ART. XXXIV.—*The Origin and Significance of Spines: A Study in Evolution;* by CHARLES EMERSON BEECHER.

[Continued from page 268.]

VII. *By repetition.* (B_2.)

UNDER the consideration of spine production by repetition, it is proposed to include local repetition or duplication of spines on or about a primary spine, the limit of this repetition resulting in a generally spinose condition.

It has been shown that intermittent stimulus produces growth, and furthermore that growth can only take place with proper nutrition. Under local stimulus, the currents of the circulation or forces of nutrition are set up in an organism toward the center of stimulation. The nutrient matter is brought to this point, and more or less of it is expended in building up a structure which is the reciprocal or direct resultant of the stimulus.' Now, since all motion is primarily rhythmic,[66] and the repetition of parts an almost universal character among organisms,[5] it would appear that the foregoing conditions would be favorable to the repetition or reproduction of the structures. In this way, it is easy to account for the growth of spines that cannot be explained as the direct result of external stimuli (A), or by any process of decrescence (C, D). The nature of the influence seems to be similar to induction in electrical physics, or to the force or stimulus of example in human conduct.

Stated as a concrete case, a simple spine produced by any primary cause may be taken, and it will be granted that the vital or physiological adjustments produced in its growth and maintenance have brought about or induced an harmonic condition in the adjacent tissues. Subsequent growth will most naturally repeat the previous structures, so that in addition to the primary spine, there will be other smaller spines on or about it, together constituting either a compound spine or a group of spines.

Carrying this repetitionary process to a maximum, there would result a generally spinous condition. As a possible illustration of this, no class of organisms probably exhibits so many kinds and series of repetitions of all sorts of external structures as the Echinodermata, and it is significant that this is a typically spiniferous sub-kingdom.

Except in a few classes of organisms, compound spines are relatively rare as compared with simple spines. They are very common among the Radiolaria, which furnish the greatest complexity occurring anywhere in the organic world. (See Plate

I.) They are also quite frequent among the Echinoidea, but more rare among the Asteroidea and Crinoidea.

Compound antlers are especially characteristic of the modern Deer family, though compound horns are but rarely found elsewhere among the mammals. The Prong-horn Antelope of America is the only living species of hollow-horned ruminant having this character. It, of course, is not intended that extra pairs of horns, which being separate, and often originating on different portions of the skull, should be considered as compound horns in the sense employed here. Likewise compound spines arising through suppression of organs or structures are not to be included here, as the compound thorns on the Honey-locust representing aborted branches.

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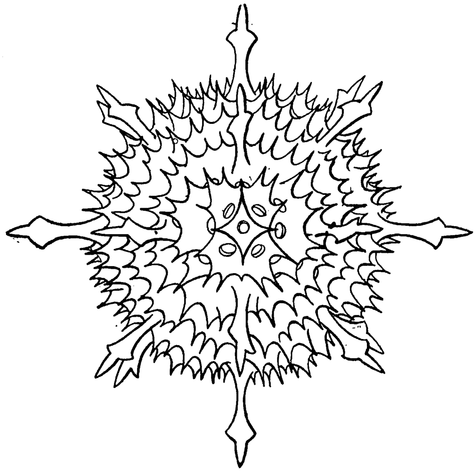

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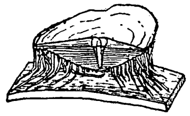

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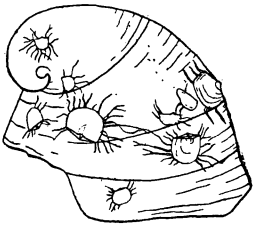

FIGURE 51. *Acontaspis hastata.* A Radiolarian, showing multiplication of spines by repetition. × 200. (After Haeckel.)

FIGURE 52. *Strophalosia keokuk.* An attached Brachiopod, showing the spines extending from the ventral valve to and along the surface of attachment. × 2.

FIGURE 53. A Gastropod shell (*Platyceras*) to which are attached a number of *Strophalosia keokuk.* Natural size.

The fin-spines of fishes are often compound, and sometimes are made up of several elements as in the spines of *Edestus* (*E. vorax*). Quite a number of Mollusca develop compound spines, as in many species of *Spondylus* and *Murex.* They are also not uncommon among the Crustacea and Insecta. Compound spines are infrequent in the Brachiopoda, being developed in but few species (*Spirifer hirtus*[31]). The Foraminifera also present but few examples (*Polymorphina Orbignii*[9]).

A number of generally or highly spinose types will now be noted to illustrate the limits of the repetition of spiny structures, the first spines having probably arisen through the operation of some primary cause, and the derived or secondary spines being produced, it is believed, by the law of repetition.

The Radiolaria have already been frequently mentioned, but as they are the most spiniferous of all classes of animals, and represent the highest degree of spine differentiation attained (figure 51 and Plate I), another brief notice will be of interest. These spines furnish characters of high taxonomic value, although generally speaking they seldom have more than specific importance among other classes. The Echinoidea and Asteroidea must also be noticed in this connection, though from the nature and origin of their spines, they do not conform to the mode of spine growth in other classes.

Productus, *Productella*, *Strophalosia*, *Aulosteges*, and *Siphonotreta* represent highly spinose genera among the Brachiopoda. *Strophalosia* is a form in which the ventral valve is cemented to some object. Whenever the valve rises well above the object of support, the spines are free like those frequently present on the dorsal valve; otherwise the spines extend root-like along the supporting surface (figures 52, 53).

Aulosteges presents a still further tendency to complete spinosity, for not only are both valves covered with spines, but the deltidium also.

Spondylus (figure 30) and *Murex* are well-known types of very spiny forms of Mollusca. *Acidaspis*, *Terataspis*, etc., hold the same place among the Trilobita; *Echidnoceras*, *Lithodes*, etc., among the Decapoda; and the Spiny Box-fish (*Diodon*), Pipe-fish, etc., among the Pisces. The higher animals also furnish examples of extreme spinosity, as in the Horned-Toad (*Phrynosoma*), the genera of Ceratopsidæ, gigantic Cretaceous Dinosaurs, and the Echidna and Porcupine.

All these forms present numerous spines, some of which cannot be explained as having arisen directly from external stimuli, for they are in comparatively well-protected regions out of the way of external stimuli. Neither can all of them serve for offense and defense, as they are often not located in the most advantageous positions; nor are they differentiated out of any previous ornaments or special structures. In fact, no factor of spine genesis except the one of repetition seems to be sufficient to account for their development.

VIII. *Restraint of environment causing suppression of structures.* (C_1.)

The previous categories of spine production (I–VII) have been brought about by some process of growth or concrescence through external and internal agencies. There still remain for discussion the formation of spines by processes of decrescence caused by extrinsic restraint (C), or intrinsic deficiency of growth power (D). The lack of vitality or growth force generally stands so directly as the result of an unfavorable environment, that it is often difficult or impossible to distinguish between their action. Furthermore, as in the case of many parasites, it may be seen that the environment may be quite favorable as regards temperature, nutrition, etc.; but unfavorable in respect to motion and use of sensory and motive organs. From the almost universal degradation and retrogression of parasitic forms, it is necessary to consider these as intrinsically deficient, and therefore lacking in the qualities of growth force which normally favor a progressive evolution. Here, also, there are apparently two intimately associated causes. In an attached animal, the absence of stimulus from disuse of an organ tends toward atrophy, and the retrogressive development serves to affect many organs in the same manner. The direct and indirect results of the restraint of the environment may therefore be expected to shade imperceptibly into each other, with only the extremes sufficiently distinct for separation.

