

NOTES ON THE ORIGIN OF BONY ARMOR*

DARWIN'S eager search for origins and the dramatic pulse given to the study of the unfolding of life which arose as a result of his physical and intellectual voyages has since encouraged the investigation of obscure comparative phenomena as related to the organic world. Whether the concern exists for the explanation of the hereditary process as a biochemical mechanism or the defense of a family tree of fossil horses, the student begins his research secure in the belief that the complex arises from the simple and that the causal factors governing the changes in presently observed phenomena may be, in a large measure, extended into the past. Consequently this inquiry into certain early stages in the development of the vertebrate skeletal system must start with a review of the functional and developmental aspects of living animals. Anatomical characters may be compared directly, but functional characteristics become less confirmable as one examines unfamiliar fossil organisms. Not infrequently, however, living primitive forms bear an astonishing resemblance to those of the remote past. Such ancient fragments as scales, plates, and teeth of extinct fish packed in the sands of an Ordovician bay present a challenging early exhibit in the testimony offered by fossil bone. These elements are intact as to general anatomic structure, and after over 400 millions of years retain the fundamental mineral crystal pattern. Such stability of form conveys microscopic details of the channels for nerves, blood vessels and fibres much as they existed in the living organism.

Bone, then, is a sediment within the provincial system of

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the vertebrate body and finally becomes a sedimentary rock in the terms of the geologist. Comprised of the mineral apatite, its structure has long been known through studies of X ray diffraction patterns. Both in the living body and in vitro this remarkable mineral presents huge surfaces for reaction with its small crystals set within the collagen framework of the body. A length of 200-780 angstrom units, a width of 30-50, and a thickness of 20-50 yield a computed surface area of nearly 100 acres for a man of average weight.¹ The tremendous surfaces offered result in much interchange between the components of the apatite lattice and the body fluids and even after death this tissue responds to the action of waters held in the sediments. The following experiments are illustrative:

Work with rabbits² involved the maintenance of a relatively constant level of labeled phosphate in the blood plasma and a measurement in the skeleton after a fifty-day period. This constituted an excellent test of the mobility of bone phosphorus; one fourth of this element was replaced in the actively growing ends of the limb bones, forty percent in the shoulder blade, and a complete turnover in the actively growing incisor tooth root.

In the test tube,³ phosphorus 32 was placed in solution in a measured amount and its exchange with skeletal tissues and synthetic apatite was noted. After a period of eight hours, thirty percent of the active element was found in the bone, less than twenty-five percent in the apatite, slightly more than five percent in a sample of dentine, and one percent in tooth enamel.

¹ Robinson and Watson (1952); (1955); McLean (1958).

² Hevesy, Levi and Rebbe (1940).

³ Falkenheim, Neumann and Hodge (1947).

It is evident that the soft organic tissues, particularly collagen and chondroitin sulfate, serve as binding materials for the minerals. Divorced from the body, the skeletal system continues to show a greater capacity to react than the synthetic mineral component. Resistant combinations of fiber and minerals as found in the teeth are more stable than other parts of the hard anatomy, and consequently teeth or tooth-like structures, and homologs such as the more primitive integument of fish, are preserved with little modification through hundreds of millions of years.

The climate of the internal animal is modified by glands of internal secretion. Many of these regulators affect bone salts and in the simpler vertebrates were exposed to the environmental waters. Naso-hypophysial openings were dorsally placed or opened into the oral cavity. The endostyle, traceable to the thyroid gland, is functional as an organ of nutrition both mechanically and physiologically in the lancet (*Branchiostoma*) and larval cyclostomes. Other regulatory structures in higher forms appear first in the region of the branchial or gill pouches. The parathyroid, thymus, and ultimobranchial series may well have been concerned more directly in the process of nutritional regulation in the most primitive vertebrates. It is significant that much of the tissue formerly exposed to an external fluid environment maintains its anatomical position and possibly much of its function with the internal fluids. Here most of these glands are concerned now, as in the past, with the accumulation or release of minerals of the body.

Hyperactivity of the pituitary gland results in gigantism,⁴ while removal halts cartilage bone growth sequences and quickly results in effects commonly observed in old age.⁵

⁴ Becks, Simpson and Evans (1945).

⁵ Evans *et al.* (1948).

Overactivity of the thyroid gland causes an increased excretion of calcium and deficiencies in bone structure (osteoporosis). Removal of the thyroid retards both growth and form of the skeleton. The closely associated parathyroids have a profound effect on mineral metabolism both in mobilizing calcium and phosphorus from the bone and possibly in the recovery of salts by way of the kidney tubules. Excess hormone from this gland results in overstimulation and destruction of bone cells, fibrous tissue formation in Haversian canals, and other pathological changes.⁶

Reproductive cycles⁷ result in the activity of these glands in relation to the oestrogenic hormones, and reserves of minerals are deposited as spongy tissue in the marrow cavities of the long bones of birds, there to await the demands of egg laying. In mammals calcium is quantitatively connected to the growth rate of the young as to its availability in milk.⁸ Two hundredths of a percent in humans is noted in connection with a doubling of the birth weight in 180 days. Cow's milk had 0.12 percent of calcium and the weight of the calf doubled in 47 days; while the dog, with 0.32 percent calcium in its milk, required only seven days to achieve twice the birth weight of the young.

