Pharyngeal Denticles (Placoid Scales) of Sharks, with Notes on the Dermal Skeleton of Vertebrates

BY GARETH J. NELSON[1]

In many species of Recent sharks, the dermal skeleton of the bucco-pharyngeal cavity is well developed and, like the dermal skeleton of the body surface, consists of numerous, independent, non-growing denticles (placoid scales). The pharyngeal denticles are known to exhibit the same sort of intraspecific and interspecific variation as those of the body surface: they may be relatively few or numerous, small or large, sparse or closely packed, and of a form either simple or highly differentiated (Steinhard, 1903; Imms, 1905; Fahrenholz, 1915; Daniel, 1934; Beaumont, 1959; Peyer, 1963, 1968). In addition, the denticles of the bucco-pharyngeal cavity as a whole are arranged in various patterns, which thus far have been little studied but which form the subject of the present paper. The arrangement of pharyngeal denticles, varying as it does from species to species, is of potential systematic importance at specific and higher levels. The objective of the present paper, however, is not to exploit this potentiality in an exhaustive study of numerous species, with a view toward defining each, or groups of them, by means of characters of the pharyngeal denticles. Rather, the objective is to discuss what seem to be the main phyletic trends in denticle arrangement, against a background of what is known of the history of the dermal

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skeleton of the buccopharyngeal cavity in other vertebrates (Nelson, 1969a).

As regards their arrangement, the pharyngeal denticles of sharks are of more interest than are those on the body surface, for the pharyngeal denticles in some sharks (some galeoids) participate in the formation of specialized structures (pharyngeal pads) apparently analogous to certain dermal bones (the upper and lower pharyngeal tooth plates) of teleostomes. That these pharyngeal pads are structures peculiar to sharks, in the sense that they have developed during elasmobranch evolution, is hardly to be doubted. This conclusion has some direct bearing on the problem of the history of the elasmobranch dermal skeleton as a whole, and indirectly on that of the history of the vertebrate dermal skeleton. Accordingly, an effort is made to discuss the present results in as wide a context as possible, including considerations of fossil vertebrates such as ostracoderms, arthrodires and acanthodians, and Recent vertebrates, including cyclostomes.

MATERIAL AND METHODS

The material consists of preserved elasmobranch specimens, for the most part included in the collections of the Department of Ichthyology, the American Museum of Natural History. Many of the specimens used were near-term embryos or juveniles. Few bona fide adult specimens were available. Nomenclature follows Bigelow and Schroeder (1948). The abbreviations used are: California Academy of Science (C.A.S.) and the American Museum of Natural History (A.M.N.H.).

Specimens were usually studied after making an incision through the jaw articulation on the right side, and continuing it posteriorly through the external gill slits, so as to expose the full extent of the buccopharyngeal cavity. Specimens selected for photography were decapitated, and a complete frontal section was made by means of an incision on the left side. The material was then stained in alizarin (in aqueous 2 per cent potassium hydroxide) and bleached in a weak solution of hydrogen peroxide. Preserved slime and epidermis were removed from the buccopharyngeal surface with a brush, and the material photographed, generally after submersion in 40 per cent isopropyl alcohol, by means of a Polaroid MP-3 camera and Kodak Contrast Process Ortho film. Retouching photographic negatives or prints was not employed.

of Sciences, and Dr. R. F. Nigrelli, Osborn Laboratories of Marine Sciences, who made specimens available for dissection, and to Dr. J. W.

FIG. 1. *Notorynchus maculatus,* C.A.S. No. 1968–XII: 2, pharynx. A. Dorsal part, ventral view. B. Ventral part, dorsal view. ×1.
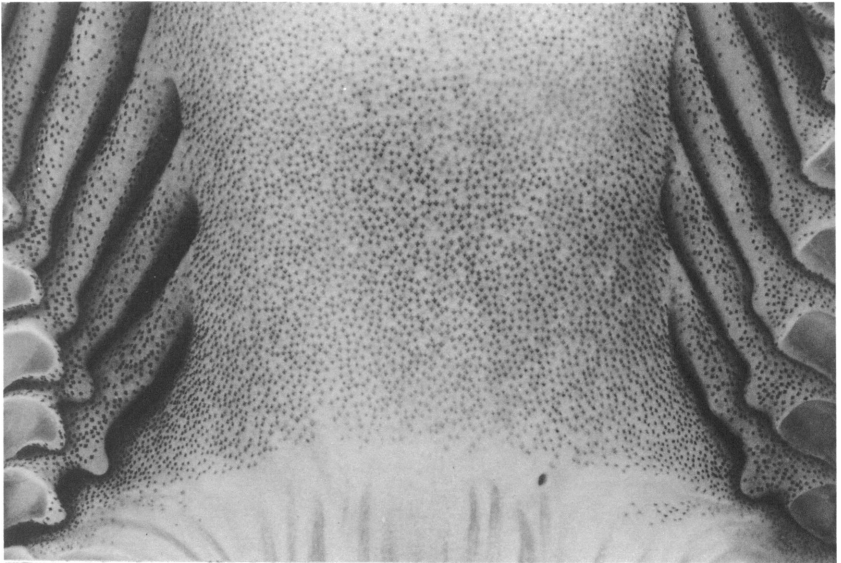
FIG. 2. *Notorynchus maculatus,* enlarged detail of figure 1B. ×2.

PRIMITIVE PATTERNS OF PHARYNGEAL DENTICLES

Many species of Recent sharks have denticles covering much or all of the buccopharyngeal surface (figs. 1–6, 10–16), in what probably is a primitive condition. That a well-developed dermal skeleton, extending from the jaw margin to the pharyngo-esophageal boundary, probably is a feature primitive for gnathostomes has been noted (Nelson, 1969a), primarily on evidence from various studies of teleostomes. On the basis of the present study, as well as the earlier ones of Steinhard (1903) and Fahrenholz (1915), it is apparent that the dermal skeleton of the bucco-pharyngeal cavity had the same anteroposterior extent in primitive elas-mobranchiomorphs as it did in primitive teleostomes. Accordingly, this feature may with greater confidence be considered primitive for the group Gnathostomata as a whole, and perhaps advanced relative to the condition of fossil and Recent Cyclostomata (see also Jollie, 1968, p. 95), from the buccopharyngeal cavity of which a mineralized dermal skeleton, so far as known, is absent (see however, Stensiö, 1964, p. 158; cf. Ritchie, 1964, p. 9; and the rejoinder of Stensiö, 1968, pp. 37–38).