The influence of an unfavorable environment as effecting the character and growth of plants and animals is well shown in desert or arid regions, and the flora has been made the subject of especial study by Henslow.[33] In such regions, the first thing to impress the observer is the small size of the species. Next to diminutive size, the scantiness of life is a striking feature, for large areas are common in which life is almost wanting. An examination of these plants reveals a series of characters not usually present elsewhere, among which may be mentioned the development of a minimum amount of surface, constituting what is known as consolidated vegetation; next their uniform gray color, due either to excessive hairiness or a coating of wax; and lastly, their frequent spinescent characters.

The spines on desert plants are a feature of such general occurrence that it has led to the notion that vegetable spines are always associated with unfavorable conditions and are therefore suppressed structures. This is probably incorrect, for in plants as in animals, spines may be developed by the progressive differentiation of previous structures; as in the angular edges of the leaf-stems of many Palms becoming spiniferous; or, as will be shown, suppressed structures may arise from deficiency of growth force. In all cases, spines may or may not serve for protection. Thus, while they are not always an indication of unfavorable environment, those occurring on desert plants may generally be so considered, for they are developed out of structures which are normally of vital physiological importance.

An animal or plant having spines and living in a favorable environment, involving freedom of motion for animals, and abundance of nutrition without extremes of temperature or dryness for both animals and plants, will, it is believed from the discussions and analyses of spine genesis in its various phases, develop these features in most instances, without the sacrifice of organs and structures having important physiological and motor functions. Thus, ordinarily, among animals it is found that spines arise as excrescences or outgrowths of exoskeletal or epidermal tissues, without seriously affecting the function of the organ or organs upon which they are located. Such cases may clearly belong to the most progressive series, and in fact usually occur there.

On the other hand, if it is found that a leg, a wing, a digit, or other organ is developed into a spine, this is always accomplished by a process of retrogression, resulting in the greater or lesser suppression of the part in question. It is also seen that this kind of spine occurs most frequently in retrogressive series or in others showing arrested development, and the necessary interpretation seems to be either that the environment is or has been unfavorable, at least so far as the particular organ or set of organs is concerned, or that the vital power has declined. Both influences are intimately associated, and the latter is often the direct result of the former.

The stunting effects of aridity and barren soil on our common plants is familiar to all. Among the plants of the desert is found every evidence of similar stunting combined with adaptations to resist the unfavorable conditions of deficient water supply, excess of radiation, etc. The diminution in size applies not only to stature, but to the leaves and branches, especially the parenchymatous tissues or parts of the plant engaged in aëreal assimilation. Consonant with these changes, the drought and other conditions produce a hardening of the mechanical tissues, which is of great aid in resisting the extreme heat and dryness of the desert. Sometimes a deposit of wax affords a similar protection.

The reduction of the leaves takes place in various ways. They may simply become smaller in every dimension and finally be reduced to mere scales, or an aphyllous condition may be established. They may grow narrower and narrower until only the hardened veins or midrib remains; or leaves may be developed only for a short time, and, in the case of compound leaves, after the shedding of the leaflets, a spiniform leaf axis remains, as in *Astragalus Tragacantha*[35] (figures 55, 56). The suppression of branches tends towards the same end;

namely, either to their complete disappearance or to their partial suppression into hard spiniform processes or thorns. Thus, both leaves, branches, and other parts of the plants may become reduced to their axial elements, bringing about what is commonly termed spinescence.

The spiny character of these plants is therefore one of the results of an arid environment, and it may or may not be of sufficient frequency to give an especial character to a particular desert flora. There is, moreover, a secondary influence which has an effect in determining the abundance of spinose plants in desert as well as in many other situations. This relates to the destruction of the edible unarmed species by herbivorous animals, and the comparative immunity of the spiny types. Thus, in old pastures, the prevailing flora is apt to be one that is offensive to grazing animals. This character is generally given by poisonous plants or those having a disagreeable flavor, or by those whose form or spiny structures afford protection.

This secondary influence by grazing animals may have had some effect in determining the particular abundance of spiny plants in certain desert regions, and their comparative infrequency in other similar regions. In either case, the unfavorable environment brings about a suppression of structures, and one type of this action results in the production of spines. These represent the limits of retrogression before the part becomes entirely obsolete.

Wallace has criticised Henslow's views on the origin of xerophilous plants and their distribution. It is believed that the views here offered remove some of the objections, and bring the opinions of these authors into greater accord.

Under arid conditions, bracts, stipules, leaves, and even branches may become spinescent. Some forms in which the spinose character has not as yet become permanently fixed by heredity, when transported or found living in moister and richer soils, develop normal leaves or branches, and lose their spinescence; others, like the Cactus, retain their spines under similar changes; while still others, as *Acanthosicyos horrida*,[33] cannot be artificially cultivated, and have become truly xlerophilous types.

As examples of plants which lose their spines by cultivation, the Pear, species of Rose, Plum, etc. (Henslow), may be cited. According to Henslow,[33] others, as *Onomis spinosa*, have an especially spiny variety (*horrida*) living on sandy sea-shores, while in more favorable natural situations, the same plant becomes much less spiny, and under cultivation loses its spines. M. Lothelier[42] also found that by growing the Barberry (*Berberis vulgaris*) in moist air, the spines disappeared, the parenchyma of the leaves being well formed between the ribs and veins. Dry atmosphere and intense light both favored the production of spines.

Henslow[33] cites the genus *Zilla* as a desert plant in which the branches are transformed into spines, *Echinops* for a similar modification of the foliage, *Fagonia* for spiniform stipules, and *Centaurea* for spinescent bracts. As further illustrations taken not only from desert plants but also from others commonly found in dry, rocky, or unfertile situations, the following examples may be taken, some of which are familiar cultivated species. The stunting of branches into spines is common among neglected Pear and Plum trees, and is a normal character in the Hawthorn, Honey-locust, *Cytisus* (figure 54), *Vella*, etc. Leaves transformed into spines are characteristic of the Cactaceæ of America, the columnar Euphorbiaceæ of Africa and southern Asia, and are also familiar in the half-shrubby Tragacanth bushes (figures 55, 56) so common in southern Europe, especially in the eastern portion, and in the ordinary Barberry (figure 13). Spiniform stipules are usually present in the species of *Robinia*, of which the Common Locust (*Robinia pseudacacia*) furnishes a well-known illustration (figure 57). Spiniform bracts are best known among the Thistles (*Cirsium lanceolatum*, *C. horridulum*, etc.).

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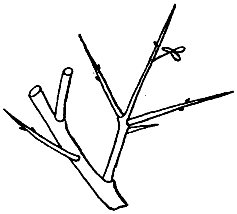

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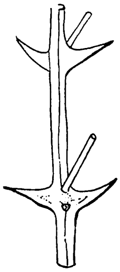

FIGURE 54. The spiny *Cytisus* (*C. spinosus*), showing suppression of branches into spines. (After Kerner.)