The outer green leaves of plants constitute the primary source of calcium for most land animals and the plants depend upon the soil minerals for their growth. Loss of these minerals due to erosion, especially during regressions of the sea, could result in mineral wealth for aquatic organisms and poverty for many land forms. Changes in the fauna during Pleistocene time, when thermal changes and cyclic rise and fall of the seas strongly affected the quality of plant life, have

⁶ Becks *et al.* (1950).

⁷ Snapper (1940).

⁸ Bunge (1898).

been observed on all continents by the students of the higher mammals. Darwin in 1832 described the "perfect catacomb for monsters of extinct races" as he reviewed the Punta Alta Pleistocene remains and, with the instincts of an ecologist, attempted to account for a food supply for the varied assortment of sloths, glyptodonts, and armadillos. He accepted the anatomical findings of the famous anatomist Owen and presented the following interpretation of the habits of these giant edentates:

With their great tails and their huge heels firmly fixed like a tripod on the ground, they could freely exert the full force of their most powerful arms and great claws. Strongly rooted, indeed, must that tree have been which could have resisted such a force! The Mylodon, moreover, was furnished with a long extensile tongue like that of the giraffe, which, by one of those beautiful provisions of nature, thus reaches with the aid of its long neck its leafy food.

The giant sloths and most of the large edentates have become extinct after having merged in time with the coming of man to South America. The largest of vertebrates, the whales, remain to testify as to the availability of nutrients in the sea gained in part from the extensive erosional processes characteristic of the Quaternary. Erosional cycles of the early Paleozoic and the primitive plants invading the land may similarly have unlocked a mineral treasure for the early agnathous fishes. The presence of their remains near shorelines and in shallow bays and estuaries suggests that the concentration of nutrients where river meets sea was a condition which stimulated the development of early fish then as today. Certainly not the least of the factors concerned with the development of bone was the availability of minerals, and it is to be assumed that in the long period of evolution of the naked chordates and unossified early vertebrates many were attracted from the sea to fresh water. One may suppose that

anadromous and catadromous habits might have been fixed prior to the appearance of a hard plate or scale integument.

Skeletal elements with minerals suspect of calcium and phosphatic components have been found in trivial numbers in Lower Ordovician deposits of Esthonia and in the Middle Cambrian St. Albans shale of Vermont⁹. Of the latter remains, the genus *Archaeognathus* may be a fibrous conodont. Most abundant¹⁰ of these early fossils are the scales, plates, denticles, and conodonts of the Mid-Ordovician Harding Sandstone as exposed in the region of Canyon City, Colorado, and geologically related areas of the western United States. Specimens were first collected in 1877 by S. F. Eammons and I. C. Russell of the United States Geological Survey. Aably assisted by a local citizen, W. T. Stanton, they accumulated a limited associated invertebrate assemblage which led to the surprising conclusion that these rocks were Silurian or even Ordovician in age. The fragmentary fish remains naturally presented a challenge to paleontologists since they then represented the world's oldest known vertebrates.

Walcott confirmed and reported the stratigraphic observations of the previous workers and visited the locality in 1890. At that time he established contacts of the Ordovician section with underlying prepaleozoic and overlying Carboniferous limestones. Reports followed in 1891 and 1892 resulting in the descriptions of three species of fishes. Distinctively ornamented scales were placed in the species *Astraspis desiderata* and provisionally assigned to the "ganoid" suborder Placodermata. Other less ornate plates were referred to the group Crossopterygii as *Eriptychius americanus*. Fragments then mistakenly diagnosed as notochordal sheath remnants

⁹ Orvig (1958); Howell (1937).

¹⁰ Walcott (1892).

were referred to the group Chimaeroidea as the species *Dictyorhabdus priscus*. Walcott's paper was discussed by a distinguished group of paleontologists including Zittel, Claypole, Jaekel, Hall, and Cope. Their comments in some cases expressed doubts as to the affinities of the specimens and stimulated Walcott to prepare microscopic sections of the scales. These clearly showed dentine tubules, pulp cavities, lamellae, and lacunae supposedly showing the presence of osteoblasts; thus the undoubted piscine affinities of the finds were demonstrated, but the classification remained uncertain.

Cope (1893) correctly placed the specimens in the group Agnatha.

Valliant (1902) examined some material from the type locality and found spaces filled with limonite which he interpreted as evidence favoring the presence of bone cells. His specimens were not classified.