ADVANCED PATTERNS OF PHARYNGEAL DENTICLES

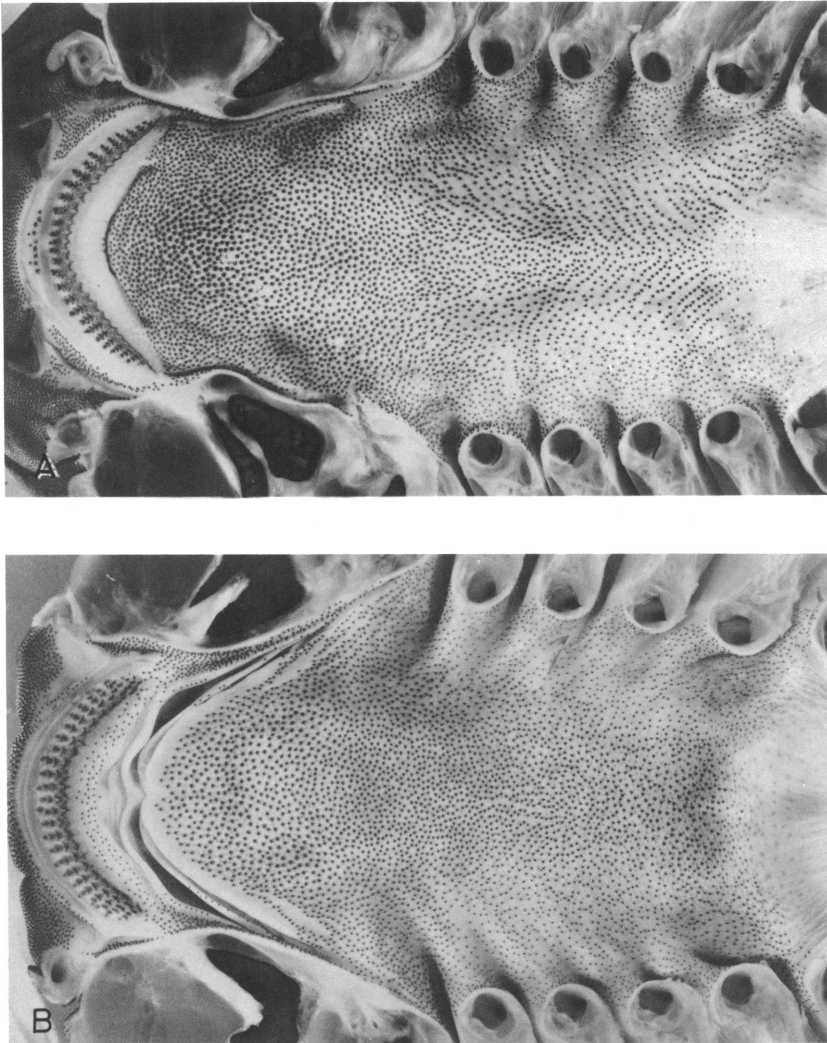Among Recent sharks there are species with variously reduced pat-

FIG. 3. *Ginglymostoma cirratum*, A.M.N.H. No. 3801, pharynx. A. Dorsal part, ventral view. B. Ventral part, dorsal view. × 1.

terns of pharyngeal denticles. Some examples are species of the genus *Mustelus*. In *M. manazo* (fig. 5C, D), denticles occur over the entire bucco-pharyngeal surface. In *M. lunulatus* (fig. 5A, B), denticles tend to be confined to an anterior area, although some are present along the gill slits, and others form part of paired lower pharyngeal pads supported by the
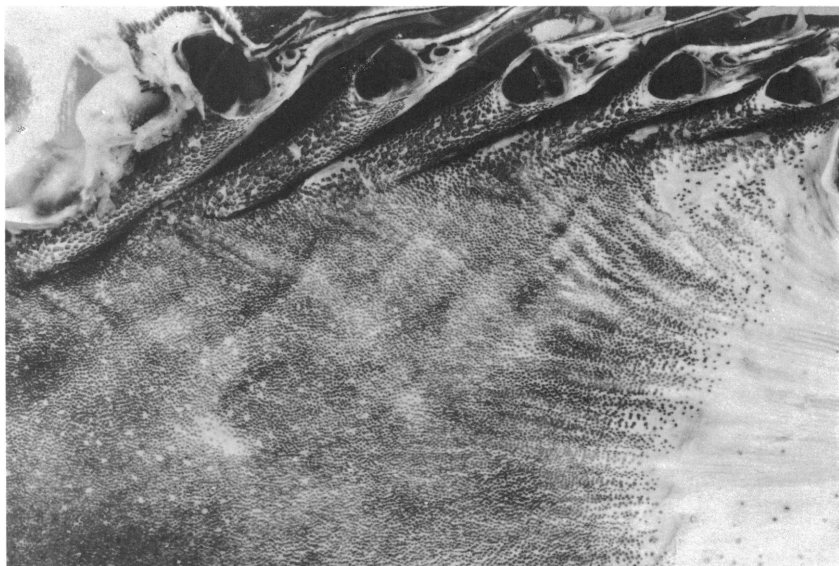
FIG. 4. *Chlamydoselachus anguineum*, A.M.N.H. No. 13813, upper rear portion of left side of pharynx, ventral view. ×1.5.

fourth ceratobranchials and paired upper pharyngeal pads supported by the most posterior pharyngobranchials. In *M. canis* (fig. 7A–D), denticles are confined to an even smaller area anteriorly, although others are present along the gill slits and on the lower and upper pharyngeal pads. Comparisons between these three species lead to the conclusion that, as regards the extent of pharyngeal denticles, *M. manazo* is the most primitive, *M. canis* is the most advanced, and *M. lunulatus* is intermediate (see also Niu, 1936).

The very distinctive arrangement of denticles of *Mustelus canis* was found to be relatively constant regardless of the size of the specimen examined. In a small embryo, the patch of denticles over the first basibrachial is well formed, even though denticles have not yet developed posteriorly (fig. 7A). The juvenile condition (fig. 7C) is hardly different from the adult (fig. 7B). Thus, even though ontogenetic series of other shark species have not been available for study, there is some reason to believe that the denticle pattern of the buccopharyngeal cavity of sharks may be a stable and definable character within the species in which it occurs.

Other examples of denticle reduction, not very different from those mentioned, are provided by species of the genus *Galeus*. In *G. eastmani*
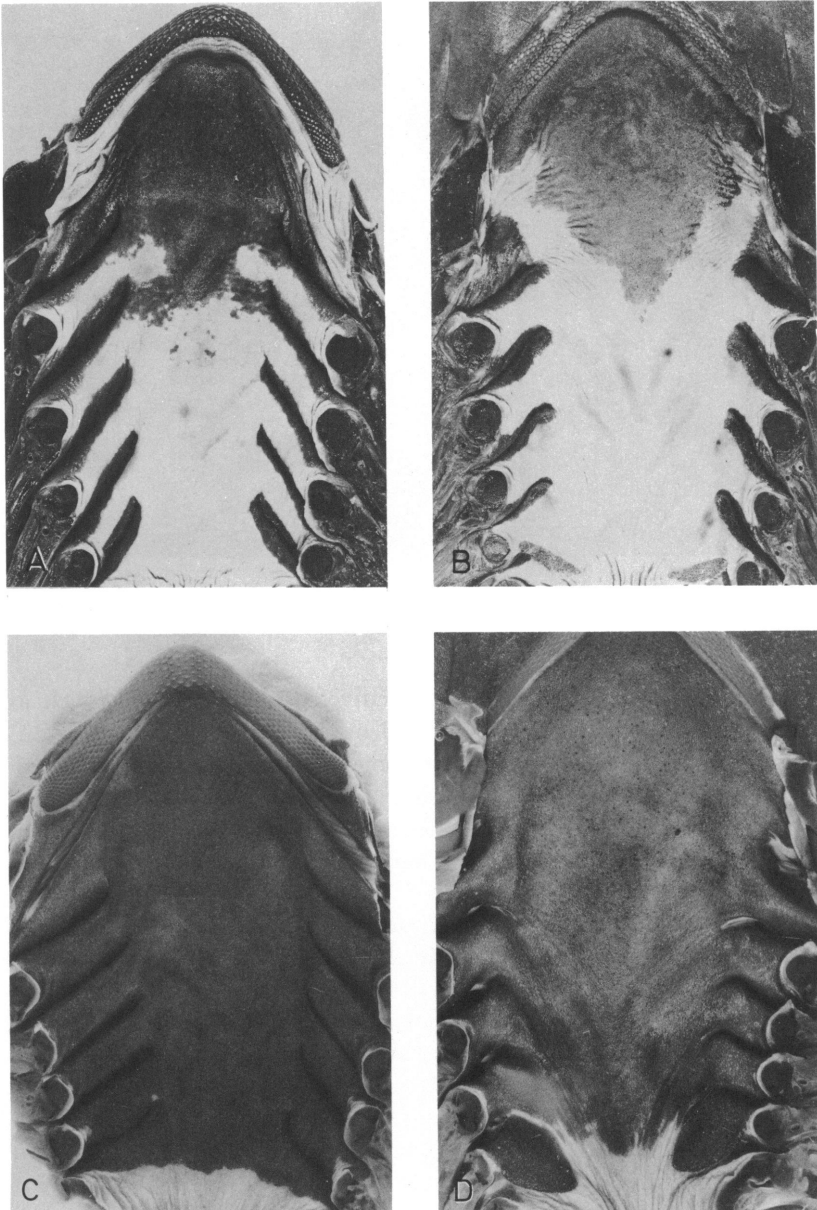
FIG. 5. Pharynx. A, B. *Mustelus lunulatus,* A.M.N.H. No. 15671. A. Ventral part, dorsal view. B. Dorsal part, ventral view. C, D. *Mustelus manazo,* A.M.N.H. No. 26685. C. Ventral part, dorsal view. D. Dorsal part, ventral view. All ×1.