FIGURE 55. A single leaf of Tragacanth (*Astragalus Tragacantha*) from which the three upper leaflets have fallen. (After Kerner.)

FIGURE 56. Leaf axis of the same, from which all the leaflets have fallen. (After Kerner.)

FIGURE 57. Twig of Common Locust (*Robinia pseudacacia*), showing spines representing stipules.

As the restraint of an environment acting on an animal so generally results in the disuse and atrophy of the organs affected, most cases will have to be considered under the head of disuse. Therefore, while the environment is the primary factor, its influences are mainly exhibited through secondary or resultant conditions. In some cases, however, it is possible to interpret a vestigial or suppressed structure directly into terms of an unfavorable environment. Thus, if the probable origin of the vestigial hind legs of a Python is considered, it leads to the belief that they represent legs which were of functional importance to some of the early ancestors of this snake. The gradual elongation of the body and the consequent change from a walking or direct crawling habit to a mode of progression chiefly by horizontal undulations, necessarily brought the legs into a relation with the environment which was unfavorable either for their function or growth. Their suppression is complete in most snakes, but in the Python, the hind legs are represented by two spurs or spines (figure 58). On the interior of the body they are supported by vestiges of femora and ilia, showing their true affinities with hind limbs. Some snake-like Batrachians (as *Amphiuma* and *Proteus*) still retain short and weak external limbs. These would undoubtedly soon be lost by a change from aquatic to terrestrial or arboreal habits.

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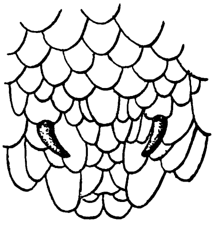

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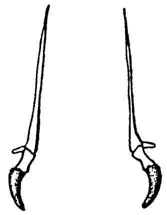


FIGURE 58. Portion of skin of Python, showing the spurs which represent the suppressed or vestigial hind legs. × $\frac{1}{8}$. (After Romanes.)

FIGURE 59. Bones of suppressed legs of Python. All but the claw-like termination are internal. × $\frac{1}{8}$. (After Romanes.)

In explanation of the nodes and spiniform processes on the epitheca of *Michelinia favosa*, it may be suggested that they represent aborted corallites, or attempts at budding. This coral belongs to the order Porifera, which has been shown by the writer[7] to have very pronounced tendencies toward proliferation, and on the interior of the colony, these attempts result in the production of mural pores. Most of the species of *Michelinia* are hemispherical or spherical. *M. favosa* is inclined to be pyriform in shape, rising above the object of support, and thus presenting a rather large epithecal surface. Manifestly the lower side of the corallum is unfavorably situated for the growth of corallites, and any efforts at proliferation on the part of the peripheral corallites is apt to result in stunted outgrowths. There is here a very close connection between restraint of environment and deficiency of growth force. If the whole corallum is taken into consideration, the restraint of the environment may be taken as preventing the growth of corallites on the lower side. If one of these single stunted corallites is considered, it may be said that the deficiency of growth force through lack of nutrition caused its suppression.

IX. *Mechanical restraint.* (C_2.)

Among the factors of spine genesis, mechanical restraint is probably of the least importance. It can only rarely happen that an organism is forced to grow a spine contrary to the natural tendencies of normal development. Yet as there are occasional types of spiniform structures which can best be explained as due to the mechanical restraint of the environment, it is necessary to notice them in order to make the categories of origin as complete as possible.

The illustrations will be taken chiefly from the Brachiopoda and Trilobita. The recent Brachiopod *Mühlfeldtia truncata* is semi-elliptical in outline, and has a very short stout pedicle which holds the shell so closely to the object of support that the beak is truncated from abrasion and resorption. In specimens attached to a small branch of a coral, thus allowing the cardinal extremities of the shell to project beyond the object of support, the ends of the hinge are generally rounded. Specimens growing on a large flat surface have the cardinal extremities angular or submucronate. Similar variations are to be observed in other living species of Brachiopods (*Cistella*, some *Dallina*, etc.). Some of the extinct genera show more highly developed cardinal extremities which are often very characteristic of certain species, though considerable variation is found to exist. It is evident that these elongated hinge lines have arisen from the mechanical necessities of a functional hinge, and their greater or less extent is also to a degree dependent upon the nature of the object of support which furnishes a stimulus to the growing ends of the hinge. A marked example is shown in *Spirifer mucronatus*, with the cardinal angles extended into spiniform processes (figure 60). Similar features are presented by many other species of *Spirifer*, *Orthis*, *Leptæna*, *Stropheodonta*, etc.

60.

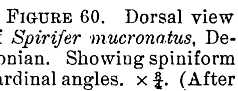
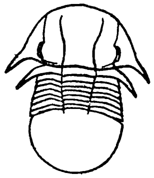


FIGURE 60. Dorsal view of *Spirifer mucronatus*, Devonian. Showing spiniform cardinal angles. × ⅔. (After Hall and Clarke.)

In the Trilobites, the pygidium, or abdominal portion, consists of a number of consolidated segments, and the segments of the thorax are successively added in front of this tail piece. The first thoracic segment is therefore formed between the cephalon and pygidium, and its form is mechanically in agreement with the requirements of the animal for bending the body, and with the adjacent margins of the cephalon and pygidium. In a way, it may be said that the segment is moulded by the adjacent parts, and may therefore take its form from the cephalon (figure 61), or from the pygidium, as in the examples following:

61



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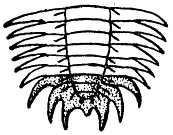

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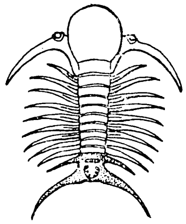

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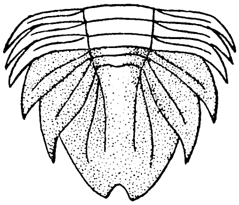

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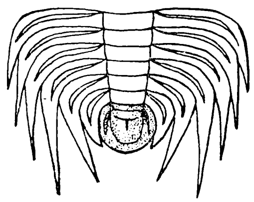

FIGURE 61. *Illænus* (*Octillænus*) *Hisingeri*, Ordovician, Bohemia. A Trilobite showing spiniform pleural extremities of first thoracic segment, corresponding to the genal spines of the cephalon. × ¾. (After Barrande[4].)

FIGURE 62. *Cheirurus insignis*, Silurian, Bohemia. Pygidium and six thoracic segments. × ¾. (After Barrande.)

FIGURE 63. *Deiphon Forbesi*, Silurian, Bohemia. Entire specimen showing spiniform pleural of segments corresponding in direction to those of the pygidium. (After Barrande.)

FIGURE 64. *Lichas scabra*, Silurian, Bohemia. Pygidium with three thoracic segments, showing spiniform ends of pleura. × ¾. (After Barrande.)

FIGURE 65. *Paradoxides spinosus*, Cambrian, Bohemia. Pygidium and six free segments. × ¾. (After Barrande.)

