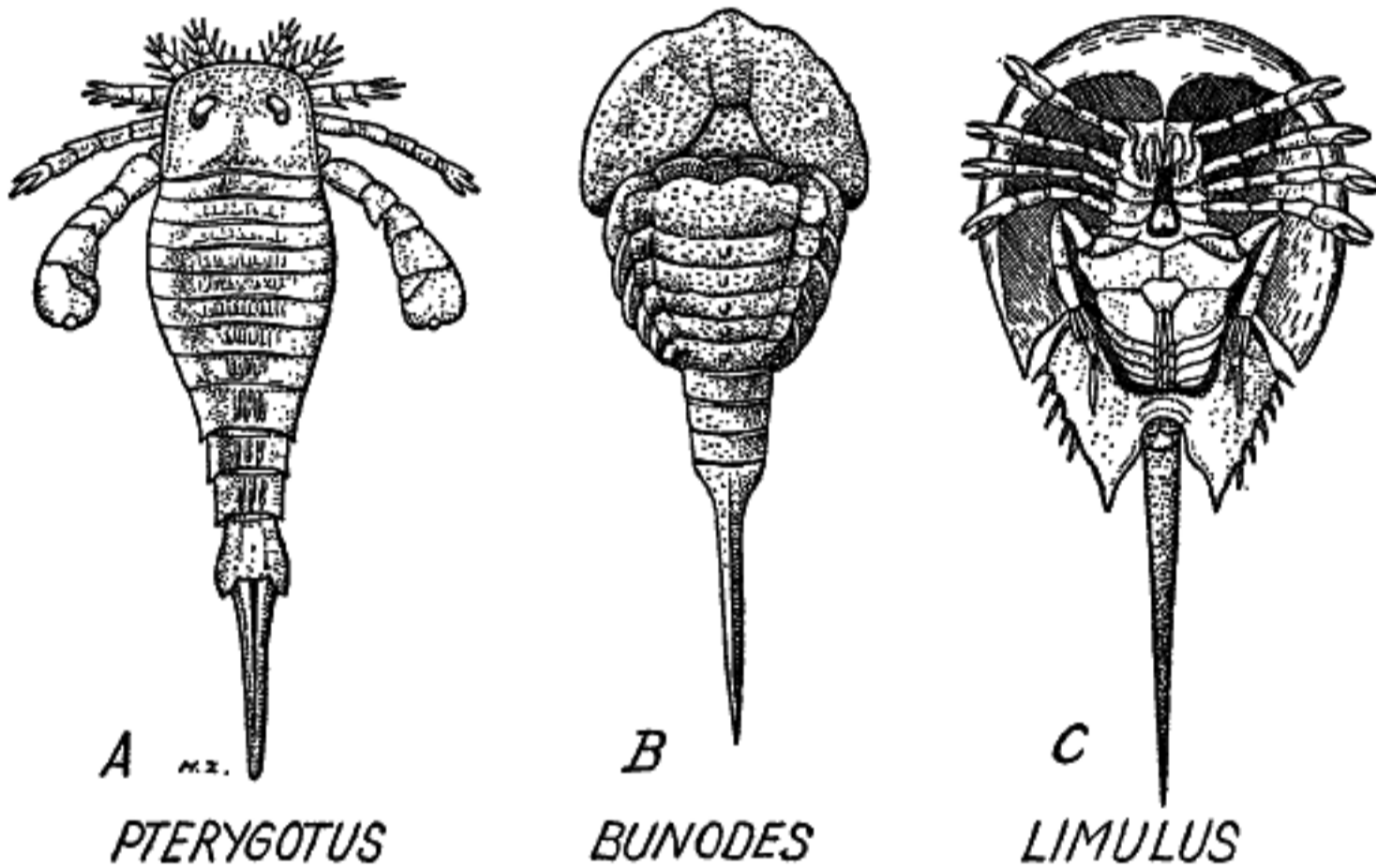PTERYGOTUS   BUNODES   LIMULUS

FIG. 2. POLYISOMERISM AND ANISOMERISM IN PRIMITIVE ARACHNIDS
A. *Pterygotus anglicus*. From Abel, after H. Woodward.
B. *Bunodes lunula*. After restoration by Patten.
C. *Limulus polyphemus*. After Abel. Under side, showing anisomerism of head-shield and thorax.

ences in growth rates in different segments as compared with the body as a whole (J. S. Huxley, 1932, p. 8).

If next we compare an ordinary crab with a spider crab (Fig. 1C) we note that in the latter the exoskeleton is covered with numerous small excrescences and that the very long appendages in a general way look much alike, so that the really high specialization of this form is masked by a false impression of uniformity or lack of differentiation. This is an example of sec-

head segments become variously fused and distorted in connection with the great enlargement of the paired cranial ganglia and their partial concrescence into a true brain. A similar fusion of primitive neuromeres has generally been supposed by embryologists to have taken place in the remote ancestors of the vertebrates. For this and other reasons the late Professor William Patten (1912) brigaded the Arthropoda and the Vertebrata in a superphylum which he named the Syncephalata.

He also showed how (Fig. 3), according to his theory, the shield and paired eyes of the primitive eurypterid grew around on to the opposite side of the animal and the eyes turned inside out to produce the paired eyes of the earliest ostracoderms; how the several cranial nerves of the arachnids were transformed into those of the typical vertebrates. But after many years of fairly frequent and close study of

To palæontologists both Patten's and Gaskell's theories must stand at present as capital examples of the power of convergence and of mere coincidence to produce deceptive similarities between widely unrelated forms. In other words, it appears that independently in the Arthropoda and in the Chordata the progressive evolution of a complex locomotor apparatus along somewhat similar lines
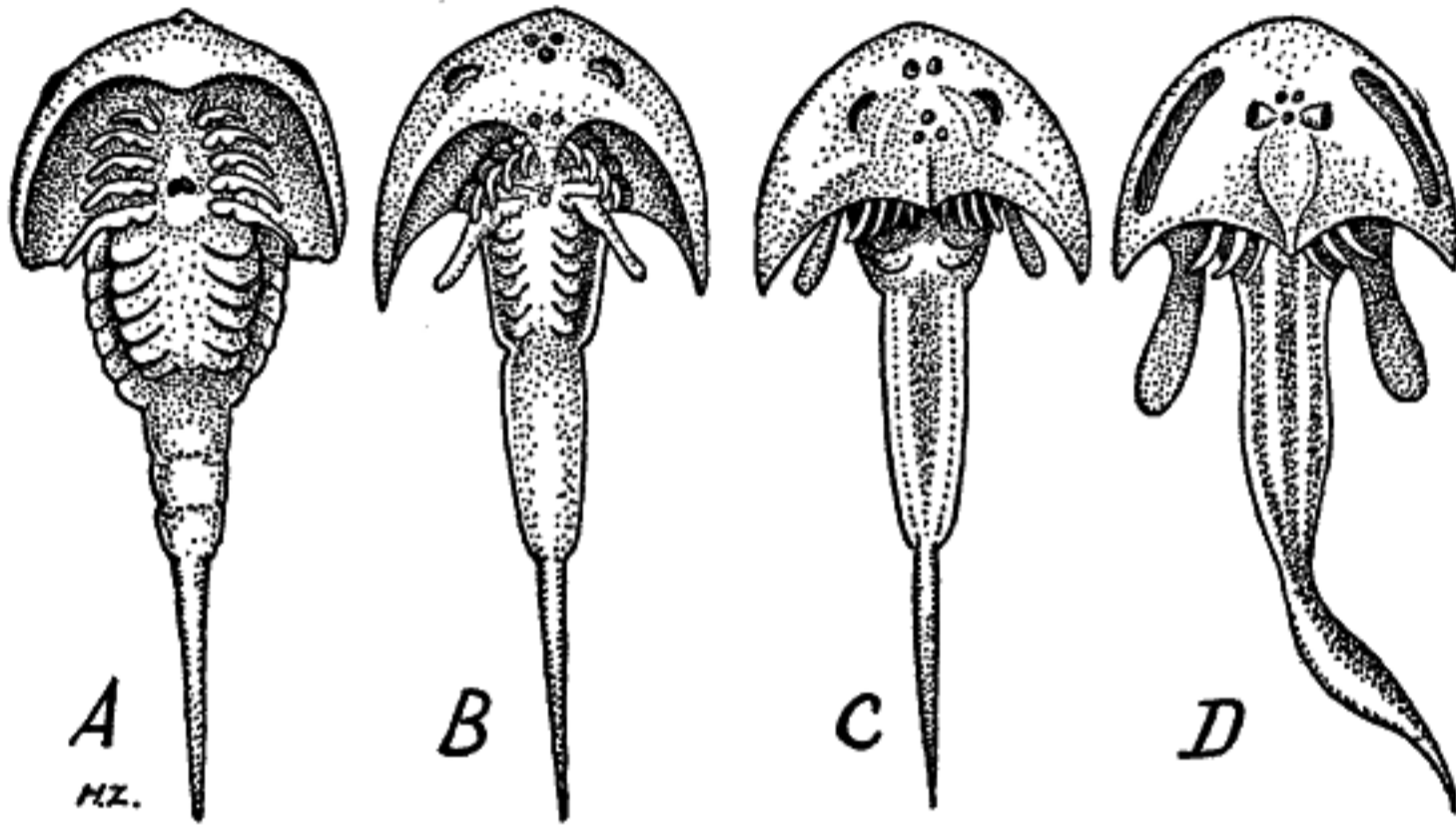