FIG. 6. *Squalus acanthias,* A.M.N.H. No. 2102, pharynx, ventral part, dorsal view. ×1.

(fig. 9C, D), some denticles are confined to an anterior area, much as in *Mustelus canis.* The arrangement of denticles on the gill arches is different, however, for there is a continuous cover of denticles in *Galeus,* whereas in *Mustelus* denticles are absent from the mid-point of the arches. In *G. melastomus* (fig. 9A, B) denticles are present only on the gill arches. In both species of *Galeus* there are neither lower nor upper pharyngeal pads.

Varying amounts of reduction in area occupied by pharyngeal denticles are shown in other species (figs. 1, 8, 13–15). In small specimens of the genus *Scyliorhinus* (*S. stellaris, S. retifer*), no denticles could be observed; nor could any be observed in a small *Squatina* (*S. californica?*) or in a specimen of *Pliotrema warreni* (other species without pharyngeal denticles are listed by Fahrenholz, 1915, pp. 409–410).

As already noted by Fahrenholz (1915, pp. 408–409) reduction of denticles first seems to take place posteriorly rather than anteriorly, and dorsally rather than ventrally. The postero-anterior reduction is apparent in many species examined in this study (figs. 1A, 5A, 5B, 7, 8, 9C, 9D, 11A, 13A, 15A) and dorsal rather than ventral reduction of denticles is apparent in *Notorynchus* (fig. 1) and in many of the galeoid species examined (figs. 11, 13, 15).
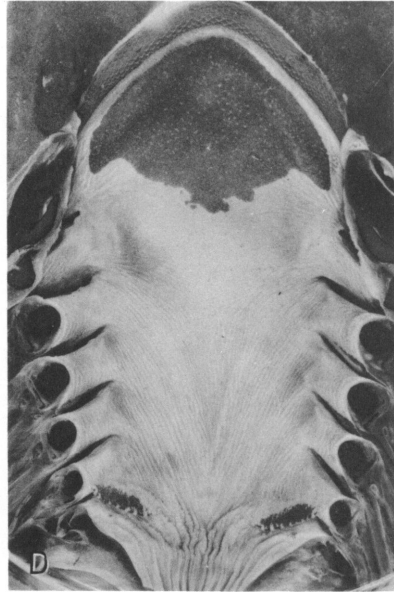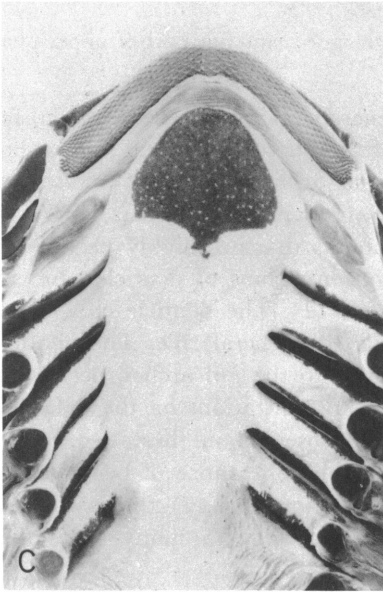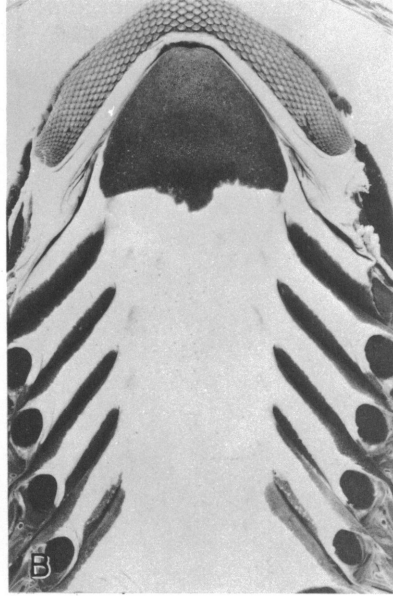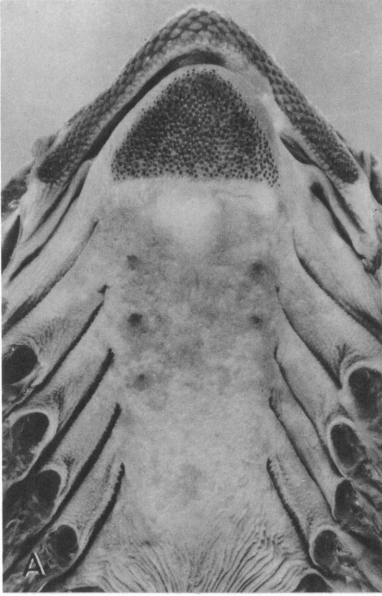
Fig. 7. *Mustelus canis.* A. A.M.N.H. No. 19475, pharynx, ventral part, dorsal view. ×2. B. A.M.N.H. No. 15667, pharynx, ventral part, dorsal view. ×0.5. C, D. A.M.N.H. No. 29393. C. Ventral part, dorsal view. D. Dorsal part, ventral view. ×1.

FIG. 8. *Heterodontus* sp., A.M.N.H. uncatalogued, anterior part of upper pharynx, ventral view. ×1.

Not all species conform to these generalizations. *Squalus acanthias*, for example, retains denticles over most of the buccopharyngeal surface but they are rather sparse and ventrally tend to occur near the midline, or the gill slits, but not between (fig. 6; Sayles and Hershkowitz, 1937).

Some species have denticle arrangements that are highly peculiar in other ways. *Heterodontus* (fig. 8) has concentrations of denticles directly behind the jaws, both dorsally and ventrally. The denticle crowns are directed anteriorly not posteriorly as is the general rule. The denticle concentrations of *Heterodontus* are anterior to the gill arches, occupying much the same position as the denticle concentrations on the palate of *Notorynchus*. Other interesting similarities observed in these two genera concern (1) the gill arches, which have the appearance of being secondarily concentrated and posterior in position and (2) the jaw teeth, which include two basic types (anterior teeth with many cusps and posterior teeth without cusps).