During growth, the new segments are added in front of the anal segment, so that after the number of abdominal segments is complete the thorax is increased by the successive addition of what in earlier moults were pygidial segments. By this means, the pygidium generally controls or determines the character of the segments of the thorax. If the pleura of the pygidium are extended into spiniform processes, the pleural ends of the segments are also spiniform, as in *Lichas* (figure 64), *Ceraurus*, *Cheirurus* (figure 62), *Deiphon* (figure 63), *Acidaspis*, *Dindymene*, etc.

Likewise, if the pleura or their distal ends are directed posteriorly nearly parallel to the axis, the mechanical necessities of motion require that the portions of the free segments pointing backward should be free, thus making the ends of the thoracic pleura generally appear as retrally curved spiniform extensions. Extreme examples of retrally directed pleura accompanied by small pygidia are shown in *Paradoxides* (figure 65), *Holmia*, *Olenellus*, *Elliptocephala*, etc. Genera having the ends only of the pleura directed backward are generally less inclined to form spiniform terminations. In contrast with these, it is found that all the Trilobites having the pleura directed outwards and with entire pygidial margins, do not ordinarily develop long pleural spines; as *Asaphus*, *Illænus*, *Agnostus*, *Phacops*, *Calymene*, etc.

The examples of the caterpillars of moths belonging to the Schizuræ, described by Packard[54] as mimicking the serrations of the leaves upon which they feed, have previously been noticed in this essay, under the head of mimetic influences. The initial cause of the spines may possibly be explained as in part due to the mechanical conditions. During their early existence the larvæ feed on the lower side of the leaves, and have no spines. Later they feed on the edges of the leaves, and at the same time acquire dorsal spines. The conformation of the animal to the serrated edge of the leaf would produce corresponding elevations and depressions on the back. The location of these would be fairly constant from the habit of the animal of feeding chiefly between the denser leaf veins which determine and terminate the serrations. The raised parts of the animal would receive the greatest amount of stimuli, and at these points spines would naturally appear.

The processes producing the spines noticed in this category (IX) are classed with others under decrescence, for the reason that the growth is restrained or controlled by mechanical necessities. If the restraint were absent, it is probable that a more expansive growth would take place or that other structures would be correspondingly benefited.

X. *Disuse.* (C_3, D_2).

In causing the reduction or atrophy of an organ, the effects of disuse have generally been recognized by most observers. In this way, the origin of many of the so-called "rudimentary organs" has been satisfactorily explained by Darwin[14] and others. Two classes of structures are evidently comprised within the common definition of rudimentary organs, namely, nascent and vestigial organs.

Nascent structures indicate the beginnings or initial stages of organs, while vestigial structures are the remnants left after the functional suppression of organs. The suppression is usually caused by unfavorable conditions or by disuse, which produce either a retardation of growth or a retrogressive development. In both cases, the results are similar. By retardation, an organ is prevented or restrained from functional development and is therefore useless as a normal organ. By retrogression, an organ gradually reverts to an initial type, loses its function, and becomes a vestigial structure. In most instances, a change of food or habit, or the substitution of a new and functionally higher structure, causes the disuse of some organ, which, under previous conditions, was of use to the animal.

Nascent structures, or the beginnings of organs, are generally made up of active tissues that only require stimulus and nutrition to perfect their function. On the other hand, suppressed or vestigial structures are composed of comparatively inert tissue and are in consequence largely made of the mechanical elements of secretion of the organism. It may therefore be considered that true rudimentary or nascent organs are potentially active, and suppressed structures are inert. It is with the latter class, the inert, that a study of spine genesis by atrophy is chiefly concerned.

The gradual loss of function through disuse, and the consequent loss of nutrition with the concomitant rapid decrescence of active tissues, brings about a change in the ratio of active and inert structures. The progression of this process naturally results in the production of a structure having a maximum of inert or mechanical tissues, and a minimum of active constituents. Moreover, it has already been shown that the axial elements are the most persistent, and therefore the last to disappear; also that the peripheral appendages and outgrowths of any organ first show the action of decrescence. Evidently, the conditions here described are favorable for the production of spines out of an organ primarily possessing distinct active functions. The axis of an organ gives the necessary form, and the hard tissue the structure, so that the whole will conform to the definition of a spine given early in this paper; namely, a stiff, sharp-pointed process.

The restraint of the environment was found to be one cause for decrescence of organs. Another, which is properly the subject matter of the present section, is disuse; and lastly, it will be seen how the deficiency of growth force may bring a similar suppression of structures.

There is considerable difficulty in selecting particular examples which will conform clearly to the strict requirements of these three categories. In a certain sense, some of the examples of spines produced by decrescence may belong to more than one category. However it does not prevent the acceptance of any one of the three as primary causes. Thus, it may be urged that disuse has caused the atrophy of leaves into spines among many desert plants, or produced a similar reduction of the limbs in a Python. While this may be true from one point of view, yet the manifest unfavorableness of the evironment in both, seems to be a sufficient reason for making it the primary factor. On the other hand, many parasites showing similar atrophies are not dependent upon a large number of active organs for their food and maintenance. After finding a host, an abundance of food is at hand, and the environment may be considered a favorable one. All the organs, except those of nutrition and reproduction, then become more or less useless and dwindle away, leaving vestigial organs, or disappearing altogether. Furthermore, a change of habit, as from climbing to flying, will necessarily cause the atrophy of some of the structures used for climbing, and the hypertrophy of others for flying.

Most of the examples illustrating the production of a spine through the atrophy of an organ by disuse are to be found in the legs and digits of animals. The process bears considerable resemblance to the formation of spines on many plants by the suppression of leaves, branches, etc. They will be noticed here, although properly these vestigial structures among animals are more strictly of the nature of claws, or at the most, spurs.

Many parasitic plants, especially among the Balanophoreæ, are reduced to a simple stem bearing the inflorescence. The leaves are represented by scales which are often spiniform, though seldom of sufficient stiffness to entitle them to be called spines. In desert plants, many of which have a similar type of growth, the hardening of the mechanical tissues by the effects of drought has converted similar leaf structures into spines, while the parasitic plants are not normally subjected to such continuous dryness and extreme heat, and therefore the mechanical tissues seldom become hardened.

Parasitic animals, especially among the Crustacea and insects, often show a reduction in the number of joints in the legs, and even in the number of limbs themselves. The terminal claws generally persist, and are sometimes longer than the rest of the leg; as in the Itch mite, *Sarcoptes Scabei*, and in the female of the parasitic Copepod *Lernæascus nematoxys* (figure 66).