FIG. 3. PATTEN'S THEORY OF THE ORIGIN OF THE VERTEBRATES
After Patten

A. Diagram of hypothetical marine arachnid, based chiefly on *Bunodes lunula.* The animal is lying on its "back," or functionally dorsal surface, revealing the primitive mouth and paired appendages.

B, C. Hypothetical stages showing the overgrowth of the shield on to the originally ventral surface, which gives rise to the dorsal surface of a vertebrate. The overgrowth of the shield is referred to a great increase and coalescence of the neuromeres beneath it. The cephalic appendages give rise to the extrabranchial cartilages and postoccipital appendages.

D. Larval ostracoderm (*Cephalaspis*), showing complete transmigration of the shield and paired eyes on to the now dorsal surface.

From the palæontological viewpoint there is little warrant for the postulation of either such a major shift of the shield or the derivation of the vertebrate branchial skeleton from cephalic appendages.

Professor Patten's theory I am unable to accept his proposed homologies between the cranial nerves of arachnids and those of vertebrates. Gaskell's version of the arthropod theory of the origin of vertebrates, while equally ingenious, requires even greater demands upon our credulity in accepting its drastic transformations of the primitive gut of arthropods into the lining of the neural tube of vertebrates (cf. Delage and Hérouard, 1898, p. 350).

required a more and more complex control system; that is, a primitive state of polyisomerism in the locomotor parts and their corresponding nerve segments, through emphasis, concrescence and loss of parts, gradually gave way to differentiation or anisomerism in both phyla. But in spite of the convergence in external appearance between eurypterids and ostracoderms it must be admitted that the brain and cranial nerves of *Limulus* are

profoundly different from those of the larval lamprey or even from those of the Devonian ostracoderms as described by Stensiö.

The mouth-parts of invertebrates show annelids, echinoderms, etc., serve to drive a current of water into the mouth. Here the polyisomerism of the cilia is evident.

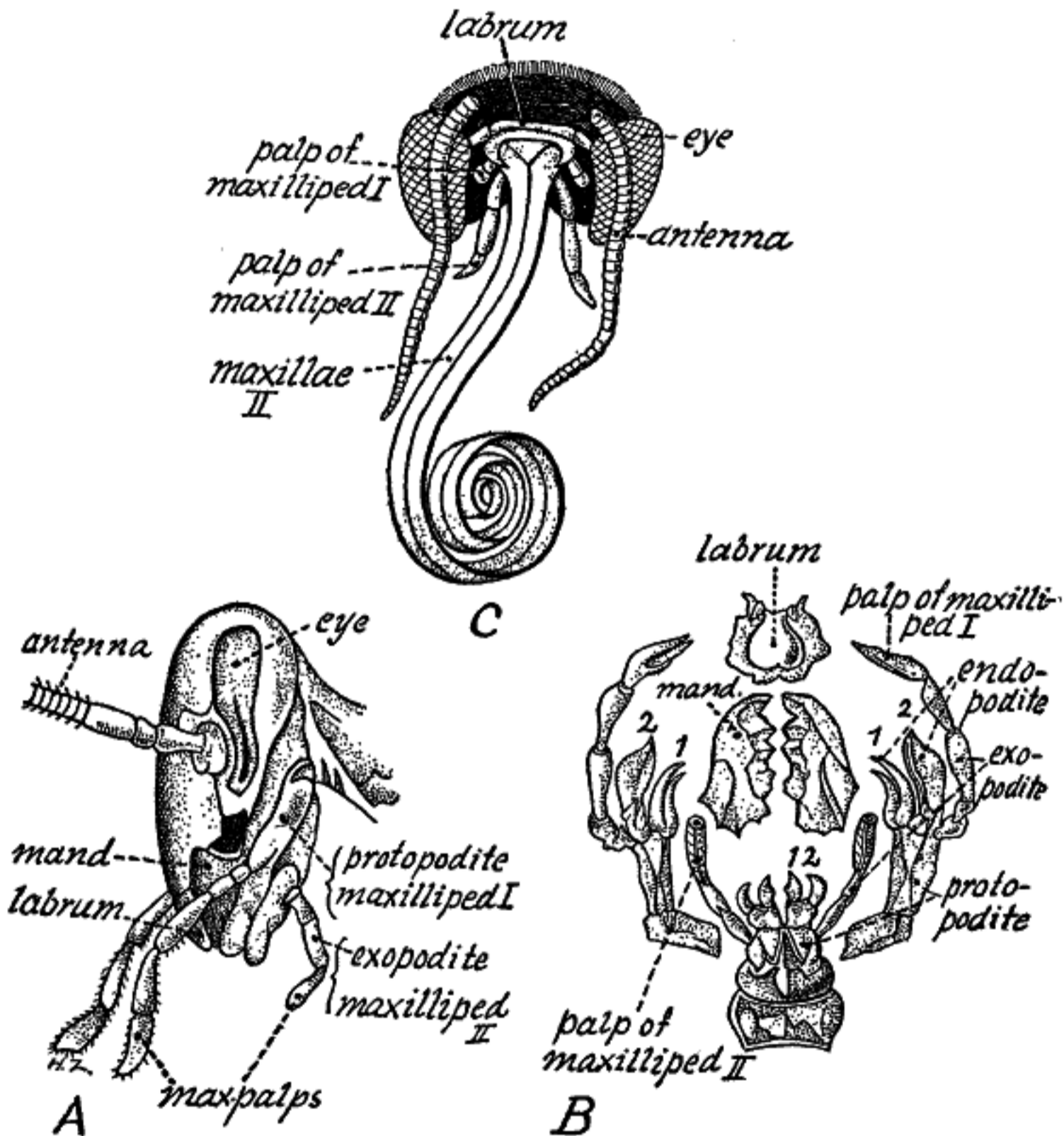The starting-point for the more or less complex jaw-parts of crustaceans, arach-

FIG. 4. POLYISOMERISM AND ANISOMERISM IN THE MOUTH PARTS OF INSECTS
Modified from Parker and Haswell, after Lang

A. Head of cockroach, showing maxillary palps derived from exopodites of cephalic appendages.
B. Mouth parts of cockroach, showing primitive relations of exopodites and endopodites to protopodites.
C. Extreme anisomerism in mouth parts of Lepidoptera, showing proboscis made up of the fused endopodites (maxillæ) of "maxilliped II."

the same principles of growth and evolution as do their varied locomotor apparatus. Perhaps the simplest forerunners of jaw-parts are the ciliated bands which in various Protozoa and in the larvae of nids and insects is to be seen in the much more primitive conditions in trilobites, where the functional jaws are merely the proximal parts of the first two pairs of segmental appendages.

It has long been known that among the insects there are many steps from the primitively isomerous mouth-parts of the cockroaches (Fig. 4A, B) to the excessively specialized anisomerous mouth-parts of the Lepidoptera (Fig. 4C).