PHARYNGEAL PADS

In some ways the most interesting aspect of shark pharyngeal denticles is their participation in the formation of pharyngeal pads, which otherwise are fleshy structures supported by certain of the paired ele-
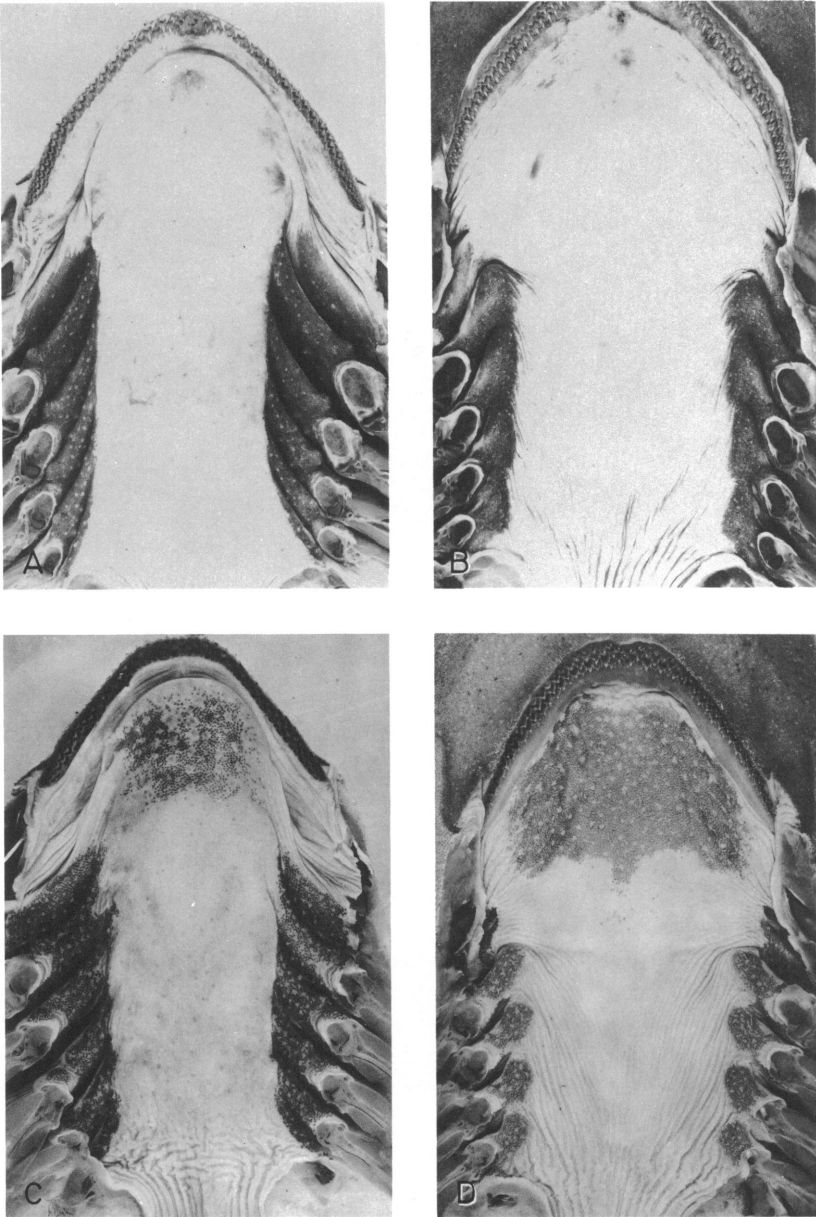
FIG. 9. Pharynx. A, B. *Galeus melastomus,* A.M.N.H. No. 4116. A. Ventral part, dorsal view. B. Dorsal part, ventral view. ×1. C, D. *Galeus eastmani,* A.M.N.H. No. 29396. C. Ventral part, dorsal view. D. Dorsal part, ventral view. ×2.
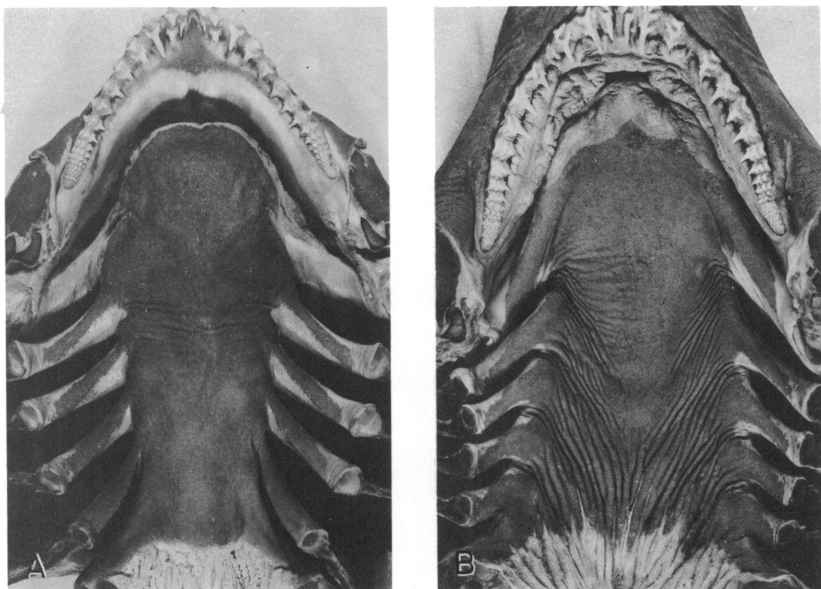
FIG. 10. *Carcharias taurus*, A.M.N.H. uncatalogued, pharynx. A. Ventral part, dorsal view. B. Dorsal part, ventral view. ×0.2.

ments of the visceral endoskeleton. One pair of lower and one pair of upper pharyngeal pads have already been noted for *Mustelus* (figs. 5, 7). In some carcharhinids at least two lower and three upper pairs of pads occur (figs. 13, 15, 16B), with the scales forming the rear border of the pads lined up in distinct rows. The condition in *Carcharhinus milberti* is similar (figs. 14, 16A) except that the scales are not lined up in rows. Neither are the scales so aligned in *Sphyrna*, even though one pair of upper pharyngeal pads is prominently developed (figs. 11, 12A). In *Scoliodon*, pads occur ventrally on all of the branchial arches (but not on the hyoid), and dorsally on the posterior four arches, with the most posterior pads, supported by the fifth arch, very small (fig. 15). In *Scoliodon*, the scales forming the posterior border of the pads are aligned in distinct rows.