Among many aquatic Crustacea and Limuloids, the specialization and seggregation of the ambulatory and swimming appendages towards the head or anterior regions of the body have produced a corresponding suppression of appendages on or near the extremity of the abdomen. This statement of fact is the basis of the principle of cephalization of Dana,[12] who applies it especially to the Crustacea, as follows: "There is in general, with the rising grade, an abbreviation relatively of the abdomen, an abbreviation also of the cephalothorax and of the antennæ and other cephalic organs, and a compacting of the structure before and behind; a change in the abdomen from an organ of great size and power and chief reliance in locomotion, to one of diminutive size, and no locomotive power." Audouin's law that among the Articulata, one part is developed at the expense of another, may be also noticed here as affording a further explanation of the suppression of the posterior appendages correlativê with the greater development of the parts anterior to them. In a Crustacean using its tail for propulsion, as the Lobster (*Homarus*), the telson is broad and flat, and the adjacent segment has a similar development of the appendages. In other forms, as the Horse-Shoe Crab (*Limulus*) and the Phyllocarids, the tail is not used for propulsion, and at best serves chiefly as a rudder, while some of the legs on the anterior part of the abdomen or on the thorax are large and strong and are often provided with paddles. These groups, the Limuloids and Phyllocarids, show a greater or less suppression of the last abdominal appendages, and in many genera, the body terminates in a spiniform telson or tail spine. The process of suppression may or may not result in a spine. In the crabs, the abbreviated abdomen is folded under the cephalothorax, and in *Lepidurus* and *Pterygotus* the telson is a scale or plate-like organ. For the most part, however, the abbreviation of the abdomen and the suppression of its appendages have reduced the telson to a spine, as in *Limulus* (figure 67), *Eurypterus*, *Stylonurus*, and *Prestwichia* among Limuloids; and *Olenellus* among the Trilobites. In addition to a telson spine, the Phyllocarids have two lateral spiniform cercopods, the three spines together constituting the post-abdomen, as in *Ceratiocaris*, *Echinocaris* (figure 68), *Mesothyra*, etc.

Although the last abdominal segments of the Horse-Shoe Crab have lost their appendages and show evidences of suppression, yet the tail spine is a large and useful organ, for it is of just the proper length to enable the animal to right itself after being overturned, which it is unable to do with its feet alone. The process of natural selection has doubtless in this way contributed to the development and retention of the long spine. This use cannot be ascribed to the tail spines of the Phyllocarids, though they evidently were important aids in directing movement, and also offered some degree of protection.

The terminal claws on the phalanges of the wings of some birds are nearly all that remains of the external fingers, or digits. In the Hoactzin of South America (*Opisthocomus cristatus*), the young bird has a thumb and index finger, both provided with claws, and climbs about much like a quadruped, using its feet, fingered wings, and beak. According to Lucas,[43] a rapid change "takes place in the fore limb during the growth of the bird, by which the hand of the nestling, with its well-developed, well-clawed fingers, becomes the clawless wing of the old bird with its abortive outer finger." Similar claws or spurs occur on a number of other birds, some having functional wings, as in the example just described, and others having only vestiges of wings, as in the Wingless Bird of New Zealand (*Apteryx*, figure 69).

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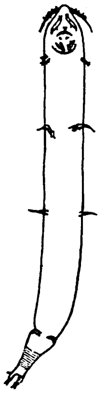

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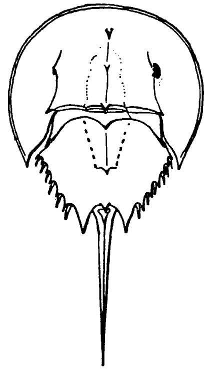

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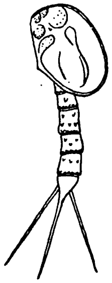

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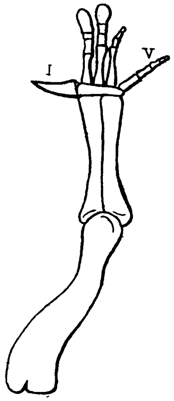


FIGURE 66. Female of *Lernæascus nematoxys.* A parasitic Copepod, showing suppression of limbs. Enlarged. (After Claus.)

FIGURE 67. Horse-Shoe Crab, *Limulus polyphemus*, showing telson spine and abbreviated abdomen. Reduced.

FIGURE 68. A Devonian Phyllocarid, *Echinocaris socialis*, showing spiniform telson and cercopods.

FIGURE 69. Wing of *Apteryx australis.* × $\frac{1}{8}$. (After Romanes.)

FIGURE 70. Skeleton of right fore limb of the Jurassic Dinosaur, *Iguanodon bernissartensis*, showing suppressed first digit. × $\frac{1}{30}$. (After Dollo.[16])

Another example may be taken from the Dinosaurian Reptiles. The Jurassic genus *Iguanodon*, from England and Belgium, belongs to a group (Ornithopoda) in which the number of functional digits varies from three to five in the manus, and from three to four in the hind feet. In this genus, the hind foot had three functional toes, representing the second, third, and fourth of a normal pentadactyl foot. The first is represented by a slender tarsal bone alone, while the fifth is completely suppressed. The manus, or fore foot, of this animal shows the second, third, fourth, and fifth digits of functional importance as digits, while the first is shortened and atrophied to the condition of a stout spur, standing out at right angles to the axis of the leg, as shown in figure 70. The fore legs of *Iguanodon* and others of the same order were short, and apparently used more for prehension than locomotion, and in *Iguanodon*, the suppression of the pollex, or thumb, into a spur doubtless provided the animal with a powerful weapon. Here is seen the suppression of a digit by loss of normal function, resulting in a protective structure of considerable value.

XI. *Intrinsic suppression of structures and functions.* (D_1.)

The most obvious and direct relationship between an unfavorable environment and the suppression of structures to form spines was afforded by desert plants. In illustration of the intrinsic suppression of structures by deficiency of growth force, the vegetable kingdom again seems to offer the clearest evidences of a like relation between cause and effect. Instead, however, of taking an unfavorable environment, in the present instance a favorable environment must be assumed, and then a type which expresses in various ways its deficiency of growth force must be sought.

In the desert plants, it was found that no single family exclusively constituted the desert flora, but that a considerable variety of types were present, and that some of these belonged to perfectly normal families commonly living under ordinary favorable conditions. Moreover, it was evident that there were certain types of form and habits of growth which were especially characteristic of plants living in desert or similar unfavorable regions. Therefore, to illustrate clearly intrinsic restraint or suppression of structures, it will be necessary to take an environment which, in most respects, may be considered as favorable, and also a type of plant life presenting evidences of a deficiency of growth force.

The great groups of plants commonly known as brambles and climbing plants appear to meet most of the requirements. They abound in regions where the greatest luxuriance of vegetation is found, and are therefore chiefly characteristic of the tropics. Kerner[38] estimates that there are two thousand species of the true climbing plants in the torrid zone, and about two hundred in temperate regions. Tropical America has the largest number of species, the flora of Brazil and the Antilles being especially rich. In the sombre depths of the tropical forest, the climbing plants, or "lianes," are not so abundant as in the open glades and along the edge of the forest, where the amount of light is greater and the conditions of existence more favorable. As far as richness of soil, amount of light, and degree of temperature are concerned, it must be admitted that their environment is as favorable as that of any of the associated plants having different habits of growth. The difference between the strong and erect plants and the comparatively weak and climbing forms is therefore not an extraneous one. It resides within the plant structures themselves, and is an intrinsic character or an expression of hereditary vital forces.

The law of recapitulation demands that each individual during its development shall pass through an epitome or recapitulation of its ancestral history. In view of the fact that the young seedlings of climbing plants and brambles have the erect form and proportions of normal erect foliage stems, it is safe to infer that they have been derived from erect forms. Further evidence is afforded from the absence of climbing plants in the earlier terrestrial floras. It is obvious, therefore, that they have been developed out of erect forms by a process of degradation.