Woodward (1921) referred *Astraspis* to the Cephalaspidae on the basis of microsections. He did not figure his specimens and his brief statement contains no defense of his diagnosis.

Eastman (1917), Stensiö (1927), Stetson (1921), Bryant (1934), and Orvig (1958) agree that *Astraspis* and *Eriptychius* be assigned to the order Heterostraci of the class Agnatha. Stetson found scales in association with these genera which he classified as Coelolepids of the genus *Thelodus*.

Conodonts associated with the Canyon City fauna were studied by Kirk (1929), Branson and Mehl (1933), and Sweet (1955). Basal structures attached to conodonts were described as having the same appearance as the ostracoderm plates by Kirk, but Bryant, in a more detailed histologic study, could not confirm this observation. Branson and Mehl (1944) state:

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Most investigators assume that they represent the jaw armour of an extinct order of primitive fishes. This opinion is based on the chemical composition, nature of growth additions, and actual attachment of many specimens to jaw substance.

It is possible that the Harding conodonts may be referred to immature stages of the associated ostracoderms as internal supports for a gill raker feeding mechanism; those with a basal attachment may have persisted in adult forms. Ellison (1944) showed the apatite crystal structure to be present and a chemical composition close to that of bone. Foss (1958)* finds the Harding Sandstone conodonts and intimately associated fish plates to be quite similar as to pattern when studied by X ray diffraction techniques.

Bryant's (1936) description of the scale anatomy of *Astraspis desiderata* based on a study of thin sections shows a close relation to exist with the Drepanaspidae. He defined basal, intermediate, and superficial zones, delineating them on the basis of variations in the canal systems and the contrasts in tissue layers. Vertical canals were found basally but described as "meandering" in the middle layer. The surface of the bone was found to be tuberculate with either stellate or oval prominences. Transparent enameloid substance capping the tubercle was shown to have a hardness of 5.5 on the Moh scale. It was soluble in hydrochloric acid, had no laminar structure, and was not similar optically to enamel or ganoine. Dense acellular tissue was beneath the cap with laminae penetrated with subparallel fibres. Bryant compared these with the Fibres of Sharpey and suggested that they radiated from a pulp cavity. Stained sections gave these the appearance of very fine tubes.

Neither cell spaces nor tubulets were described for the

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middle layer. Vascular canals were found to open between the tubercles, the aspedin, or acellular bone, forming concentric lamellae around the vessels. Cavities resembling lacunae for osteocytes were found to be largely the results of post-mortem erosion.

The basal layer was characterized as thick with distinct parallel lamellae with usually unbranching vertical canals extending to the vascular system of the middle layer. Fibres were described extending upwards in parallel groups.

Bryant found *Eriptychius* (pl. II, 3) to have a dentine ridge ornamentation with microstructure similar to that of *Astraspis*. Coarse dentine tubules were described as branching, originating in the pulp cavity and extending to the surface.

The middle layer was acellular with a labyrinthine appearance as a result of the branching of the abundant vascular canals extending to the pulp cavities and the surface.

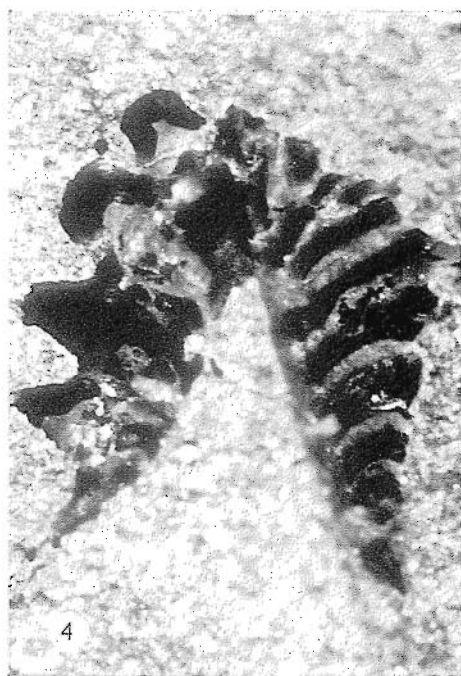
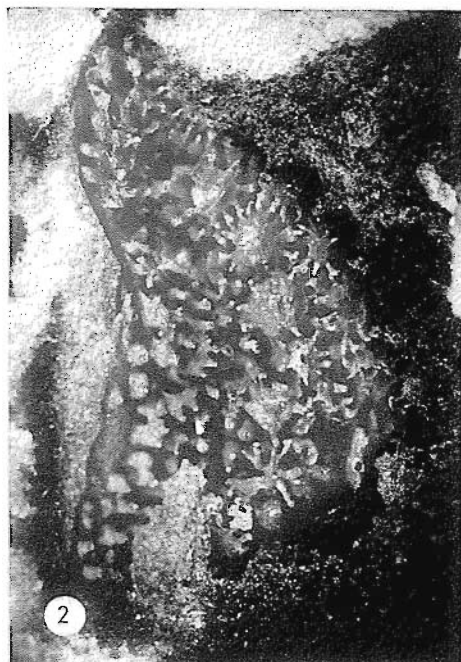
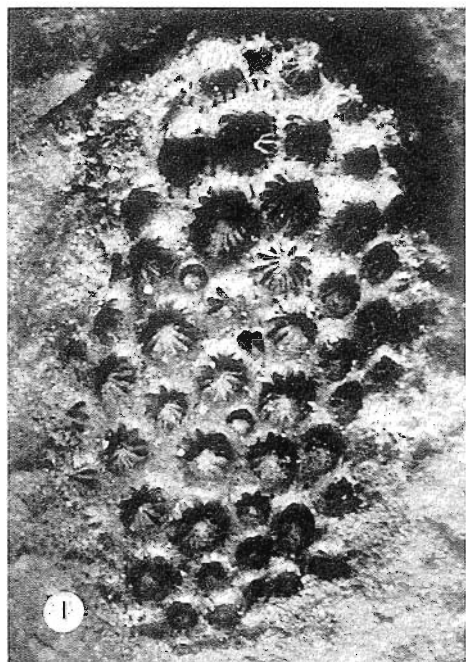
Horizontal layers of aspedin were described in the basal layer where primarily vertical canals characterize the vascular system.