Molluscs

Although molluscs are not metameric animals they often display serial repeti-
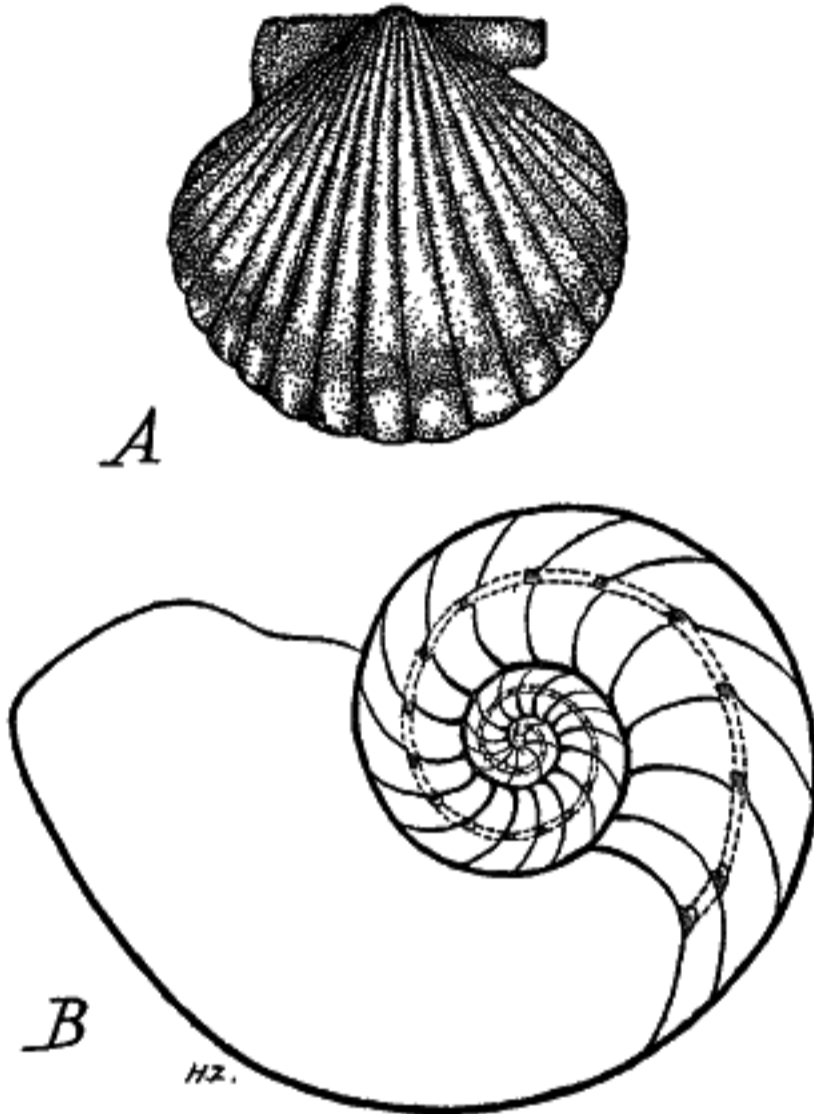
A

B

FIG. 5. SECONDARY POLYISOMERISM IN MOLLUSCS

A. Radial polyisomerism in *Pecten*. After A. G. Mayer.

B. Spiral polyisomerism in *Nautilus*. Section of shell, after Parker and Haswell.

tions of certain features which are an expression of the phenomenon here called secondary polyisomerism, following upon an earlier anisomerism: for example, the ridges or folding of the shells of many pelecypods or the eyes on the mantle of scallops. Such alternate elevations and depressions imply temporal acceleration of growth and spatial distribution of neutral nodes, which processes seem to be among

the causes of polyisomerism. Secondary polyisomerism is beautifully illustrated in the successive chambers of cephalopods. In the more elaborate types of sutures of fossil nautiloid shells we witness the evolution of polyisomerism of the second, third and even higher orders.

There seems to be good evidence that the primitive mollusc was bilaterally symmetrical until a constant difference in growth rates of the two sides of the mantle conditioned what might be called a spiral symmetry.

Thus polyisomerism is due to the summation of rhythmic pulses of growth operating in tissues of more or less homogeneous material, i.e., in any of the three primary germ layers or their products. Hence polyisomerism, as a direct result of rhythm in cell division, is perhaps as fundamental and far-reaching a property of living things as growth and subdivision.

The opposite phenomenon, anisomerism, is due to the undue emphasis or prolongation of growth of certain parts, which are thus thrown out of harmony with the rest. A more remote contributing cause of polyisomerism and its opposite may be the diurnal and seasonal variations in the environment, as clearly registered in the lines of growth in shells, fish scales and tree trunks.

The highly organized radula, or rasp, of predatory molluscs includes a great number of tiny denticles arranged in various ways in longitudinal rows on a movable, strap-like tongue, which can be jerked back and forth over the shell of the victim. These polyisomerous denticles are also diagnostic in different species and genera, and here we notice the obvious but fundamentally important fact that polyisomeres are always specific or even individual, so that although the processes that produce polyisomerism may be similar or identical in different cases, the material that goes

into the product is always specific and diagnostic, possibly even of the individual, if sufficiently delicate tests of age and nutritional factors were available.

Echinoderms

The combined results of long periods of polyisomerism, anisomerism and secondary polyisomerism in the arthropod group and their allies have produced many extraordinary types of body, but in the echinoderms still more amazing transfor-

with five well developed "arms" may be more primitive than the asymmetrical bag-like *Aristocystites*. These five arms, which were of course primarily like the puckered corners of the bell-like mouth of a jellyfish, were of great functional importance in collecting and passing along minute food particles to the mouth. From the first they exhibited a pentameral polyisomerism, not only in respect to their general ground-plan but in the comparison of their extremely numerous small parts, such as

A   B   C   D
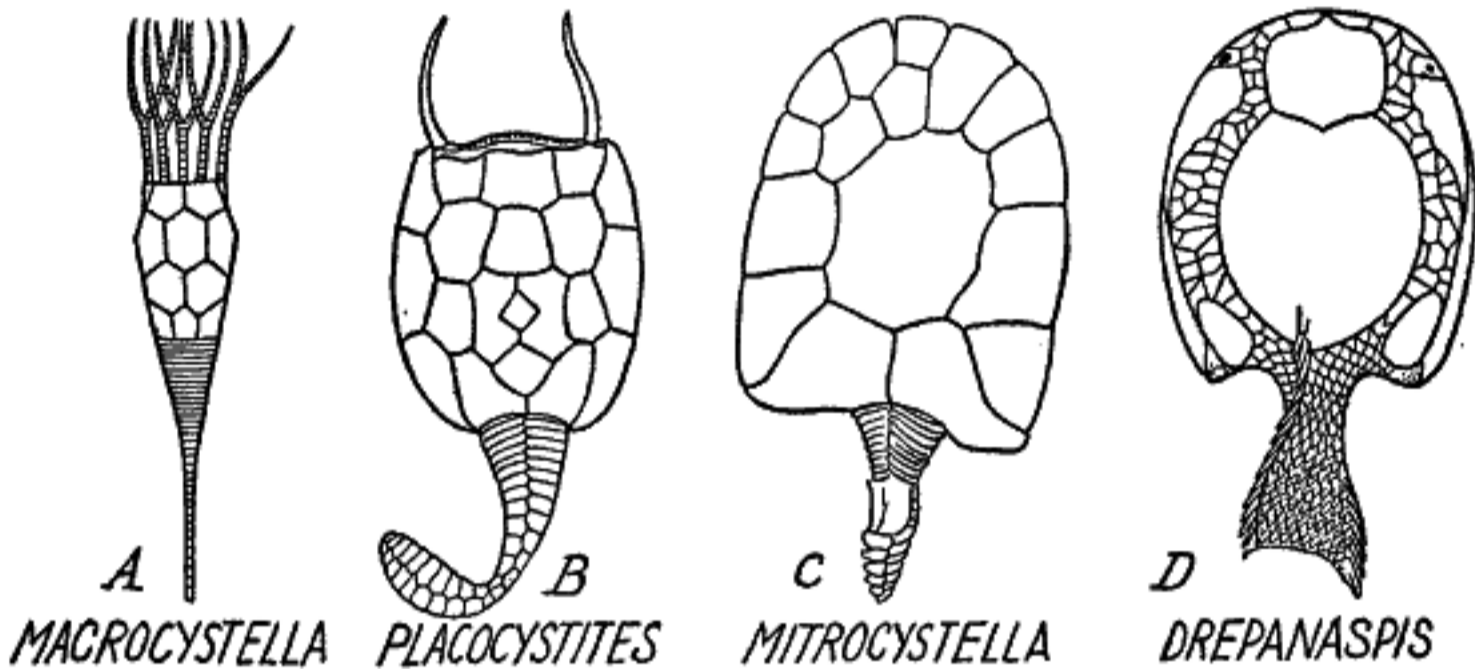MACROCYSTELLA   PLACOCYSTITES   MITROCYSTELLA   DREPANASPIS

FIG. 6. COMPARISON OF ECHINODERMS AND PRIMITIVE CHORDATE

A. Relatively primitive cystoid, *Macrocystella*. After E. W. Berry. Showing quinqueradiate polyisomerism.

B. Upper Silurian carpoid, *Placocystites forbesi*. From Abel, after Bather. Showing secondary dorso-ventral asymmetry and bilateral symmetry.