Pharyngeal pads apparently are analogous to the consolidated upper and lower pharyngeal tooth plates of teleostomes, and presumably function in moving food from the pharynx into the esophagus. Such food would be in the form of relatively large pieces, either whole animals, or large parts of them, which when bitten off, could be swallowed whole. It is not demonstrable on present evidence that the pharyngeal pads of

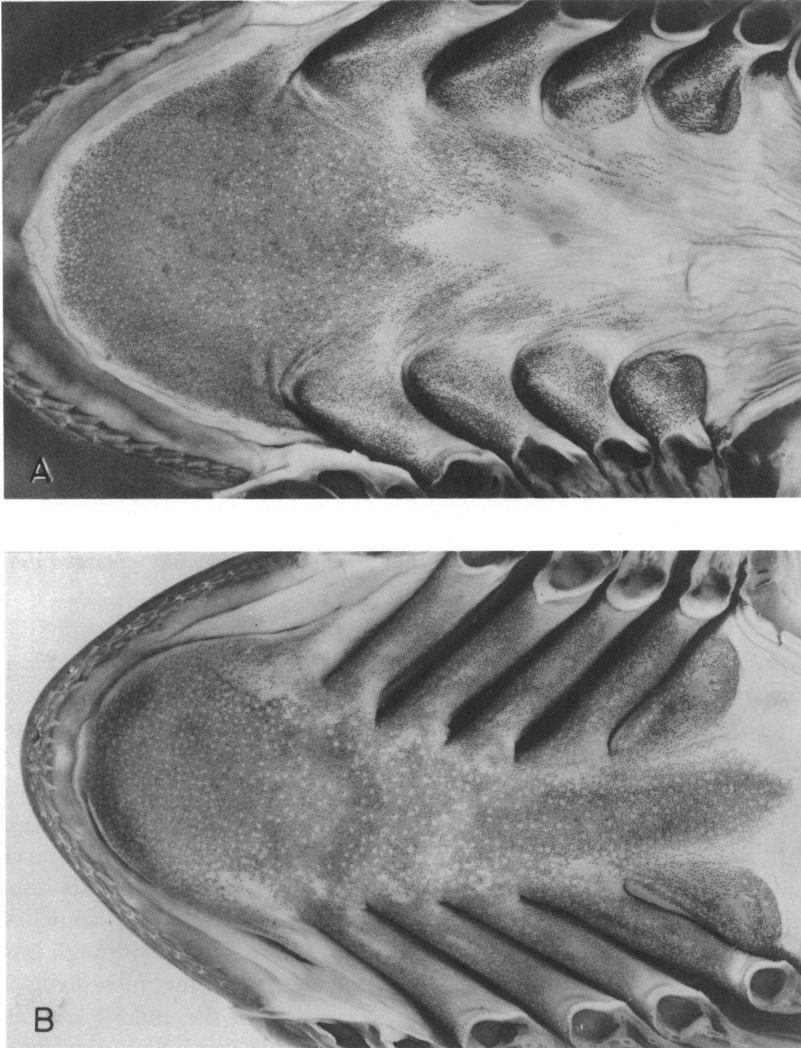FIG. 11. *Sphyrna zygaena*, A.M.N.H. No. 29392, pharynx. A. Dorsal part, ventral view. B. Ventral part, dorsal view. ×1.

sharks actually function in this way. Hence the above interpretation of their function is entirely hypothetical, but nevertheless appears to be relatively certain.

From the form and arrangement of pharyngeal denticles on the gill arches of sharks, it is apparent that certain areas are functionally more
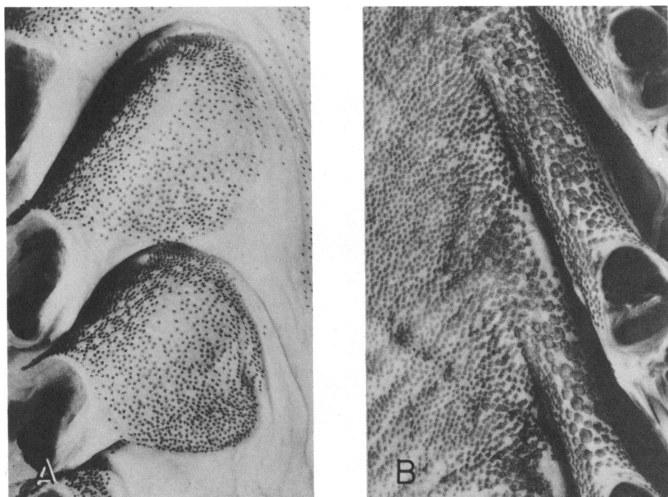
FIG. 12. Ventral views of upper, rear parts of pharynx. A. *Sphyrna zygaena*, enlarged detail of figure 11A. ×3. B. *Chlamydoselachus anguineum*, enlarged detail of figure 4. ×3.

important than others. Thus, even in a form as generalized as *Chlamydoselachus*, enlarged scales occur in certain areas on the gill arches (figs. 4, 12B; Nelson, 1969a, pl. 92, figs. 3, 5). Such areas of differentiated scales can be compared with the areas occupied by pharyngeal pads of other sharks, and to the areas occupied by consolidated tooth plates of teleostomes. In sharks the ceratobranchials (especially the fourth and fifth) and one or more posterior epibranchials commonly support pharyngeal pads or enlarged scales. In teleostomes, the ceratobranchials (especially the fifth but sometimes the fourth) and the infrapharyngobranchials commonly support, or are fused with, large tooth plates, although basibranchials, hypobranchials, and epibranchials are sometimes involved. There are, of course, between the arrangements of the endoskeletal elements of sharks and teleostomes important differences which may determine the various areas of differentiation of the dermal skeleton of the buccopharyngeal cavity. But aside from the fact that in sharks the epibranchials in large measure support the upper pharyngeal pads, whereas in teleostomes the infrapharyngobranchials support the upper pharyngeal tooth plates, one cannot resist concluding that both groups of gnathostomes have tended to differentiate the dermal skeleton of the buccopharyngeal cavity in about the same ways. Meaningful comparisons perhaps could also be made between the well-formed patches of
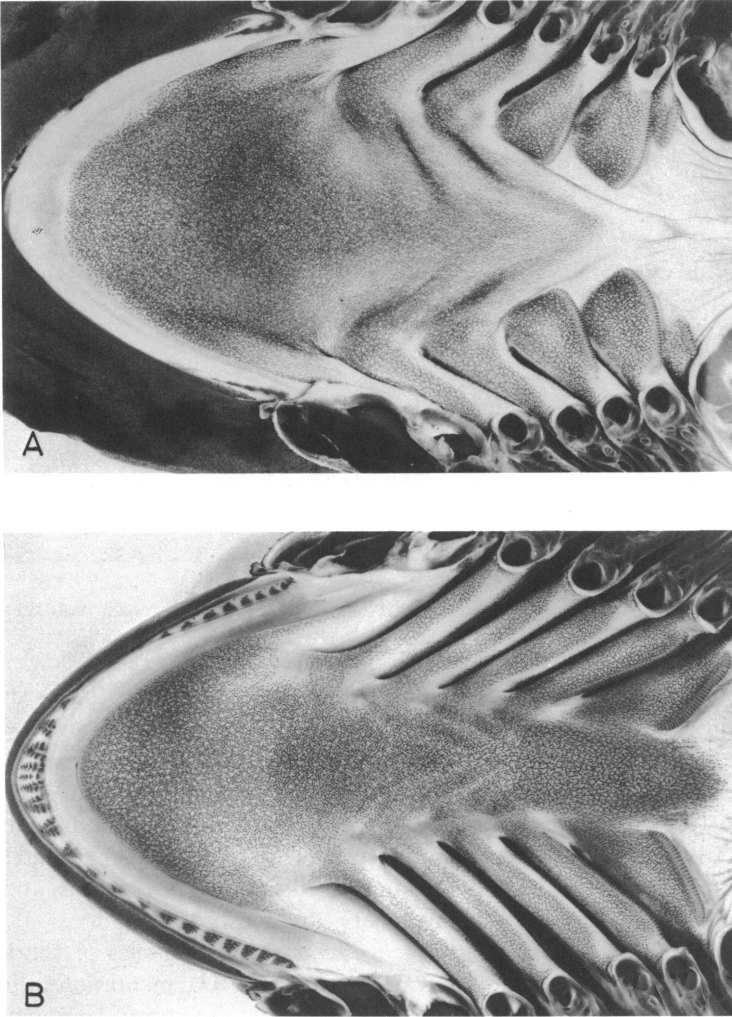
FIG. 13. Carcharhinidae, genus and species indeterminate, A.M.N.H. No. 15683, pharynx. A. Dorsal part, ventral view. B. Ventral part, dorsal view. ×1.