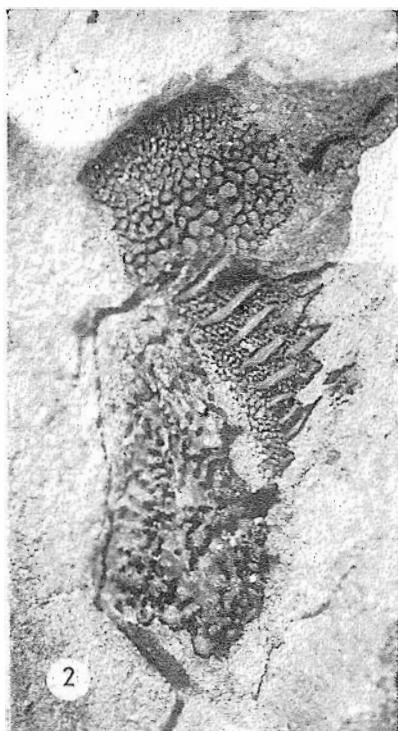
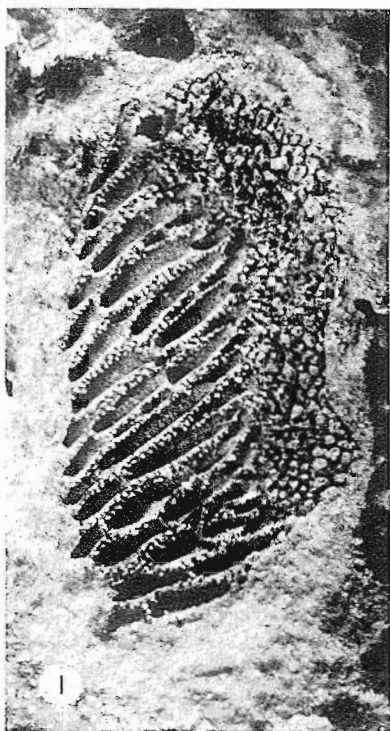
This detailed study of Bryant confirmed most of Walcott's observations and clearly made the elements comparable to heterostracan plates as described by Stensiö (1932; fig. 69). Ørvig (1958) describes similar forms from the Upper Ordo-

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PLATE I. *Astraspis*

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| 1. <i>Astraspis desiderata</i> | × 14 |
| Bone removed. View of impressions of stellate caps as seen from medial aspect. | |
| 2. <i>Astraspis desiderata</i> | × 14 |
| Bone removed. View of casts of reservoirs as seen from above. | |
| 3. <i>Astraspis</i> sp. and associated elements. | × 9 |
| 4. <i>Astraspis</i> sp. | × 30 |
| Thick section of angular plate with bone removed. The reservoirs are shown in position beneath the stellate cap impressions. | |





vician of the Bighorn Mountains of central Wyoming, and his very clear drawings depict essentially the same microstructure noted by previous workers in the older Harding collections. *Pycnaspis splendens* (Ørvig, 1958) and the earlier described specimens of Walcott show the vertebrate exoskeleton to have attained a considerable state of complexity by Ordovician time.