C. Lower Silurian carpoid, *Mitrocystella barrandei*. From Abel, after O. Jaekel. Showing dorso-ventral asymmetry and incomplete bilaterality.

D. Devonian ostracoderm, *Drepanaspis*. From Zittel, after Traquair. Showing nearly complete bilaterality.

mations have been attained by the accumulation of an infinite number of small steps. On account of the bilaterality of the larva of *Antedon* it is believed by high authorities that the radiate symmetry of echinoderms was first developed in adaptation to sessile life by an early bilateral and free-moving pre-echinoderm. While that may well be true of the pre-echinoderms, by the time the echinoderms themselves first became known in geological history they were already attached forms and it is even possible that some of the early sea-lilies

the tube-feet, ampullæ and supporting plates. Contact of the larva with the ground, however, induced a marked regional anisomerism manifested by the outgrowth of an attaching organ or stalk, which eventually in its turn became secondarily polyisomerous.

However, with the instability and as it were recklessness that characterizes Nature, some of the beautiful sea-lilies sacrificed their five-rayed symmetry by habitually bending over on one side. As the calyx touched the bottom on one

side and the race gradually became adjusted to this new position, a dorso-ventral asymmetry was gradually imposed, together with a cephalo-caudal asymmetry and eventually a bilateral symmetry. Several stages in this process are seen in the early group of echinoderms called Carpoidea. Thanks chiefly to the researches of Bather in England and Jaekel in Germany, many genera of these queer lop-sided creatures have been made known to science and an excellent brief review of the group may be found in O. Abel's *Lehrbuch der Paläontologie* (1920, pp. 280, 281). When the calyx was bent over and acquired a dorso-ventral asymmetry it developed a bilateral articulation with the stalk, which in turn tended toward bilateral symmetry, while the lower end of the latter, formerly serving as a kind of root, acquired a spatulate, tail-like expansion. Meanwhile, as a result of the induced tendency toward dorso-ventral asymmetry and bilateral symmetry of the calyx, certain genera (e.g., *Placocystites*, *Mitrocystella*, Fig. 6) began to display a somewhat vague suggestion of the general appearance of the "head shield" of certain ostracoderms (e.g., *Drepanaspis*, Fig. 6), while the stalk, as above noted, furnishes an amusing suggestion of an ostracoderm tail.

In another carpoid named *Cothurnocystis* the calyx is markedly asymmetrical, bearing on one side a row of small openings (Fig. 7) which Dr. Torsten Gislén (1930) has compared with the asymmetrical gill-openings of the larva of *Amphioxus*.

Of course we cannot yet be sure that all these resemblances are not due to the "long arm of coincidence," which has brought about hosts of what the late Professor Bashford Dean (1908) called "Unnatural History Resemblances," such as the "crucifix" on the underside of the skull of certain catfishes, the "samurai's

face" on the back of certain Japanese crabs and the "Arabic inscription" on the tail of a certain fish. And whenever such spurious resemblances are pointed out the memory is quick to supply additional "evidence" from independent quarters. So also in the case of the ostracoderm-like appearance of some of the carpoid echinoderms we recall that zoölogists have long suspected that there was a remote connec-
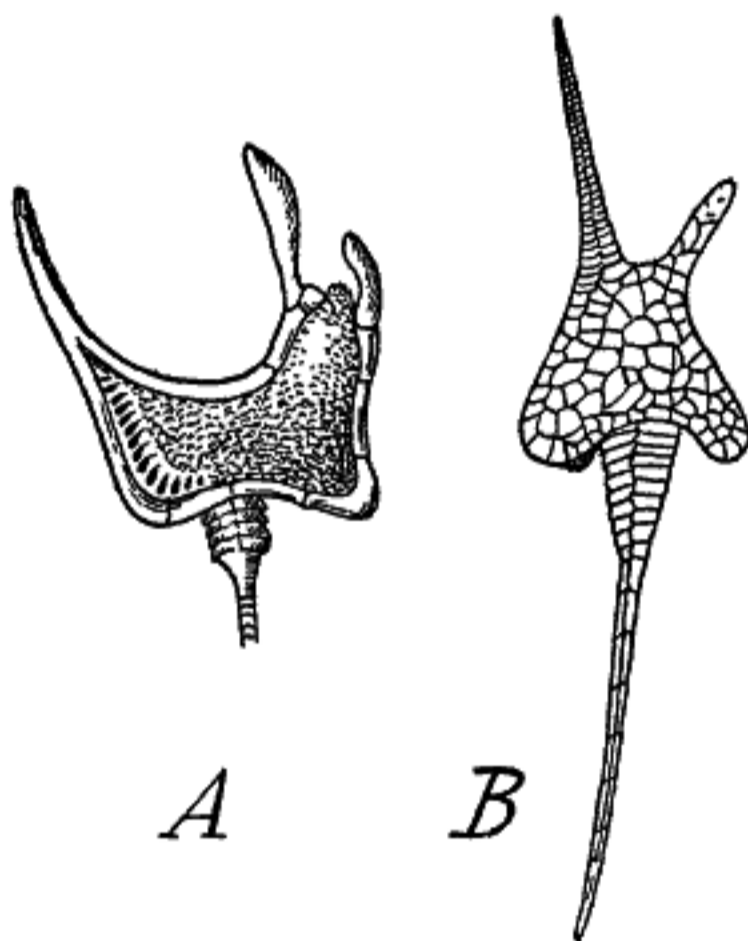

FIG. 7. ASYMMETRICAL SILURIAN CARPOIDS
From Abel, after Bather

A. *Cothurnocystis elizae*. Showing marked asymmetry and supposed "mouth openings" (? branchial openings).
B. *Dendrocystites scotticus*. Showing tail-like stalk. The marked asymmetry and general appearance is somewhat suggestive of an ascidian larva.

tion between the echinoderms and the vertebrates, not only because of the "Tornaria" larva of *Balanoglossus*, which resembles that of certain echinoderms, but also because both form their mesoderm from enterocoelic pouches.

Meanwhile it must be admitted that so far as known there is a profound morphological gap between any known echinoderm and the oldest known vertebrates. This would be still more con-

spicuous if proof were found for Jaekel's view (quoted by Abel, 1920, p. 279) that the reduction of the mouth-plate in the carpoids is correlated with the evagination of the gut in front of the mouth, as occasionally happens in the holothurians, so that the food was both caught and digested outside the body! Nevertheless even greater miracles seem to have happened than the hypothetical loss of the preoral part of the gut and the development of a new mouth, transformations long ago demanded by embryologists. An echinoderm that had lost its arms would have left only a sac-like gut with a minimum of nervous system. It would thus have far less to get rid of as a preliminary
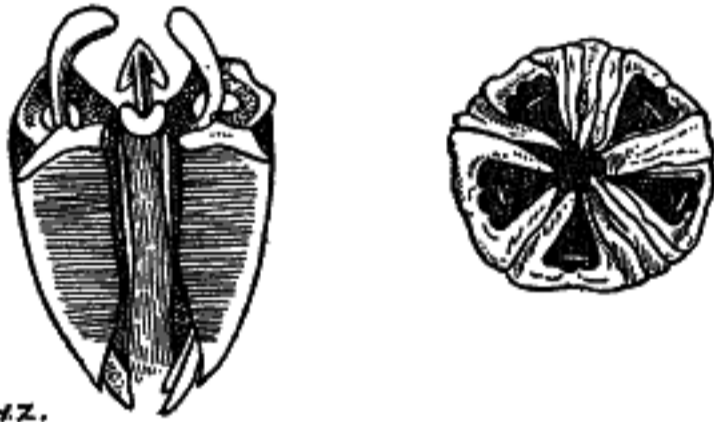

FIG. 8. "ARISTOTLE'S LANTERN"

After Parker and Haswell. Showing quinqueradiate polyisomerism

before starting on the upward road to the vertebrates than would the far more highly organized arthropods.