The next striking feature to be noticed in climbing plants is their extreme slenderness, due to the general suppression of the plant body. They may attain lengths not reached by the highest trees, and yet the diameter of the trunk is but a minute fraction of the length. The Climbing Palm, or Ratan, has stems of great length and tenuity. It has been stated that stems two hundred meters long have been observed having a uniform thickness of only from two to four centimeters.[38] The diameter of such a stem would be only one or two ten-thousandths of its length. The length of the internodes is another conspicuous character in climbing plants, and both this and the slenderness of the stems suggest the results obtained by growing ordinary plants in the dark, where the conditions are adverse to increased vitality.

The transfer of function from one part of the plant to another, usually by a process of retrogression or degradation, is also very common. The first growth above the ground is a leafy stalk. Later, after the plant has attained a considerable height, the lower portion puts out quantities of rootlets and loses its foliage. The rootlets may be mere dry threads or points of support for the stem ; or, if they happen to encounter a crevice containing soil, they develop into true absorbent organs. In others, the ends of the growing stems or any point on the stems, upon reaching the earth, may put out vigorous roots. These facts seem to show a lack of positive differentiation throughout the plant, which admits of the substitution of a lower structure for a higher, by the suppression of a higher function.

Lastly, the general spininess of climbing plants and brambles is a well-known and conspicuous character. Kerner[38] says that "most, if not all, plants which weave into the thicket of other plants are equipped with barbed spines, prickles and bristles." These spiniform processes seem to fall naturally into two classes. First, those produced by the suppression of stipules, leaves, petioles, branches, etc., and second, those appearing as simple eruptions on the surface.

71 72 73

FIGURE 71. Leaf of Ratan, *Dæmonorops hygrophilus.* Reduced. (After Kerner.)
FIGURE 72. Leaf of Ratan, *Desmoncus polyacanthus.* Reduced. (After Kerner.)
FIGURE 73. Bramble, *Rubus squarrosus.* Reduced. (After Kerner.)

The suppression of normal plant organs into special structures, as tendrils and claspers, is extremely common, and, as already shown, this process if carried far enough without complete suppression will favor the production of a spiniform growth representing the axial elements of the organs. The classes of organs thus affected are practically the same as those in desert plants, though varying somewhat in manner and degree. The consolidated type of plant body is naturally absent, for, in this respect, the diffuseness of climbing plants is quite antithetical. It does not seem necessary to give a long list of examples among the climbers, illustrating the suppression of organs into spines. Although apparently not of rare occurrence, spines produced in this way are not as common as among desert plants. Two figures of the pinnate leaves of Ratan are introduced here to show the suppression of a number of the terminal leaflets into spines (figures 71, 72). In *Machærium* the stipules are converted into thorns.[62] A tropical *Bigonia* (*B. argyro-violacea*) has normal full-sized simple leaves, and suppressed leaves bearing two opposite leaflets on one stalk, and ending "in a structure which divides into three limbs, with pointed hooked claws, and which is not unlike the foot of a bird of prey."[38]

By far the greater number of spines on climbing plants are of the nature of prickles, and are not produced by the suppression of any particular organ or organs, but appear usually without any very definite order. They represent outgrowths of the superficial layers, and hypertrophied plant hairs, or trichomes. The cause of these cortical eruptions is not clear, although they seem to be intimately connected with the general suppression of the plant body. They are therefore a secondary and not a direct result of suppression. Bailey[2] asserts that, "probably the greater number of spinous processes will be found to be the *residua* following the contraction of the plant body." This connection is very apparent in the consideration of the suppression or contraction of various plant organs, but is less obvious when applied to the surface of the whole plant, though doubtless it is the true explanation. In continuation of this idea, it may be suggested that the prickles represent aborted attempts on the part of the plant, through hereditary influences, to recover its former normal proportions. Or, they may exhibit the action of the law of repetition acting in an organism where the initial cause of spine production is the intrinsic suppression of such structures as leaves, petioles, stipules, etc. The subsequent repetition of spines on other parts of the organism results in a series of homoplastic spines which are not homologous with those first formed.

The prickles on climbing plants and brambles may often serve for purposes of protection (D_3), and enable the plant to cling to a support, but these utilitarian properties cannot be considered as an initial cause. Natural selection, also, probably has fostered the development of certain types of spiny climbers and the production of adaptive characters. Nevertheless, in studying these forms, it is necessary to revert to the original consideration of the localized suppression of normal plant structures, and to the general suppression of the plant body as affording a more primary conception of the causes and modes of spine growth among climbing plants.

In many cases of retrogressive series of animals, there seems to be a close parallelism with some of the characters observed among the climbing plants. If the Ammonite family during the Cretaceous, or near the close of the Mesozoic, is taken as an example, it cannot be said that the environment of these old age or pathologic series is unfavorable in respect to food temperature, etc., for with them are associated many vigorous progressive series of other organisms. Neither can it be said, that in many cases the animals perished on account of over-specialization, though this was evidently the cause of the extinction of a large number. The return to a condition of second childhood in old age cannot be called a progressive specialization, since it clearly points to a deficiency of growth force.

Old age types, or phylogerontic forms, among animals may show the same attenuation or suppression of the body as do climbing plants. Thus, *Baculites*, considered by Hyatt as a typical phylogerontic type, has a very attenuate shell, and some species, after attaining a certain diameter, cease to increase in any direction except length. On account of being a chambered shell, it is manifest that the growth of the animal must have practically ceased, while its secretive activities were continued and confined largely to lengthening the shell. Other related genera of Cephalopods show a similar attenuation of the shell, evincing a stoppage of growth in the animal. Among the Mollusca, it seems quite likely that attenuation of form often accompanies decreased growth power.

The pathologic varieties of the Steinheim *Planorbis*, as described by Hyatt,[35] or of the recent *Planorbis complanatus* described by Piré,[57] are further illustrations of this attenuation accompanying the uncoiling of the shell. The sedentary *Magilus*, immersed in its coral host, is also an example, for not only does the shell cease to increase in diameter, but the whole interior, except a small cavity at the end, is filled with a solid deposit of lime. Similar examples could be multiplied indefinitely. Since, however, but few of them are spiniferous, their consideration does not properly come within the scope of the present discussion, though, as is well known, some of the attenuate forms often enlarge and contract periodically, such enlargements frequently leaving prominent laminæ or nodes that are sometimes differentiated into spines. They suggest the observations on growth, senescence, and rejuvenation, made by Minot,[48] who showed that in guinea pigs from a very early age, the increments of growth are in a steadily decreasing ratio to the increase of weight of the animal. This led to the general conclusion, that the whole life of an individual is a process of senescence or growing old.

Spines arising by a real pathologic or diseased condition of the individual can have little or no effect in producing a normal spiniferous variety or species. However, some note should be taken of them, especially as they may be congenital, and thus appear through several generations. In the human species, the peculiar skin-disease known as ichthyosis sometimes produces spiniform excrescences, and the victims are commonly called "porcupine-men." The most celebrated instance was the Lambert family. Haeckel[27] gives the following account of this family: "Edward Lambert, born in 1707, was remarkable for a most unusual and monstrous formation of the skin. His whole body was covered with a horny substance, about an inch thick, which rose in the form of numerous thorn-shaped and scale-like processes, more than an inch long. This monstrous formation of the outer skin, or epidermis, was transmitted by Lambert to his sons and grandsons, but not to his granddaughters. The transmission in this instance remained in the male line, as is often the case." Other similar examples are cited by Gould and Pyle,[21] and the disease is described as "a morbid development of the papillæ and thickening of the epidermic lamellæ."