Further collections from the type locality at Canyon City and environs permit some additional observations on the internal anatomy of the plates and scales and the demonstration of a small section of articulated material. This collection was studied by means of thin sections, acid etching and X ray diffraction analysis. The disposition of the scales and plates within the sandstones and siltstones suggests a relatively shallow bay zone (20-30 fathoms) for the former and a considerably deeper environment of deposition for the latter. Gould and Stewart (1956; figs. 2, 5) show shell and algal sand of dimensions similar to the Harding scales at the depths suggested. Since the least worn scales are present in shallower water, but beyond wave base, and the but

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PLATE II. *Eriptychius*

1. *Eriptychius americanus* × 11
Bone removed. View of impressions of elongate dentine ridges and area of overlap as seen from within.
2. *Eriptychius americanus* × 10
Bone removed. View of casts of elongate reservoirs and associated vascular structures as seen from above. Basal canals of another plate are seen in the upper central part of the photograph and poorly formed reservoirs of *Astrapis* in the lower center.
3. *Eriptychius americanus* × 5
Five associated lateral body plates as seen from within. Dark, elongate impressions of dentine ridges are visible in the matrix. These are covered in some areas with the light-shaded bone.

slightly worn plates remain intact even in the fine sediments, it is assumed that *Astraspis*, *Eriptychius*, and associated materials were marine in habit.

Treatment of specimens collected at the Cripple Creek Shelf Road locality with five percent phosphoric acid resulted in the removal of the aspedin and the exposure of fine details of the negative impressions of sculpture, the extent and branching of the vascular channels, and the distribution and relations of cavities beneath the sculptured eminences. Negative impressions of the sculpture of *Astraspis* show the distinct stellate pattern with as many as sixteen rays in the larger tubercles, the number decreasing in the smaller stellae (pl. I, 1). Beneath the enameloid stellate caps and the supporting dentine base there are reservoirs which conform in distribution with the tubercles. These are connected with adjacent reservoirs, and vertical vessels extend to the surface of the plates around the tubercles (pl. I, 2). The reservoirs are connected to the base of the plate by the vertical channels which branch to meet the edges of the reservoirs as well as extending directly into the lower central portion of the reservoir (pl. I, 4). Thin sections frequently give the impression of a labyrinthine set of cavities in the reservoir areas. It is possible that these cavities were occupied by mucus secreted by underlying glands and also the channels were occupied by nutrient vessels and nerves serving peripheral structures such as chromatophores and sense organs.

Eriptychius (pl. II, 1; 2) in acid-etched specimens has clearly revealed negative impressions of the dentine eminences. These are surrounded by marginal vessels extending to the surface of the plate. Coarser vertical channels are present in the area of overlap which occupies the front

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third of the width of the element. The elongate cavities are replaced by siltstone and underly the eminences. These are not in communication with neighboring reservoirs and appear to be served with more numerous but less branched vessels than those described above for *Astraspis*. The mucous pores are emphasized in lines on some plates possibly showing the existence of a primitive lateral line. In some specimens there are channels of varying size in the area of overlap; some of these may have been occupied by connective tissue fibers functioning as connectors for adjacent elements.

Five imbricated body plates were found at the type locality in the Old Quarry one mile west of the city limits of Canyon City, Colorado. The largest is 1.3 cm. long and from 0.35 to 0.40 cm. wide, and the bone, including ornamentations, is slightly more than one millimeter thick. The anterior one third or more of the plate provides a surface for overlap which suggests the function of active mucous glands which may have provided a lubricant as well as a protective surface for the body. As illustrated, the armor is viewed from the inside. Much of the ornamentation has been lost but remains evident by the impressions registered in the matrix. Fragments of the bony base remain (pl. II, 3) and the aspedin is preserved between the adjacent plates to show clearly the direction of overlap.

The existence of the reservoirs and the complexity of the systems of channels show the bone to have enough surface exposed to the vascular system to serve as an effective calcium and phosphorous reservoir. The considerable surfaces for overlap suggest an active but well armored animal. The absence of carbonized or sulfide material in the specimens and the replacement of the cavities by fine siltstone exotically

colored by oxides of iron is suggestive of a death assemblage which was not derived secondarily from an estuarine or fresh water source.

White (1958) argues the case for a marine distribution to account for the presence of later ostracoderms in contemporaneous beds in North America and Europe. *Archegonaspis* is from the Ludlow of Europe and the Salina of the United States. *Pteraspis* is reported from Europe, Spitzbergen, and Nova Scotia in the Lower and Middle Dittonian, and *Protaspis* from the Upper Dittonian and higher deposits in both Europe and the United States. Fresh water routes for this distribution can be obtained only by assuming continental connections or fresh water adaptations as a part of the life cycle.

White (1935, 1958) also convincingly assembles a series of pteraspids to show that the geologically earlier forms produced armor only after the full growth had been attained. Later heterostracans became ossified at more youthful stages in their life histories. Early pre-metamorphic stages of both the pteraspids and the osteostracids, as noted by Westoll (1945), may in instances have been characterized by a small animal devoid of armor. Certainly a considerable period of time was spent in the evolution of unarmored chordates and vertebrates and it is not unlikely that adaptations were early made to a fresh water habit. Clandestine evolution¹¹ may have been an important process in the very favorable nutritional conditions in barrier-guarded bodies of brackish water supplied by mineral-rich rivers. In such an environment in the early Paleozoic, accelerated growth rates and a hastened attainment of the reproductive capacity may have led chordates or primitive vertebrates into fresh water.