Consequently the nascent "Carpoid theory" of the origin of the vertebrates, which no one except Dr. Torsten Gislén has as yet had the courage even to imply, may eventually prove to be the final key to the classical problem of the origin of the vertebrates.

We have already noted that the five arms of primitive sea-lilies are practically projecting folds around the mouth. Thus the tube-feet in the "arms" of the starfishes now serve as locomotor organs by a change of function.

The beautiful mechanism known as Aristotle's lantern in the sea-urchin is made up of five sets of tooth-like plates with several rows of supporting plates and lever arms, operated by five principal muscles and a number of accessory muscles and their controlling nerves—all set in a ring around the mouth. If taken to pieces by an amateur this amazing example of so-called "design in nature" might prove as distressingly polyisomerous as the parts of a radial motor of an airplane.

The complexities of Aristotle's lantern seem to have been too much for even Nature herself to modify successfully, for so far as I can gather from the literature it is found only in the sea-urchins and holothurians.

Protochordates

Balanoglossus and the ascidians, derived, doubtless at different times, from the earliest echinoderm-chordate forerunners, are each highly specialized and in some respects degenerate but in different ways. While *Balanoglossus* is perhaps a protochordate masquerading under the habitus of a marine worm, the colonial sessile ascidians are protochordates almost transformed into the condition of corals or bryozoöns. But for all that, the *Balanoglossus* group seems to reveal its kinship on the one hand with the echinoderms through the *Tornaria* larva of its typical species and on the other hand with *Amphioxus* through the three-pouched larva of other species, while the ascidians retain their connection with *Amphioxus* through the mode of formation of their mesoderm, the expanded pharynx with its many gill-openings and the presence of a true notochord in the larval stage.

Each of the protochordates exhibits a high degree of polyisomerism in certain parts and in different ways. Thus in the adult *Balanoglossus* the numerous branchial organs are made up of elongate U-shaped

slits with little horizontal bars connecting adjacent U's. The details of the branchial apparatus differ in the four genera of balanoglossids (Delage and Hérouard, *Les Procordés*, Pl. IV and Fig. 34). The plates of Delage and Hérouard also illustrate the polyisomerism of the cells composing any given organ and we realize that macroscopic polyisomerism depends upon the homogeneity of the microscopic components. The *Tornaria* larva of *Balanoglossus* shows a highly polyisomerous arrangement of its ciliated bands.

Amphioxus.—Perhaps the highest degree of secondary intraorganic polyisomerism is attained in the fish-like *Amphioxus*, not only in its very numerous myomeres and gonads but in its multitude of tactile cirri, its greatly expanded pharynx and high number of gill-bars. The peculiar asymmetry of the developing gill-bars, as noted above, has been compared by Torsten Gislén with the asymmetry of certain fossil echinoderms (Fig. 7); but if the protochordates have indeed been derived from the carpoid echinoderms (see p. 280 above) the transformation has completely wiped out all traces in the adult *Amphioxus*; in this connection it will be realized that as the condition here called secondary polyisomerism advances it submerges the ancient anisomerous heritage of earlier ages.

The polyisomerous ciliated bands that form the endostyle in ascidians, in *Amphioxus* and in the larval lamprey perhaps date back to a period before any kind of jaws developed, when microscopic food was ingested by the action of cilia.

Ascidians.—The ascidians also supply us with examples of the principle that a primitive state of polyisomerism may give rise to a stage of anisomerism or differentiation and that this in turn may be replaced by a secondary polyisomerism. For example, it is not impossible that the simple tunicates (Fig. 9A) as an offshoot of the chordate stem and ultimately of the echinoderm stock, may represent a secondary return to a sessile mode of life. As a sessile animal such a typical simple ascidian is strongly anisomerous in its twisted digestive tract and localized gonads. But by breaking loose from its base (Fig. 9B) and budding in chains, a *Salpa* colony (Fig. 9C) as a whole has become secondarily polyisomerous.

Since polyisomerism may be either primary or secondary we can not hope to distinguish between the two merely by inspection of a given type without regard to the taxonomy and phylogeny of the group. Amateur students of evolution have often been misled by Herbert Spencer's classic concept of evolution as implying progress from homogeneity to heterogeneity, from simplicity to complexity. We now know from hundreds of well established instances that simplicity may often be the reverse of primitiveness and that progress, at least in the later chapters of evolution, has often been from a state of high local differentiation or anisomerism to the deceptively generalized-looking simplicity of secondary polyisomerism.

REDUPLICATION IN THE LOCOMOTOR SKELETON OF VERTEBRATES

The locomotor skeleton of vertebrates has evolved in relation to the arrangement of the zig-zag myomeres and to the septa between them. These myomeres are themselves products of lateral pouches from the primitive gut, so it is not surprising that they should be found in close functional connection with the median out-pocketing of the gut, which is the primitive notochord. But whereas the myotomes very early become polyisomerous, the notochord is unsegmented and continuous from the hypophysial sac to the tip of the tail. The notochord, composed of thin-walled

cells turgid with liquid contents and covered with an elastic sheath, affords the necessary resiliency and reaction against the rhythmic contractions of the myomeres.

served impressions of the posterior half of the body show an empty space in the midline beneath the longitudinal dorsal fin-fold and between the dorsal and ventral rows of small rod-like supports of the
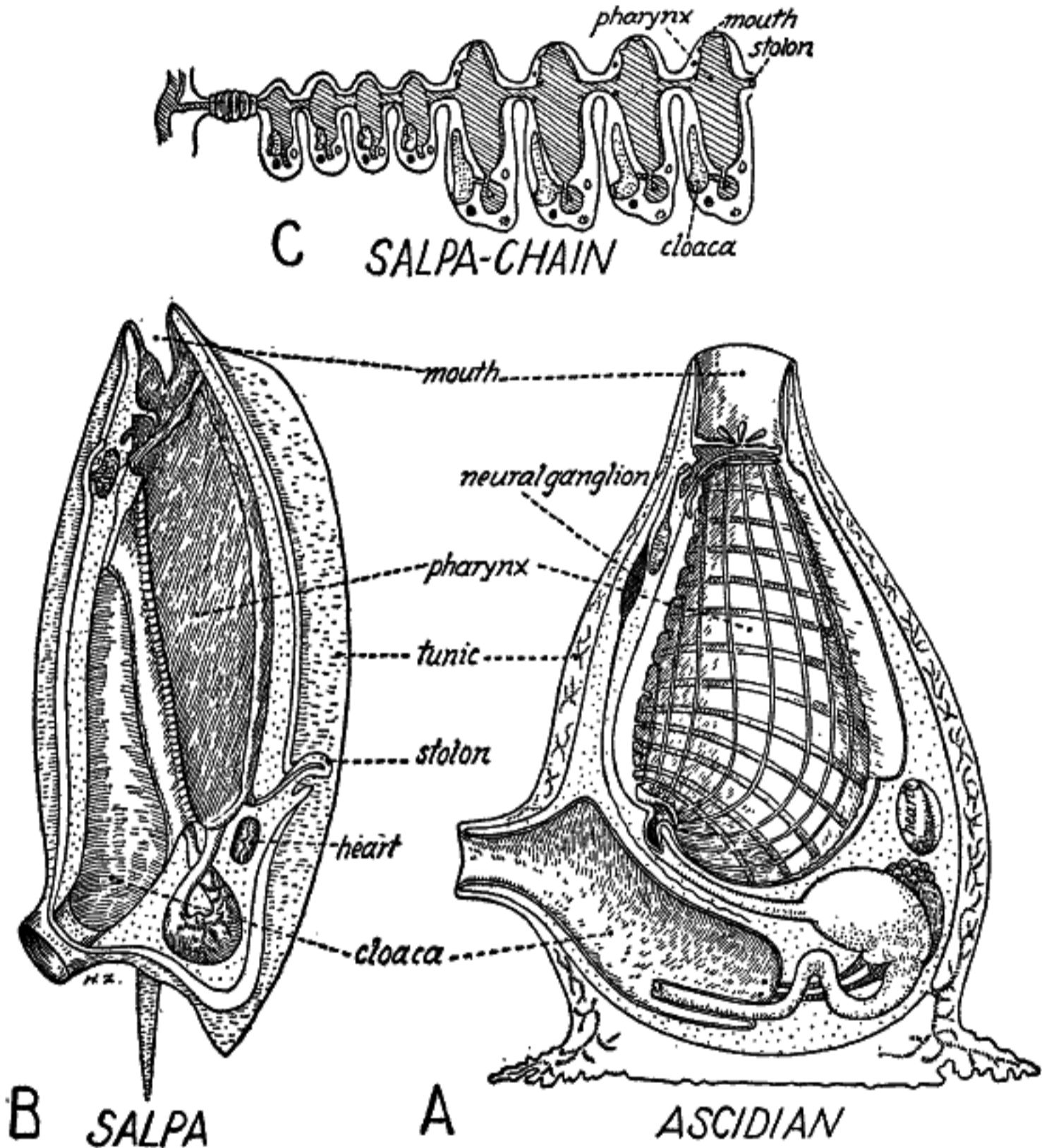
FIG. 9. ANISOMEROUS AND POLYISOMEROUS ASCIDIANS
After Delage and Hérouard