CATEGORIES OF INTERPRETATION.

Having thus far examined the factors governing the origin of spines, and found that they could be grouped into a number of distinct categories, it is now desirable to interpret these results, and endeavor to arrive at the real significance of the spinose condition.

The two main generalizations which will be discussed are, first, that spinosity represents the limit of morphological variation, and second, it indicates the decline or paracme of vitality.

Spinosity a Limit to Variation.

A number of data have already been given, leading to the belief that, on becoming spinose, organisms have reached a limit of morphological variation. They may continue to develop more and more differentiated and compound spines, but no new types evolve out of such a stock.

The subject may be treated in two ways, both leading to the same conclusion. First, the stages and processes involved in the growth of a spine itself may be studied, and next the development of spines in the ontogenies and phylogenies of animals and plants may be examined.

The growth of a spine has already been described, and it was shown that this type of growth may arise from specialization of other ornamental features, such as nodes, ridges, and lamellæ, and also from the decadence of leaves, legs, etc. These observations and numberless others which could be made will be sufficient to show that almost any kind of superficial structure, as knobs, tubercles, ridges, laminæ, reticulations, etc., has by differential growth been changed into spines; also, that organs of various kinds, as legs, branches, leaves, etc., have by atrophy been reduced to spines. In each case, the parts in their development pass through the various intermediate stages, and clearly show that the spine is a result and not a mean. Moreover, none of these structures or organs is developed through the contrary process; namely, that of beginning with spines and passing through stages corresponding to laminæ, ridges, tubercles, etc. The spine is the limit, and out of it no further structure is formed.

It is necessary to make some mention here of the movable spines of Echinoderms, which appear to form an exception to the foregoing statements. There seems to be no doubt that the fixed and movable spines, the pedicillariæ, the paxillæ, and the spheridia are homologous structures, and that all begin as spiniform skeletal outgrowths, which by subsequent growth and modification produce the structures mentioned (Agassiz[1]). The echinoderm skeleton, including spines, etc., is deposited in the midst of living tissue, and in the case of the spines cannot be directly correlated with the spines of other classes of organisms, which are either very deficient in vitality or are dead structures as soon as completed. After the movable spines of echinoderms are fully developed, the living portion is often confined to the base, and the shaft becomes simply a dead structure upon which encrusting organisms may find lodgement, a condition seldom occurring in the living spines. These finished spines never develop into anything else, and are the structures which conform to the present discussion. The embryonic condition of the spines and pedicillariæ shows that they are really more internal than external structures, and therefore remain under the full control of the ordinary processes of growth, resorption, and modification by living tissues. Furthermore, the movable spines are of such functional importance that no close homologies can be made with ordinary spines found in other classes of organisms.

In tracing the ontogeny of a spinose form, it has been found (pp. 14–17) that each species at the beginning was plain and simple, and at some later period, spines were gradually developed according to a definite sequence of stages. Usually after the maturity of the organism, the spines reach their greatest perfection, and in old age, there is first an over-production or extravagant differentiation followed by a decline of spinous growth, and ending in extreme senility with their total absence.

There are abundant reasons for believing that the radicles of groups are undifferentiated and inornate, and whenever a class has had a long existence, it has been by the continuance of such radical types or by the development of secondary or tertiary radicles, which, though differing in internal characters, still retain a primitive simplicity in superficial features. The early stages of ontogeny of any form should agree with the radical stock, and, as already noted, these stages are simple. Hyatt[34] says on this point: "the evidence is very strong that there is a limit to the progressive complications which may take place in any type, beyond which it can only proceed by reversing the process, and retrograding. At the same time, however, the evidence is equally strong that there are such things as types which remain comparatively simple, or do not progress to the same degree as others of their own group. Among Nautiloidea and Ammonoidea these are the radicle or generator types. No case has yet been found of a highly complicated, specialized type, with a long line of descendants traceable to it as the radicle, except the progressive; and all our examples of radicles are taken from lower, simpler forms; and these radicle types are longer-lived, more persistent and less changeable in time than their descendants."

A few examples will now be taken from the life histories of large groups. In the Brachiopods, the order Protremata, containing most of the spinose forms, has 4 genera and 22 species in the Cambrian of America, 20 genera and 173 species in the Ordovician, and 30 genera in the Silurian. "Then began a steady decline, with extinction in the Carboniferous of North America. In the Triassic of Europe this order is sparingly represented by small species, and is there essentially restricted to the family Thecidiidæ, which continues to have living representatives in the Mediterranean Sea" (Schuchert[64]). The superfamily Strophomenacea of this order is the longest lived and excelled in amount of specific differentiation, there being 608 species in North America alone (Schuchert). In this superfamily the early families and genera were without spines, it being only when *Chonetes* is reached that the first spines are found in the order. In this genus, they are along the hinge, and seem to make up for the weak and obsolescent pedicle. Greater spine growth occurs in the genera *Productella* and *Productus*, where, in extreme cases, the surfaces of both valves are thickly studded. During the Carboniferous, the spiny Productii attained their maximum both in number, length of spines, and in individual size, for here occur the largest species of all Brachiopods. This was the climax. The Permian genera are chiefly degenerate forms (*Aulosteges*, *Strophalosia*), and with the close of the Paleozoic, the family Productidæ became extinct. The order Protremata, to which this family belongs, likewise underwent a rapid decline, and only two simple types continued on into the Mesozoic, while but one declining representative is living at the present time.

Among the Ammonites, the chief spiny forms are those occurring just before the final extinction of the group and representing the beginning of the decline of the order (*Crioceras*, *Toxoceras*, *Ancyloceras*, *Hamites*, etc.). In the Dinosaurian Reptiles, the great horned forms, *Triceratops*, *Torosaurus*,[39] etc., mark the extinction of the entire order. The great horned mammals of the Eocene, the Dinocerata, have left no descendants, and the giant Brontotheridæ, after undergoing various horn modifications through the Miocene, continued no further.

It is not desirable, however, to convey the impression that the spines or horns are alone responsible for this wholesale extinction. It has been shown that they are undoubtedly often an expression of extreme specialization, and generally they represent the limits to which superficial structures may be differentiated. Although there may be other expressions for similar conditions, yet the presence of spines is one, if not the most evident, marker of the attainment of these limits. The presence of a spine on an organ or part indicates the limit of progression or regression of that part or organ. If the spinose condition is general, or if it dominates important functions, it then indicates the limit of progression and regression of the organism.

Spinosity the Paracme of Vitality.

The physiological interpretation of spinosity is a correlative of the morphological aspect of the same condition, and, as it was found that spinosity was a limit to morphological progress or regress, it will now be shown that it also indicates the paracme or decline of physiological progress. Both inferences are drawn from the individual or ontogenetic standpoint, as well as from the racial or phylogenetic.