¹¹ De Beer (1954).

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Concentrations of salts during conditions of drouth could create evaporite basins and the resulting conditions force the selection of another environment or result in the selection of halophilic developmental varieties. Anadromous or catadramous species thus originating could account for distributional patterns independent of marine or fresh water limitations. The modern cyclostomes so adapted may have early developed as successful carnivores near the start of fish evolution and thus have been a more effective factor than the eurypterids as a selective agency forcing the development of armor in the other less aggressive agnathids. Perhaps even now they present a fair portrait of an extremely successful early Paleozoic carnivore, just as *Branchiostoma* illustrates the marine status of the ancestral chordate.

The work of Webb and Hill (1958) shows patterns in the nutrition and development of this little chordate, which may now in our Pleistocene age of thermal and erosional cycles be experiencing some of the evolutionary stimuli gained only infrequently in the course of the earth's history. *Branchiostoma* was found to grow more rapidly, even to the point of attaining essentially adult size prior to the development of all of the branchial apertures, when living in a nutrient-rich lagoonal environment. The same species develops more slowly in seaward localities. Such growth patterns, if finally adaptive to other climatic conditions, could result in the selection of lancelets with neotenic tendencies in water of low salinity, a phenomenon suggestive of causal factors concerned with the early migratory habits of vertebrates.

Primitive visual pigments have been found by Wald (1957) in fresh water larval cyclostomes; a more advanced

pigment was observed in the salt water adapted adults. If eyes were initially evolved in fresh water environments, as implied by Wald's work, then it is possible to theorize on a set of conditions to account for the closely set eyes of certain ostracoderms as a phenomenon indicative of fresh water adapted forms forced early in their evolutionary history into hypersaline environments. Stockard's (1921) experiments on *Fundulus* whereby he succeeded in the production of cyclopia on developmental stages grown in hypertonic solutions is suggestive of the effects on forms selected among the survivors of evaporite basins of the past. The widespread and ultimately more successful radiation of fish with relatively separated orbits implies a descent of the more conventional fishes from organisms which avoided this morphogenic trap.

The first development of the hard skeletal system was probably related to the visceral arches. Fibrous conodonts may well be the remains of stiffeners for a gill-sifting mechanism. As the primitive chordate or vertebrate increased in size, such structures may have developed into true branchial teeth. The most available chondrogenic and skeletogenic material probably existed in the head region in direct relation to the visceral arches. This mesectodermal tissue is derived from neural crest cells, and in the earliest vertebrates this embryonic source was probably concerned with the formation of the visceral arches and odontoblasts just as it is known to be in recent forms (DeBeer, 1947). Consequently, the early production of multi-layered armor in vertebrates of Ordovician age is not unexpected when embryological factors are weighed. The next step in the evolution of the hard parts would be the appearance anteriorly in the visceral arches of denticles with a resistant outer

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enameloid layer supported by dense dentine overlying a base of bone. Proliferation of such denticles outward to form a shagreen-like coat may have resulted in forms such as *Thelodus*; the dispersal of flattened plates could be the source of the armor in the Pteraspids. Individual denticles may have merged in other agnatha and lost their identity, but the individuality of the tubercles of *Astraspis* and the dentine ridges of *Eriptychius* with their attendant vascular and mucous supplies hark back to a simpler design.

Both sharks and the bony fishes have the same history of initially complicated scales and it is probable that the palimpsest of enamel, vitrodentine, ganoine, cosmine, dentine, and bone may likewise be understood by reference to the simple underlying history of the branchial denticles.

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REFERENCES

- Albright, F., Bauer, W., and J. C. Aub. 1931. "Thyroid, parathyroid, and acid-base metabolism." *J. Clin. Invest.*, vol. 10, pp. 187-219.
- Becks, H. M., Simpson, M. E., and H. M. Evans. 1945. "Ossification at the proximal tibial epiphysis in the rat. I. Changes in females with increasing age." *Anat. Rec.*, vol. 92, pp. 121-134.
- Becks, H., Scow, R. O., Simpson, M. E., Asling, C. W., Li, C. H., and H. M. Evans. 1950. "Response by the rat, thyro-parathyroid ectomized at birth, to growth hormone and to thyroxin given separately or in combination." *Anat. Rec.*, vol. 107, no. 3, pp. 299-306, 5 pl., 30 figs.
- Becks, H., Collins, D. A., Asling, C. W., Simpson, M. L., Li, C. H., and H. M. Evans. 1948. "V. Skeletal changes—skull and dentition. The gigantism produced in normal rats by injection of the pituitary growth hormone." *Growth*, vol. 12, pp. 55-67.
- Boyd, E. S., and W. V. Neuman. 1941. "The surface chemistry of bone. V. The ion binding properties of cartilage." *J. Biol. Chem.*, vol. 133, no. 1, pp. 243-251.
- Branson, E. B., and M. G. Mehl. 1933. "Conodont studies number 1." *Univ. Missouri Studies*, vol. VIII, no. 1.