The primitive state of the notochord, as exhibited in *Amphioxus*, was doubtless also characteristic of the ostracoderms, in which there is a tube for the notochord behind the hypophysial fossa (Stensiö, 1927, Pl. 79). In another group of early chordates, the Antiarchi, several well preserved impressions of the posterior half

caudal fin. These spaces can hardly have been filled by anything but the notochord.

In the elasmobranchs the thick outer or fibrous sheath of the notochord was invaded by skeletogenous cells which proceeded to lay down four pairs of blocks, two dorsal and two ventral, in each

sclerotome or primitive mesodermal segment. According to Gadow (1895), the anterior dorsal and ventral blocks were at the posterior end of one segment just in front of the intersection of the oblique septa of the myomeres with the elastic sheath of the notochord, while the posterior dorsal and ventral blocks were behind this septum and at the front end of the next segment. Goodrich (1930), however, dissents from this and holds that all four pairs belong within one segment. The two dorsal pairs (basidorsals and interdorsals) rest on the dorsal half of the elastic sheath and protect the spinal cord, while the two ventral pairs (basiventral and interventral) rest against the lower half of the fibrous sheath (Goodrich, 1930, p. 18). These vertebral blocks or arches not only protect the spinal cord and nerve exits but also serve as bases for the attachments of the myomeres. Those parts of the blocks that surround the notochord coalesce to form short cylindrical centra.

The vertebral centra of sharks exhibit a high degree of intersegmental polyisomerism as well as intrasegmental polyisomerism. Their diverse patterns, afforded by the deposition of calcareous material presumably along the zones and lines of greatest stress, are in general characteristic of the various groups of elasmobranchs and have been exhaustively treated in a great monograph by Hasse.

In the chimaeroids, which are highly specialized elasmobranchs, the central portion of the vertebral column attains a stage of secondary hyperpolyisomerism, as it is composed of a very large number of similar rings. In the embolomerous type of vertebrae, characteristic of the earliest known amphibians, each vertebra consists of two checker-like discs perforated by the notochord, the second one bearing the massive neural arch. The polyisomerous

ribs, which function as lateral extensions of the vertebrae for the insertion of the lateral muscles of the myomeres, are movably articulated with the centra by two processes or heads, of which the lower or capitulum is articulated with the intercentrum; the upper or tuberculum articulates with the diapophysis of the neural arch (Watson, 1925). The neural arches articulate with each other by means of inclined paired facettes or zygapophyses, the function of which is to prevent strangulation of the spinal cord and spinal nerves during flexure of the body.

In the more ancient stegocephalian amphibians from the Lower Carboniferous there was also a high degree of primitive intersegmental polyisomerism from one end of the backbone to the other (Fig. 10). At the same time we see in these forms the beginning of regional anisomerism, since there is a rather rapid reduction of the ribs as we pass backward in the lumbar region to the sacrum and then a sudden marked increase in size of the two ribs that are expanded as a sacrum to receive the thrusts of the pelvic limbs transmitted through the pelvis. Again, behind the sacrum there is a rapid constriction of the intercostal diameter as the posterior ventral ribs, or haemopophyses, enclose only the postanal main blood-vessels.

At the other end of the vertebrate series in man, we find a high degree of regional anisomerism in the backbone, combined however with a considerable degree of intraregional secondary polyisomerism. Thus there is a sharp differentiation between the atlas and axis, between the seventh cervical and the first dorsal, between the last dorsal and the first lumbar, the last lumbar and the sacrum. In the postsacral vertebrae, especially where they are coalesced into the coccyx, the polyisomerism is partly secondary.

The great flying reptile *Pteranodon* ex-

FIG. 10. MODEL OF AN EMBOLOMEROUS AMPHIBIAN, DIPLOVERTEBRON

Based on skeletons described by D. M. S. Watson.   Showing primary polyisomerism and slight regional ani-
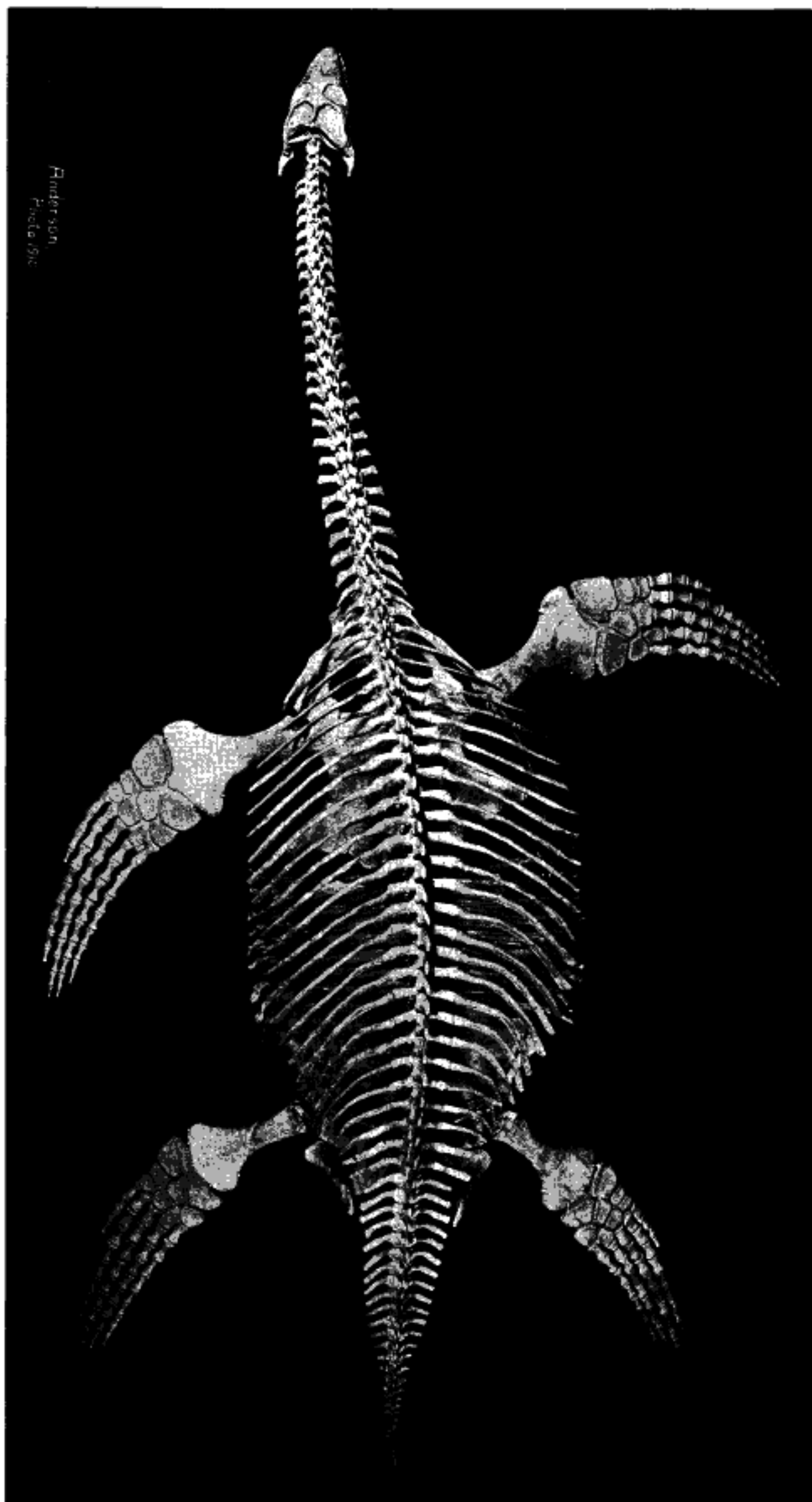somerism in axial skeleton.