denticles of *Mustelus canis* and the basibranchial tooth plates and median palatal bones (vomers and parasphenoid) of teleostomes. Indeed, even the paired dense concentrations of denticles on the palate of *Notorynchus* (fig. 1) bear some similarity to the paired vomers and dermopalatines of primitive teleostomes, such as *Eusthenopteron* (Jarvik, 1954, fig. 25).
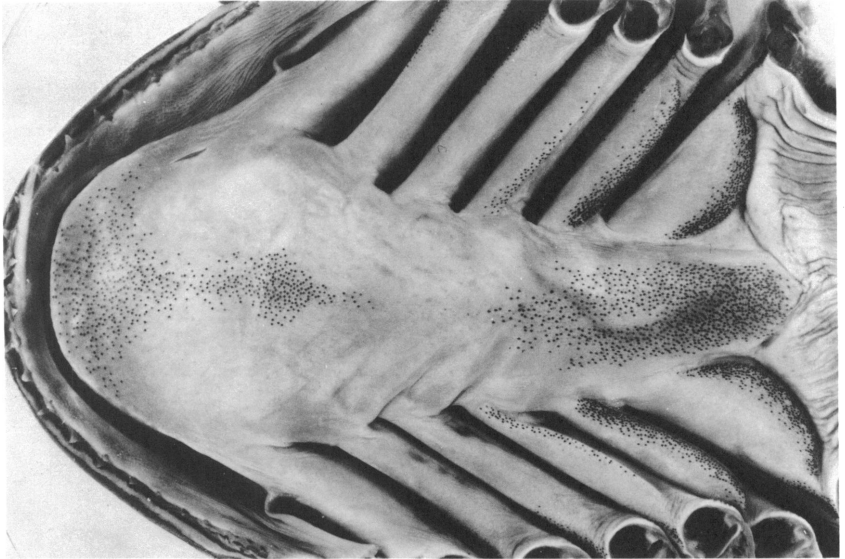
Fig. 14. *Carcharhinus milberti,* A.M.N.H. No. 29402, pharynx, ventral part, dorsal view. ×1.

This is not to say that particular patches of denticles in sharks should be considered homologous to particular dermal bones of teleostomes except in the broadest sense (that both might be differentiations of the same region of the dermal skeleton), but only that in certain ways the dermal skeleton of the buccopharyngeal cavity has tended to differentiate similarly in both gnathostome groups. Such similar phyletic tendencies (parallelisms) are to be expected in related groups of organisms and can be interpreted as indicators of phyletic relationship.

Viewed from this perspective, the pharyngeal denticles of sharks do not appear to have originated from the phyletic fragmentation of larger dermal bones. Rather, the phyletic trends associated with the arrangement of pharyngeal denticles, like those associated with the pharyngeal tooth plates of teleostomes, seem to progress toward consolidation and differentiation in localized areas supported by the visceral endoskeleton. Thus, the subdivided condition of the pharyngeal denticles can be considered to represent a primary micromeric stage (Ørvig, 1968).

This conclusion has some bearing on the interpretation of the dermal skeleton of the body surface of Recent elasmobranchs, for there is little reason to suppose that the pharyngeal denticles could represent a primary micromeric stage, and the denticles on the body surface a secon-
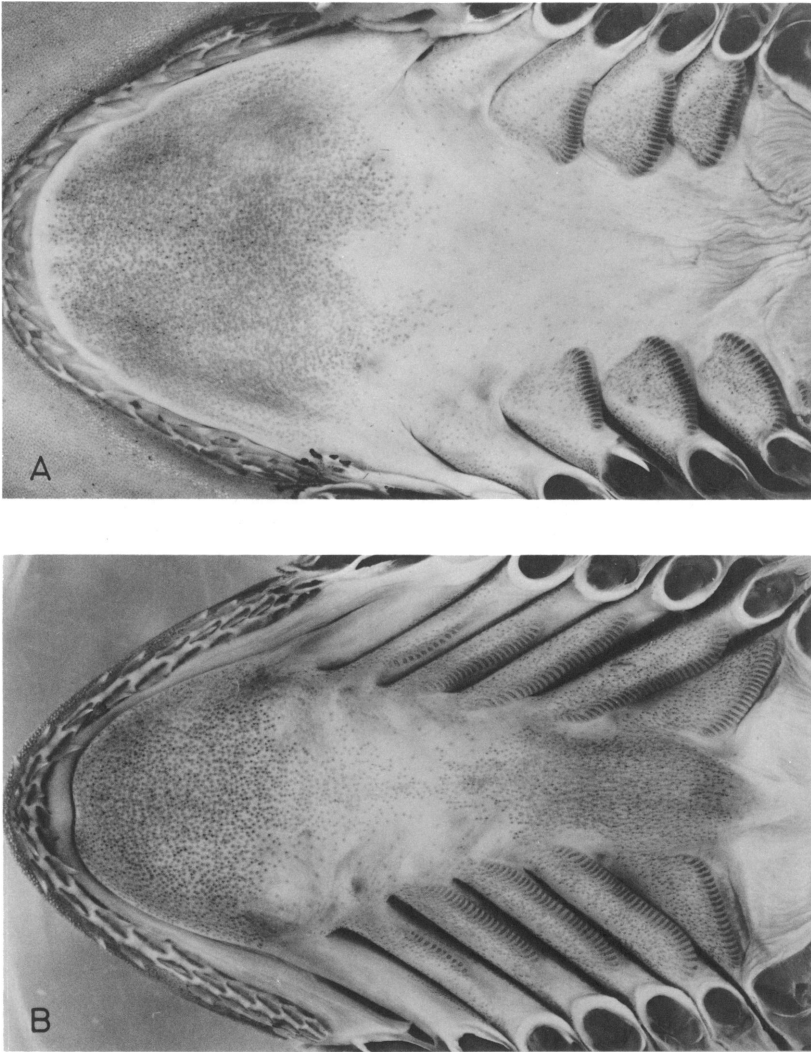
FIG. 15. *Scoliodon terraenovae*, A.M.N.H. No. 29395, pharynx. A. Dorsal part, ventral view. B. Ventral part, dorsal view. ×3.