- . 1944. "Conodonts." Shimer and Shrock, *Index Fossils of North America*.
- Brett, J. R. 1956. "Thermal requirements of fishes." *Quart. Rev. of Biology*, vol. 31, no. 2, pp. 75-87.
- Bryant, W. L. 1936. "A study of the oldest known vertebrates." *Proc. Amer. Phil. Soc.*, vol. LXXVI, pp. 409-427.
- Bunge, G. 1898. *Lehrbuch der Physiologischen Chemie*. 4th ed. Leipzig.
- Darwin, Charles. 1901. *Journal of Researches*. P. F. Collier & Son.
- De Beer, Sir Gavin. 1954. *Embryos and Ancestors*. Oxford at the Clarendon Press.
- . 1947. "The differentiation of neural crest cells into visceral cartilages and odontoblasts in *Amblystoma* and a re-examination of the germ layer theory." *Proc. Roy. Soc. London*, Ser. B, vol. 134.
- Eastman, C. R. 1917. "Fossil fishes in the collection of the United States National Museum." *Proc. U. S. Nat. Mus.*, vol. 52, no. 2177.
- Ellison, Samuel P., Jr. 1944. "The composition of conodonts." *Jour. Paleontology*, vol. 18, pp. 133-140.
- Elmdorf, E., and H. B. Pierce. 1940. "The calcium and phosphorus content of certain vegetables grown under known conditions or fertilization." *Jour. Nutrition*, vol. 20, no. 3, pp. 243-253.
- Enlow, D. H., and S. O. Brown. 1956-1958. "A comparative histological study of fossil and recent bone tissues." Parts I-III. *Texas Jour. Sci.*, vol. VIII, no. 4; vol. IX, no. 2; vol. X, no. 2.
- Evans, H. M., Becks, H., Asling, C. W., Simpson, M. E., and C. H. Li. 1948. "The gigantism produced in normal rats by injection of the pituitary growth hormone. IV. Skeletal changes: Tibia, costochondral junction and caudal vertebrae." *Growth*, vol. 12, pp. 43-53.
- Falkenheim, M., Neumann, W. F., and H. C. Hodge. 1947. "Phosphate exchange as the mechanism for adsorption of the radioactive isotope by the calcified tissues." *Jour. Biol. Chem.*, vol. 169, no. 3, pp. 713-722, 2 figs.
- Gardner, W. V., and C. A. Pfeiffer. 1939. "Sex hormones and bone changes in mice." *Anat. Rec.*, vol. 73, no. 3, Sup. no. 2, p. 21.
- Gould, H. R., and R. H. Stewart. 1956. "Continental terrace sediments in the Northeastern Gulf of Mexico." Soc. Ec. Paleont. and Mineralogists *Special Publication* No. 3, Tulsa, Okla., U.S.A., 1955.
- Heintz, Anatol. 1958. "The head of the Anaspid *Birkenia elegans* Traq." *Studies on Fossil Vertebrates*, Univ. of London, The Athelone Press, pp. 71-85, 4 figs.
- Hevesy, G., Levi, H., and O. H. Rebbe. 1940. "Rate of rejuvenation of the skeleton." *Biochem. Jour.*, vol. 34, pt. 1, pp. 532-537.
- Howell, B. F. 1937. "Cambrian *Centropleura vermontensis* fauna of northwestern Vermont." *Bull. Geo. Soc. Amer.*, vol. 48, no. 8, pp. 1147-1210, 6 pls.