FIG. 11. SKELETON OF PLESIOSAUR, CRYPTOCLEIDUS OXONIENSIS

Mounted in the American Museum of Natural History by Charles Lang.   Photograph by A. E. Anderson.
Shows marked secondary polyisomerism tending to obscure an earlier anisomerism.

hibits a high degree of regional anisomerism in the backbone, for here a number of the anterior thoracic vertebrae are coalesced into a pseudo-sacrum to receive the thrusts of the enormous pectoral limbs, while many vertebrae in the sacral region are coalesced to form a synsacrum. Even here, however, there is also a considerable degree of intraregional polyisomerism.

Secondary polyisomerism in the backbone of vertebrates is quite common; for example, among fishes we have an extraordinary hyperpolyisomerism of the column in the morays and in other anguilliform fishes of several orders. Again in the class Amphibia many exhibit this feature in a high degree, especially among the early stegocephalians and Lepospondyli as well as in such urodeles as *Necturus*, *Siren*, and in the entire order of coecilians. The same principle ran riot among the reptiles, which produced many long-bodied, small-limbed and eventually limbless forms like the glass snakes and amphisbaenians among the lizards, as well as the true serpents.

Various phyla of extinct land-living reptiles gradually became aquatic and some of them even marine in habits. As they did so, the limbs were transformed into paddles and the backbone usually became de-differentiated and secondarily polyisomerous, so that in the ichthyosaurs, for example, the centra were simple and checker-like from one end of the column to the other, nearly all traces of the sacral differentiation being obliterated. Similarly the neural arches became alike and reduced their zygapophyses, thereby facilitating the free undulation of the backbone.

In the plesiosaurs there was also a rather high degree of partly secondary polyisomerism in the elements of both the axial and the appendicular parts of the skeleton (Fig. 11).

In many cases of excessive polyisomerism of the backbone (due apparently to a multiplication of the muscle segments) there is also a corresponding polyisomerism of the integument, frequently producing rings or a regular arrangement of spots. As a result of intrasegmental anisomerism combined with intersegmental polyisomerism, one or more elements of a pattern may be stressed at an early stage of development. Subsequent growth and elongation pull out these color patches into various component parts, so that we finally witness the beautiful color patterns of the pythons and vipers. The feathers of perhaps every species of birds would furnish many examples of inter- and intraregional polyisomerism and of the opposite tendency toward anisomerism but always with a specific or individual stamp of the resulting patterns. In the phenomenon called aquintocubitalism in birds, for example, which implies the presence of fifteen primary flight feathers on each wing, a great number of species, genera and even orders of birds exhibit a general polyisomerism of these feathers, combined with specific differences in the colors, patterns and forms of the overlying wing coverts.

The accessory locomotor organs, including the fins, paddles and finally limbs, likewise go through the stage of primitive polyisomerism and anisomerism, followed by either hyper-polyisomerism or hyper-anisomerism. Thus the pectoral and pelvic fins were once part of either continuous or nodally projecting paired finfolds, supported in the earliest fishes by spines or cartilaginous rods. These paired fins were originally of the same nature as the median fins and included rigid projections of the body-wall enclosing the segmental muscles and surmounted by crests of integument strengthened by rows of denticles coalesced into spines or fin-rays.

There was, however, one enduring rea-

son for anisomerism between the pectoral and the pelvic girdles, for the former was originally associated with the head and formed the boundary between the body musculature and the orobranchial chamber, while the pelvis was associated with the exit of the digestive and reproductive tubes and was thus situated on a node of the musculature between the flanks and the tail. Also the pectoral limbs, except among the pterosaurs, never acquired an attachment to the column, whereas the pelvic limbs by the upgrowth of the ilium gained a ligamentous contact with the girdle into anterior, dorsal and posterior elements. Such triradiate sutures in the case of fish skulls arise through the mutual pressure of three bony centers which are being pushed away from each other by their equal growth rates and by the reactions generated at their intersecting peripheries.

The distal ends of the paired fins were originally polyisomerous in so far as they were supported by serially arranged muscles and skeletal rods. By coalescence of some of these serial elements the base became constricted and the fin gradually
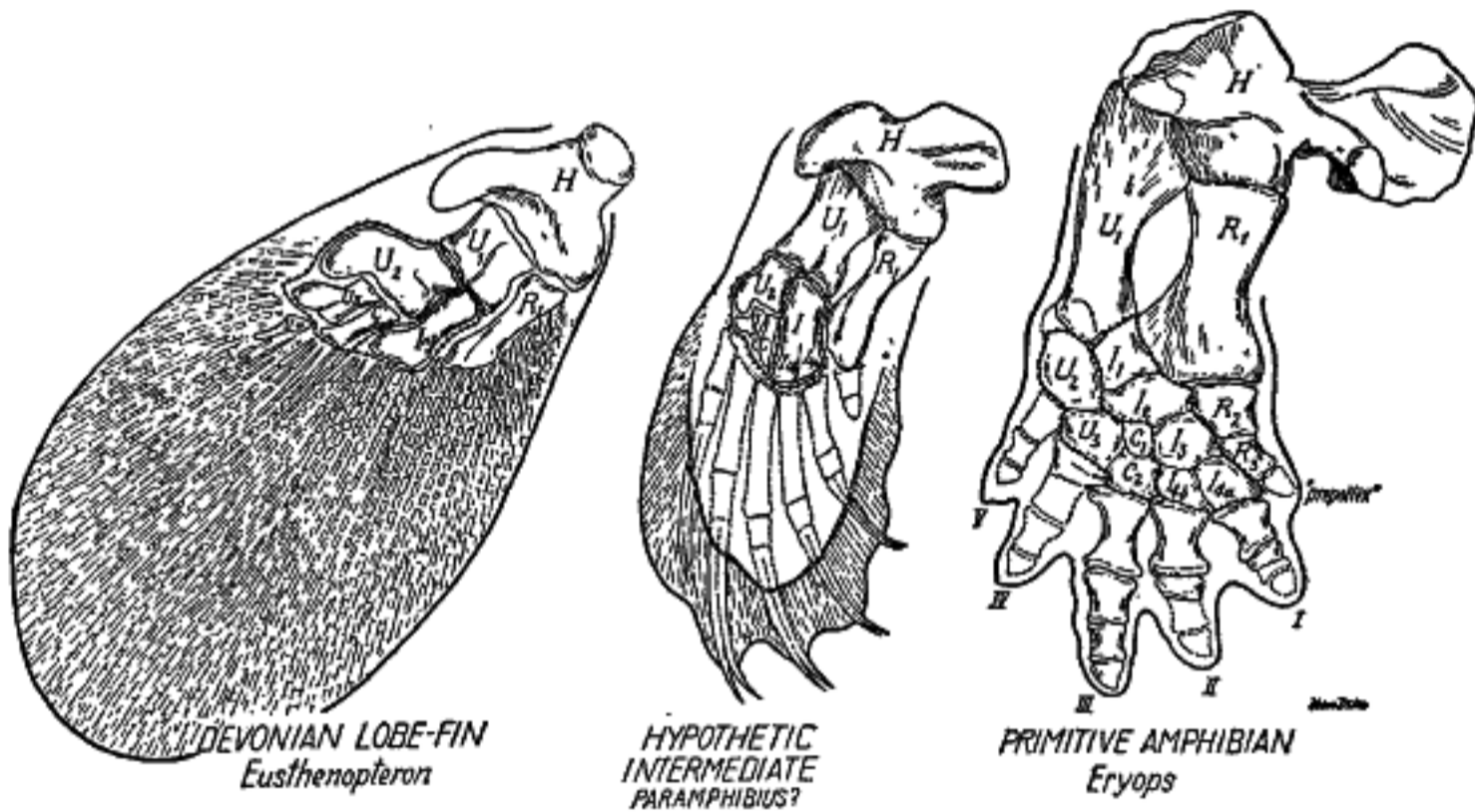