In the spinose individual, the decline of vitality has been studied by Geddes[20] in thorny plants. He concludes that they show a "gradual death from point backwards (i. e. *ebbing vitality*)." The requisite evidence is afforded in the experience of gardeners who generally consider spiny plants as "always given to die back," or as otherwise expressed, they "often prune themselves." It is difficult to adduce the same kind of evidence among animals, though there may be some degree of semblance between this self-pruning of spiniferous plants and the growth, death, and shedding of the antlers of the modern Deer. Stronger evidence of the relations of spinosity to the organism is afforded in the consideration of spines as consisting wholly of the mechanical tissues. They are more or less dead structures and are usually without special physiological function. Hence, in so far as the whole or a part of an organism is spinose, it represents the ratio between the mechanical and active tissues, or between the inert and living structures.

Morris[49] correlates the mechanical and motor defenses of animals and plants in a matter bearing upon this subject as follows: "If we examine the whole range of the animal kingdom, we find every phase of combination of mechanical and motor defense, the motion growing more sluggish as the defensive armor grows more efficient. But in the whole kingdom, motion persists as one of the defensive agencies. No animal exists without some power of motion, by whose aid it withdraws or otherwise escapes from danger." He also notes that the plant kingdom, with the exception of the minute, swimming forms, possesses no defensive motion, and that mechanical defense alone exists. Under mechanical defense are included thorns, spines, etc., together with chemical appliances, as in plants with poisonous or disagreeable juices. These facts lead to the conclusion that, in proportion as animals are spinose or armored, they exhibit a vegetative type of structure, and have retrograded.

It has been shown elsewhere in this article, that the greatest development of spinose organisms occurs just after the culmination of a group, and, as this period clearly represents the beginning of the decline of the vitality of the group, the spines are to be taken as the visible evidence of this decadence. A similar observation has been made by Packard,[54] who after passing in review the geological development of the Trilobites, Brachiopods, and Ammonites, states that "these types, as is well known, had their period of rise, culmination, and decline, or extinction, and the more spiny, highly ornamented, abnormal, bizarre forms appeared at or about the time when the vitality of the type was apparently declining."

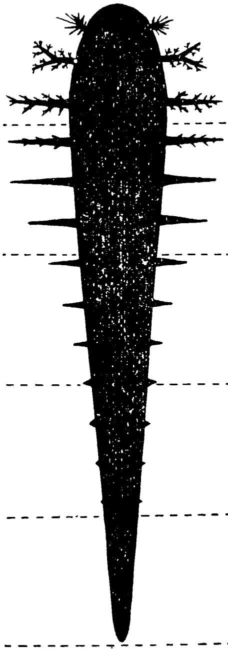
Furthermore, it is now commonly agreed that all groups have been most plastic near their point of origin, or, in other words, that during their early history, all the important or major types of structure have been developed. Their subsequent history reveals the amount of minor differentiation and specialization they have undergone. Apparently, most of the early impulses of growth, whether from the environment or from vital forces, resulted in physiological changes producing fundamental variations in function and structure. The later influences of environment and growth force are expressed in peripheral differentiation, and show that the racial or earlier characters had become fixed, and that the later or specific features were the chief variables. The stimuli which, during the early life history of a group, were expended in internal or physiological adjustments, later produce external differentiation, and in this differentiation, spinosity is the limit. The presence of spines, therefore, indicates the fixity of the primary physiological characters, together with the consequent inability of the organism to change due to its decreasing vitality.

Conclusion.

Just as all our features of terrestrial topography are included between the limits of plains and mountains, and the mountains are considered as the limit of progressive accidentation, so the spines of animals or the monticules and pinnacles of their surface may be considered as the limits of progressive differentiation. The primitive base level, or peneplain, becomes elevated, and by erosion is cut up into table lands, mèsas, and buttes, with intersecting valleys. The valleys are gradually deepened, and the country becomes rougher until a maximum is reached. Then follows a reduction of the inequalities of the surface, and finally in old age, the smooth, gently rounded outlines of geographic infancy again appear. So in organisms, the smooth rounded embryo or larval form progressively acquires more and more pronounced and highly differentiated characters through youth and maturity. In old age, it blossoms out with a galaxy of spines, and with further decadence produces extravagant vagaries of spines, but in extreme senility comes the second childhood, with its simple growth and the last feeble infantile exhibit of vital power.

The history of a group of animals is the same. The first species are small and unornamented. They increase in size, complexity, and diversity, until the culmination, when most of the spinose forms begin to appear. During the decline, extravagant types are apt to develop, and if the end is not then reached, the group is continued in the small and unspecialized species, which did not partake of the general tendency to spinous growth.

Lastly, it must be determined whether spines are really hereditable characters, and therefore can be used in studying the phylogenies of groups. No one has yet been able to show any type or set of characters which cannot be transmitted from parent to offspring. Hyatt[34] says: "Everything is inherited or inheritable, so far as can be judged by the behavior of characteristics." Furthermore, in a review of animal life, extinct and living, no one can fail to be impressed with the fact that, especially near the close of the life history of a group, or in a series of highly specialized forms, spinose characters are often considered as of supra-varietal value, and are rated of specific, generic, and sometimes of family rank, or even higher. They have therefore acquired a fixed importance in these special groups, and are recognized in the same categories with physiological and structural characters. The differences which appear at an early period in higher genera are the bases of distinction among lower genera. If the spines or other similar features do not make their appearance in an individual until a late adolescent stage, they are usually of negative value in a scheme of classification. This agrees with the general principle recently suggested by Harris,[32] that when the main features of the ornament (= spines, etc.) are foreshadowed in the larval and early adolescent stages, they are to be regarded as of taxonomic value.



Ontogeny stages.	Ontogeny condition.	Phylogeny stages.	Phylogeny condition.	Chronology.
Old age or gerontic	Paraplasis	Phylogerontic	Paracme	5
Adult or ephebic	Metaplasis	Phylephebic	Acme	4
Immature or neanic	Anaplasis	Phyloneanic	Epacme	3
Larval or nepionic	Anaplasis	Phylonepionic	Epacme	2
Embryonic	Anaplasis	Phylembryonic	Epacme	1

Diagram and table showing correlation of stages and conditions of development in the spinose individual, in its ancestry, and in time.

The preceding diagram illustrates the previous statements, and shows the correlation between the stages and conditions of growth in the ontogeny of a spinose individual, with its phylogeny, and also the chronology of groups containing spinose forms. The numbers indicating chronology simply refer to successive periods of time. In particular cases, they may be long geologic ages as Cambrian, Ordovician, Silurian, Devonian, and Carboniferous, or in other instances they may represent much shorter periods.

From the study of the ontogenies of spinose forms, it has already been ascertained that they were simple and inornate during their young stages; and from the phylogenies of the same and similar forms, it was likewise learned that they were all derived from non-spinose ancestors. It has also been shown that spines represent an extreme of superficial differentiation which may become fixed in ontogeny, and the further conclusion, that spinosity represents a limit to morphological and physiological variation, has been reached. Finally, it is evident that, after attaining the limit of spine differentiation, spinose organisms leave no descendants, and also that out of spinose types no new types are developed.

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TABLE OF CONTENTS.