dary micromeric stage derived from the fragmentation of well-developed armor such as that of the arthrodires. In fossil and Recent gnathostomes there is every indication that dermal skeletal assimilation never was restricted only to the body surface, but occurred also within the buccopharyngeal cavity. It is, of course, the non-growing character of placoid
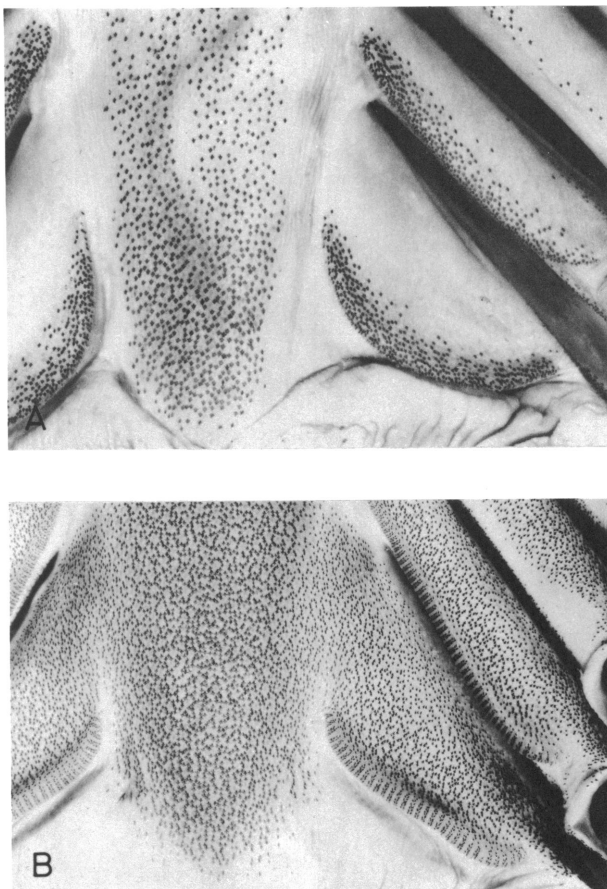
FIG. 16. Dorsal views of lower, rear parts of pharynx. A. *Carcharhinus milberti*, enlarged detail of figure 14. ×2., B. Carcharhinidae, genus and species indeterminate, enlarged detail of figure 13. ×2.

scales that probably accounts for the absence of evidence of prominent dermal skeletal assimilation from Recent elasmobranchs (see below).

THE DERMAL SKELETON OF SHARKS

The dermal skeleton of sharks has been of theoretical importance to comparative zoologists since Hertwig (1874) proposed that vertebrate dermal bones arose by the fusing together of denticles of the sort that occur in modern sharks (see also Moss, 1968). The relevance of this theory of fusion (or concrescence) continues to the present day, despite

some controversy about the detailed structure of the primitive unit of the vertebrate dermal skeleton, and whether the placoid scale is in fact the best modern representative of it (Stensiö, 1961; Ørvig, 1968; Zangerl, in Peyer, 1968, pp. 59–60). Despite such controversy one may assume with ample justification that the dermal skeleton of elasmobranchs and the dermal skeleton of teleostomes are homologous formations: in the skeleton of each group occur enameloid, dentinous, and osseous tissues (Ørvig, 1967; Moss, 1968), and in each group the skeleton has the same extent, primitively occupying the entire body surface and the entire buccopharyngeal surface, presumably developing wherever there is an ectodermal influence. That elasmobranch dermal denticles do not grow, whereas teleostome dermal scales and bones do grow, is a fundamental difference between the dermal skeletons of modern representatives of each of the two groups. It is apparent, however, that the capacity for growth is a primitive one lost during the evolution of elasmobranchio-morphs (Ørvig, 1951; Stensiö, 1961, 1962). Thus, the hypothesis that the dermal bones of modern teleostomes arose by the fusing together of non-growing denticles of modern elasmobranch type can be rejected. At least two alternative hypotheses are possible, and both have been proposed at one time or another: (1) that the dermal skeleton of modern gnathostomes arose from small, primitive units capable of growth, and (2) that no primitive unit was involved, the skeleton instead arising as a continuous sheet without primary subdivision. The former alternative represents a refinement of Hertwig's theory of fusion, and the latter, if it were further developed, would lead to a contradictory theory. At present there is abundant evidence favoring some kind of fusion theory (see below and Ørvig, 1969, p. 243).

THE VERTEBRATE DERMAL SKELETON

Perhaps the greatest problems of interpretation of the vertebrate dermal skeleton center around the possibilities that dermal bones in on-togeny and phylogeny either fuse, fragment, do both, or neither. For example, in a given location on the body surface, one may observe several small bones in one species, but only a few large bones in another (fig. 17). In many cases it is possible for specialists, after independent studies, to reach significant agreement that the many small bones represent the primitive condition, and the few large bones, the advanced condition, or vice versa, but nothing is or can be directly known about how such changes in phylogeny have actually occurred. Nonetheless, it is possible to call the one condition a micromeric condition, the other a macromeric condition, and to recognize or to postulate phyletic trends

of skeletal assimilation and regression (Ørvig, 1968; the terms "micro-meric" and "macromeric" here are used only in a relative sense, and represent a simplification of Ørvig's concepts).

Skeletal assimilation both in ontogeny and phylogeny seems to be relatively common and regression relatively rare. For this reason and others (Ørvig, 1968, pp. 380–388) it seems necessary to assume that dermal bone, when it first arose in the vertebrates, appeared in a micro-meric pattern, probably over the entire body surface. If so, the out-standingly different macromeric patterns reflected in the head armor of the osteostracans, heterostracans, arthrodires, and teleostomes arose by means of assimilative processes operative in phylogeny. Perhaps in these four cases the skeletal assimilation, occurring primarily around the head,
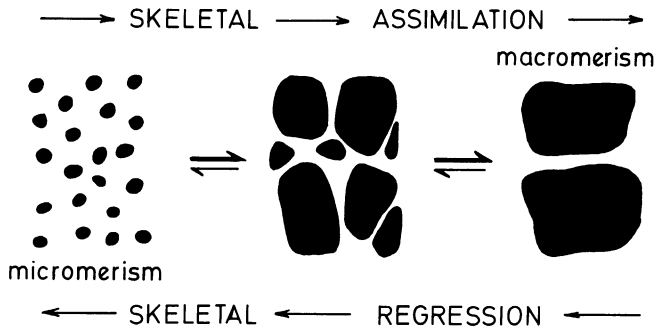
FIG. 17. Diagram illustrating phyletic trends of assimilation and regression of the dermal skeleton.

was related to specific improvements or specializations in feeding mech-anisms.

These macromeric patterns apparently developed independently, for it is not possible to speak of homologies between dermal bones of species of the four different groups, or to derive one macromeric pattern from another, except in a subjective and arbitrary way (for which, it may be added, there is ample precedent). Within each group, therefore, it seems that skeletal assimilation began at a primary micromeric stage, or per-haps even at a primary naked stage (fig. 18). Thus there is some pos-sibility that bone appeared more than once in vertebrate history (Ørvig, 1965).

The interrelationships of the major groups of Recent vertebrates are agreed on relatively well, but the relationships of fossil groups such as ostracoderms and placoderms remain relatively obscure. For this reason

FIG. 18. Diagram summarizing a comparative theory of the vertebrate dermal skeleton, with naked stages represented by open circles, micromeric stages by half-black circles, and macromeric stages by black circles.
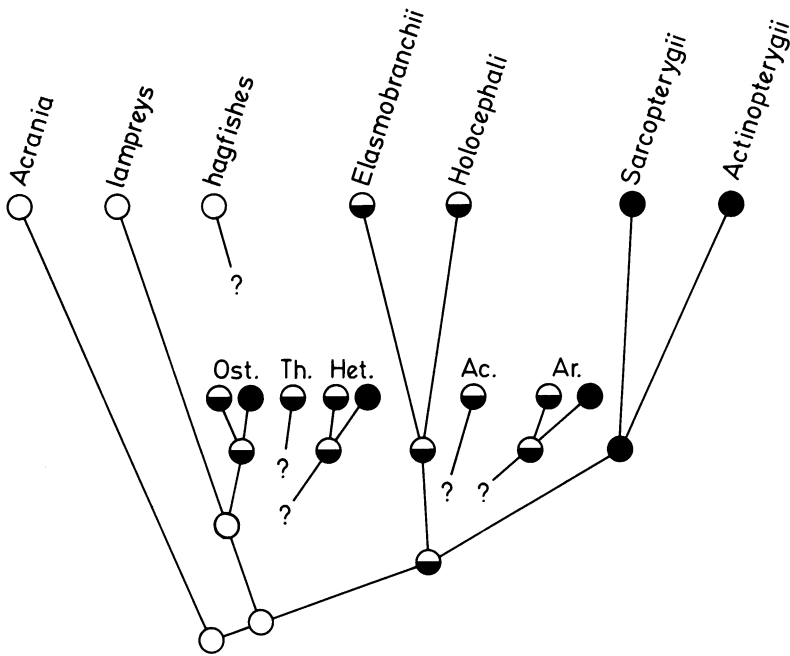
Abbreviations: Ar., Arthrodira; Ac., Acanthodii; Het., Heterostraci; Ost., Osteostraci; Th., Thelodonti.