FIG. 12. SUPPOSED TRANSFORMATION OF PECTORAL PADDLE OF DEVONIAN LOBE-FIN INTO PRIMITIVE CHEIROPTERYGISM OF AMPHIBIAN, BY ANISOMERISM AND SECONDARY POLYISOMERISM

sacral ribs, thus indirectly transmitting their thrusts to the column. The marked and persistent anisomerism of the pectoral and pelvic girdles is thus readily understandable in the light of the functional history of these elements. Nevertheless, a secondary tendency toward polyisomerism very early asserted itself, in that, especially among the Permian reptiles, each half of both pectoral and pelvic girdles came to acquire a triradiate suture centering respectively in the glenoid and acetabular depressions and dividing each changed into a paddle with a movable wrist-like base. In the fan-like paddles of the early crossopterygians (Fig. 12) one set of rods (H, U_1, U_2, U_3, U_4) became the functional axis and one member (H) of this set gave rise to the humerus or single proximal piece. When the paddle was bent sharply upon itself in pushing the body on the mud, anisomerous increase of the proximal elements took place together with some secondary polyisomerism in the elements that were to become the carpals. A similar history in the pel-

vic limb resulted in the anisomerous proximal elements and the polyisomerous extremities.

In the earliest tetrapods each of the elements of the primitive hind foot has the somewhat deceptive appearance of complete homology with the corresponding piece of the fore foot; but it is more than likely that this is largely due to intersegmental polyisomerism.

An even more complete homodynamism and polyisomerism is developed secondarily between the pectoral and pelvic paddles of typical plesiosaurs (Fig. 11).

The fore and hind limbs of birds have attained a high degree of anisomerism with little or no tendency toward secondary or tertiary polyisomerism. The skeleton of the pectoral limbs of humming-birds, for example, is excessively different in function, in general appearance and in detail from that of their pelvic limbs. The same is even more conspicuous in the penguins, where pectoral and pelvic limbs are used, although in very different ways, in propulsion through the water and on land. And yet the remote common ancestors of all birds were primitive lizard-like reptiles with similar but secondarily polyisomerous hands and feet. This case suggests that marked regional anisomerism between serially homologous parts is concomitant with equal differences in function and at present I can think of no exceptions to this rule.

CONCLUSIONS

The phenomenon of polyisomerism, whereby adjacent or serially homologous parts of the body are moulded into similar patterns, obviously results from the interaction of many forces, influences and conditions such as the following: the production of similar units of building material by the digestive system, the similar influences upon a row of homologous parts exerted by serially homologous nerves and blood-vessels, the similar effects upon all the units of the series by specific endocrine products, in stimulating or retarding growth or in changing the physical or chemical properties of any of the component tissues; finally we have to reckon with the similarities that were initiated by forces let loose by the unfolding genes.

In short, "wholeness," "specificity" and "aristogenesis" seem to be names for certain aspects of the behavior of living kaleidoscopes that slowly evolve through the ages: the little pieces ("aristogenes") that go to make up the patterns are the small units that are budded off from some rhythmically growing organ like the dental lamina; the patterns are determined in part by the primary symmetries and asymmetries of the fertilized egg, in part by secondary symmetries and asymmetries produced, for example, by the recurrent invagination of the ectoderm and the mesoderm so as to form dental caps and tooth germs; or by nodal retardation of growth in a rapidly growing strip, as in the notches and folds of rodent teeth; finally, patterns are produced by the recurrent interference between polyisomerism and its opposite, anisomerism.

As to the occasional recurrent alternation of polyisomerism and anisomerism, let us consider the long line of vertebrates that culminated in the existing narwhal. In the remote reptilian ancestors of the mammals the dentition was at first strongly polyisomerous; this we may call primary polyisomerism. In the higher cynodonts this condition began to give way to a moderate degree of anisomerism, which was progressive up to the time of the earliest creodonts; this may be called the first cycle of anisomerism. In the ancestors of the hyaenodonts the dentition as a whole was anisomerous but the upper

molars were becoming secondarily polyi-
somerous, through the emphasis of their
metastyle shears and the reduction of their
protocones. Traces of this condition are
still visible in the earliest archæocetes,
but by the time we reach the squalodonts
the teeth have begun to multiply and to
be much simplified and polyisomerous, a
tendency which culminates in the dol-
phins. Here is the phase of secondary
polyisomerism. In the immediate an-
cestors of the narwhal one pair of these
similar teeth began to enlarge; this move-
ment culminated in the excessively ani-
somerous stage of the narwhal, which has
in the adult but a single tooth left in
the form of a huge spirally wound straight
tusk. Thus we have secondary anisomer-
ism of an extreme type. The next stage
would probably be loss of all teeth (nega-
tive anisomerism).

The usefulness of polyisomerism or
reduplication is that it has enabled the
same function to be performed by many
different units, so that the necessary work
could be distributed among many; thus a
massive result could be achieved by mass
action of small units multiplied by time.
As an example we may cite the amazing
achievement of the minute teeth of the
radula of certain gastropods in boring
through the thickest part of the shell of a
clam, or the powerful mass action of the
tube-feet of a starfish in pulling open the
shell of an oyster.

On the other hand, anisomerism, or the
inequalization of parts, resulting from the
overgrowth of one part of a polyisomerous
series, has proved useful under the fol-
lowing conditions: (a) when the enlarged
anisomerous parts have been compelled
to bear the brunt of attack, as in the canine
teeth of the sabre-tooth tiger, or when
they serve as a shield, as in the plates of
the carapace of the tortoises; (b) when the
enlarged parts serve as a fulcrum, anchor
or stay for adjacent parts, as in the co-
alesced anterior cervical vertebrae that
support the immense head shield of cera-
topsian dinosaurs, or as in the enlarged
sacral ribs that receive the thrusts from
the pelvic limbs; (c) when adjacent pieces
of an originally polyisomerous series per-
form narrowly delimited parts of some
complex function, as in the several parts
of the atlas-axis complex of man.

Thus the presence of polyisomerous parts
implies mass action, the presence of ani-
somerism implies inequality of stresses,
highly differentiated functions.

In all Metazoa polyisomerism, or the
formation of numerous small unit organs
of the same type, is the next step above
cell division and the differentiation of the
primary germ layers. The quality of
specificity or individuality becomes mani-
fest in each case of polyisomerism at ear-
lier or later stages of ontogeny. Polyi-
somerism, either as between organs or as
between the smaller units that compose
them, is a universal property of living
things; it is the specificity of the polyi-
somerism that remains to be explained.
Here from a historical point of view we
emphasize the divergent, cumulative com-
pound-interest-bearing effect of an infinite
number of small conditioning factors oper-
ating on divergent hereditary lines through
geologic time.

In general the nature of protoplasm is
such that a separated part tends to assume
the form of the parent mass, hence poly-
isomerism is a result of an inherent property
of protoplasm. On the other hand, ani-
somerism, or hereditary divergence, arises
when the forces of polyisomerism are un-
evenly distributed so that one part grows
or evolves faster than its neighbors.

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