Notes on the Origin of Bony Armor 107

- Irving, J. T. 1957. *Calcium Metabolism*. Methuen's Monographs on Biochemical Subjects, London, Methuen and Co. Ltd.
- Kirk, S. R. 1929. "Conodonts associated with the Ordovician fish fauna of Colorado. A preliminary study." *Amer. Jour. Sci.*, vol. XVIII.
- . 1930. "The Harding Sandstone of Colorado." *Amer. Jour. Sci.*, vol. XX, 5th series, no. 120.
- Kyes, P., and T. S. Potter. 1934. "Physiological marrow ossification in female pigeons." *Anat. Rec.*, vol. 60, no. 4, pp. 377-379.
- Leblond, C. P., Belangar, L. F., and R. C. Greulich. 1955. "Formation of bones and teeth as visualized by radioautography." *Ann. N. Y. Acad. Sci.*, vol. 60, art. 5, pp. 630-659.
- McElroy, W. D., and Bently Glass. 1952. *Phosphorus Metabolism*, vol. II. Baltimore, The Johns Hopkins Press.
- McLean, F. C. 1958. "The ultrastructure and function of bone." *Science*, vol. 127, no. 3296.
- Munson, P. L. 1955. "Studies on the role of the parathyroids in calcium and phosphorus metabolism." *Ann. N. Y. Acad. Sci.*, vol. 60, art. 5, pp. 776-796.
- Ørvig, Tor. 1958. "*Pycnaspis splendens*, new genus, new species, a new ostracoderm from the Upper Ordovician of North America." *Proc. U. S. Nat. Mus.*, vol. 108, no. 3391.
- Robinson, J. J., and T. H. Bast. 1934. "Bone changes due to lathyrisms in rats." *Anat. Rec.*, vol. 59, no. 3, pp. 283-289, 3 pls.
- Robinson, R. A., and M. L. Watson. 1952. "Collagen-crystal relationships in bone as seen in the electron microscope." *Anat. Rec.*, vol. 114, no. 3, pp. 383-392, 8 pls.
- . 1955. "Crystal-collagen relationships in bone as observed in the electron microscope. III. Crystal and collagen morphology as a function of age." *Ann. N. Y. Acad. Sci.*, vol. 60, no. 5, pp. 529-628.
- Romer, A. S. 1942. "Cartilage, an embryonic adaptation." *Amer. Naturalist*, vol. LXXVI, pp. 394-404.
- . 1945. *Vertebrate Paleontology*. University of Chicago Press, Chicago, Ill.
- . 1946. "The early evolution of fishes." *Quart. Review of Biology*, vol. 21, no. 1, pp. 39-69.
- Snapper, I. 1940. "Different features of the syndrome of hyperparathyroidism." *Acta. Med. Scand.*, vol. 103, fasc. III-IV, pp. 321-340.
- Stensiö, E. A. 1927. "The Downtonian and Devonian vertebrates of Spitzbergen. Part I., Family *Cephalaspidae*." *Skrifter om Svalbard og Nordishavet*, no. 12.
- Stetson, H. C. 1931. "Studies on the morphology of the Heterostraci." *Jour. of Geol.*, vol. XXXIX, no. 6.
- Stockard, C. R. 1921. "Developmental rate and structural expression;

- an experimental study of twins, double monsters and single deformities. . . ." *Am. Jour. Anat.*, vol. 28:115.
- Sweet, W. C. 1954. "Harding and Fremont formations, Colorado." *Bull. Amer. Assoc. Pet. Geol.*, vol. 38, pp. 284-305.
- . 1955. "Conodonts from the Harding Formation (Middle Ordovician) of Colorado." *Jour. Paleont.*, vol. 29, no. 2, pp. 226-262; 17 figs., 3 pls.
- Valliant, Leon. 1902. "Sur la Presence du Tissu Osseux chez Certains Poissons des Terrains Paleozoiques de Canyon City, Colorado." *C. R. Acad. Sci. Paris*, vol. CXXIV.
- Walcott, C. D. 1892. "Notes on the discovery of a vertebrate fauna in Silurian (Ordovician) strata." *Bull. Geol. Soc. Amer.*, pp. 155-172, 2 pls.
- Wald, G. 1957. "The metamorphosis of visual systems in the sea lamprey." *Jour. Gen. Physiol.*, vol. 40, no. 6, pp. 901-914.
- Wald, G., and Austen Riggs. 1951-52. "The haemoglobin of the sea lamprey, *Petromyzon marinus*." *Jour. Gen. Physiol.*, vol. 35, pp. 45-53.
- Webb, J. E., and M. B. Hill. 1958. "IV. On the reactions of *Branchiostoma nigeriense* Webb to its environment." *Phil. Trans. Roy. Soc. Lond.*, Ser. B. no. 683, vol. 241.
- Westoll, T. S. 1945. "A new cephalaspid fish from the Downtonian of Scotland." *Trans. Roy. Soc. Edinb.*, vol. 61, pp. 341-357.
- . 1958. *Studies on Fossil Vertebrates*. Univ. of London, The Athelone Press.
- White, E. I. 1958. "Original environment of the vertebrates." *Studies of Fossil Vertebrates*, Univ. Lond., The Athelone Press.
- . 1935. "The Ostracoderm *Pteraspis Kier* and the relationships of the agnathous vertebrates." *Phil. Trans. Roy. Soc. Lond.*, Ser. B, vol. 225, no. 527, pp. 381-457, 97 figs., pls. 25-27.
- . 1946. "*Jamoytius kerwoodi*, a new chordate from the Silurian of Lanarkshire." *Geol. Mag.*, vol. 83, pp. 89-97.
- Woodward, A. S. 1921. "Visit to the gallery of fossil fishes, British Museum of Natural History." *Proc. Geol. Assoc.*, vol. XXXII, pt. 3.