it is questionable that the Recent cyclostomes are primitively naked, but at present only if one assumes that they have descended from known ostracoderms, that is, if one assumes that they are secondarily naked. Of course, it has become fashionable in recent years to imagine that Recent cyclostomes are ostracoderm "derivatives" and to begin a discussion of vertebrate evolution from that premise. In the opinion of the writer this practice is of little or no scientific value, for it requires assumptions that are both biased and unnecessary, and here can be dismissed without further comment (Nelson, 1969b and In press).

For an assessment of the significance of the dermal skeleton of fossil groups such as ostracoderms and placoderms, some assumptions about their relationships are necessary. Fair assumptions are (1) that, among the ostracoderms, the Osteostraci, Heterostraci, and Thelodonti are monophyletic groups, and (2) that the Osteostraci are in some way related to modern lampreys. Within each of these three groups of ostracoderms

are forms having a dermal skeleton in what apparently is a primary micromeric condition (Stensiö, 1964, pp. 112–115, 176–177, 359; Ørvig, 1968, p. 385). Consequently the common ancestor of each of these three groups can be hypothesized to have been in a primary micromeric stage (see also Stensiö, 1964, p. 359). Thus, whatever other relationships might be assumed to exist between ostracoderms and modern cyclostomes, one can conclude on present evidence either that the modern lampreys are primarily naked, or if secondarily naked, the loss of dermal bone began at a primary micromeric stage.

Among arthrodires, also, are forms having a dermal skeleton in what is possibly a primary micromeric condition (Gross, 1962). If the arthrodires were assumed to be a monophyletic group, it would be possible to hypothesize that their common ancestor was in a primary micromeric stage. Thus, whatever relationships may be assumed to exist between arthrodires and Recent groups of vertebrates, it is possible to hypothesize that the ancestor common to arthrodires and their nearest Recent relatives (whatever they are) was also in a primary micromeric stage, or a primary naked stage (see also Stensiö, 1969, p. 82). The dermal skeleton of acanthodians has a similar significance, for it appears to be primarily micromeric in all known acanthodians (Ørvig, 1968, p. 387).

For some time it has been fashionable to believe that the dermal bones of the two groups of teleostomes (Sarcopterygii and Actinopterygii in the sense of Nelson, 1969a) have arisen independently from a micromeric stage. This argument is sometimes based on the premises that early dipnoans are primarily micromeric, and that the dipnoans are sarcopterygians. In fact, the relationships of dipnoans are obscure (Jarvik, 1968a), and the interpretation of their dermal skeleton is tenuous. More noteworthy is the similarity in dermal-bone arrangement of primitive sarcopterygians and actinopterygians. If dermal-bone homology between these two groups is assumed (and there is ample justification for doing so), then their common ancestor can be hypothesized to have had a similar macromeric pattern of dermal bones in the region of the head.

The literature pertaining to dermal-bone interpretation is abundant and conflicting. Particularly difficult to interpret have proved to be fishes, both fossil and Recent, which have most or all of the dermal skeleton in the form of small scales or plates. Such forms (among the cephalaspids, anaspids, heterostracans, thelodonts, acanthodians, elasmobranchs, arthrodires, dipnoans, and chondrosteans) often have been considered primarily micromeric by one author and secondarily micromeric by another. Indeed, such disagreement has proved inevitable, for no way has been discovered to distinguish primary micromeric elements

from secondary ones on the basis of their general appearance and structural properties. Indirect types of argument have been proposed to resolve this problem (e.g., by Ørvig, 1968, pp. 385–386), but most, if not all, of them require assumptions of doubtful or at least challengeable validity, insofar as they rest on prior, biased assumptions of ancestor-descendant relationships among organisms of the past.

If it is assumed, however, that dermal bone, when it first appeared in the vertebrates, was in a micromeric pattern, then the principle of parsimony dictates that any given pattern considered micromeric must be hypothesized to be primary. If the interrelationships of the studied species are sufficiently well established, it is conceivable in certain cases that this hypothesis of primary micromerism could be rejected in favor of one found to be more parsimonious, that is, one of secondary micromerism (it should be emphasized that the "relationships" of concern
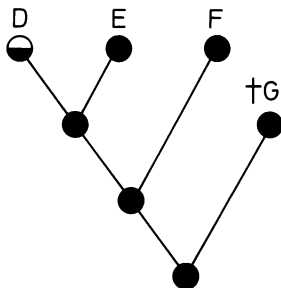

FIG. 19. Diagram illustrating a hypothetical example of secondary micromerism.

here are of the "sister-group," not of the "ancestor-descendant," type). For example, if a species (or group) D, found to be micromeric, were assumed to be related in the manner shown (fig. 19) to species (or groups) E, F, and +G, all found to exhibit a common macromeric pattern, the hypothesis of primary micromerism in D could be rejected with some confidence. Among fishes, the dermal skeleton of the sturgeons and perhaps that of the dipnoans might be, but have not yet been, the subject of argumentation of this type.

From the above considerations follows a comparative theory of the dermal skeleton of vertebrates, summarized in figure 18. In the writer's opinion this theory is the most parsimonious possible, given the assumptions of relationship mentioned above and the present state of information about structure and homology of vertebrate dermal bones. Given other assumptions of relationships, other theories, of course, would be possible. But the outlines of the general picture could hardly be changed materially without radically new conceptions of relationships of Recent

vertebrates. It is unlikely that such conceptions will be forthcoming in the near future. It is to be hoped, however, that the problems of the relationships of the fossil vertebrates, such as ostracoderms and placoderms can be studied in greater depth, so that the full biological significance of what is known of their dermal skeletons can be realized (see also Jarvik, 1968b, p. 523).

It may be added here that the theory outlined above does not depend on any assumptions of ancestor-descendant relationships among organisms of the past or present, but rather it depends upon certain assumptions pertaining to sister-group relationships, particularly those among the groups represented in the Recent fauna. The writer has commented in detail elsewhere on the relative merits of assumptions of these types (Nelson, In press).

SUMMARY

Within the buccopharyngeal cavity of many Recent sharks, there occurs a well-developed dermal skeleton, consisting of numerous, independent, non-growing denticles (placoid scales). It is apparent that the extent of this dermal skeleton, from the jaw margin to the pharyngo-esophageal boundary, is a feature primitive for the Gnathostomata.

Secondary reductions in the extent of this dermal skeleton are apparent in some Recent sharks. In others, pharyngeal denticles participate in the formation of specialized structures (pharyngeal pads), apparently analogous to the consolidated pharyngeal tooth plates of teleostomes.

These observations lead to the hypothesis that the dermal skeleton of modern elasmobranchs is primitively subdivided, that is, in a primary micromeric condition. The relevance of this hypothesis is discussed in the context of a comparative theory of the dermal skeleton of vertebrates.

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