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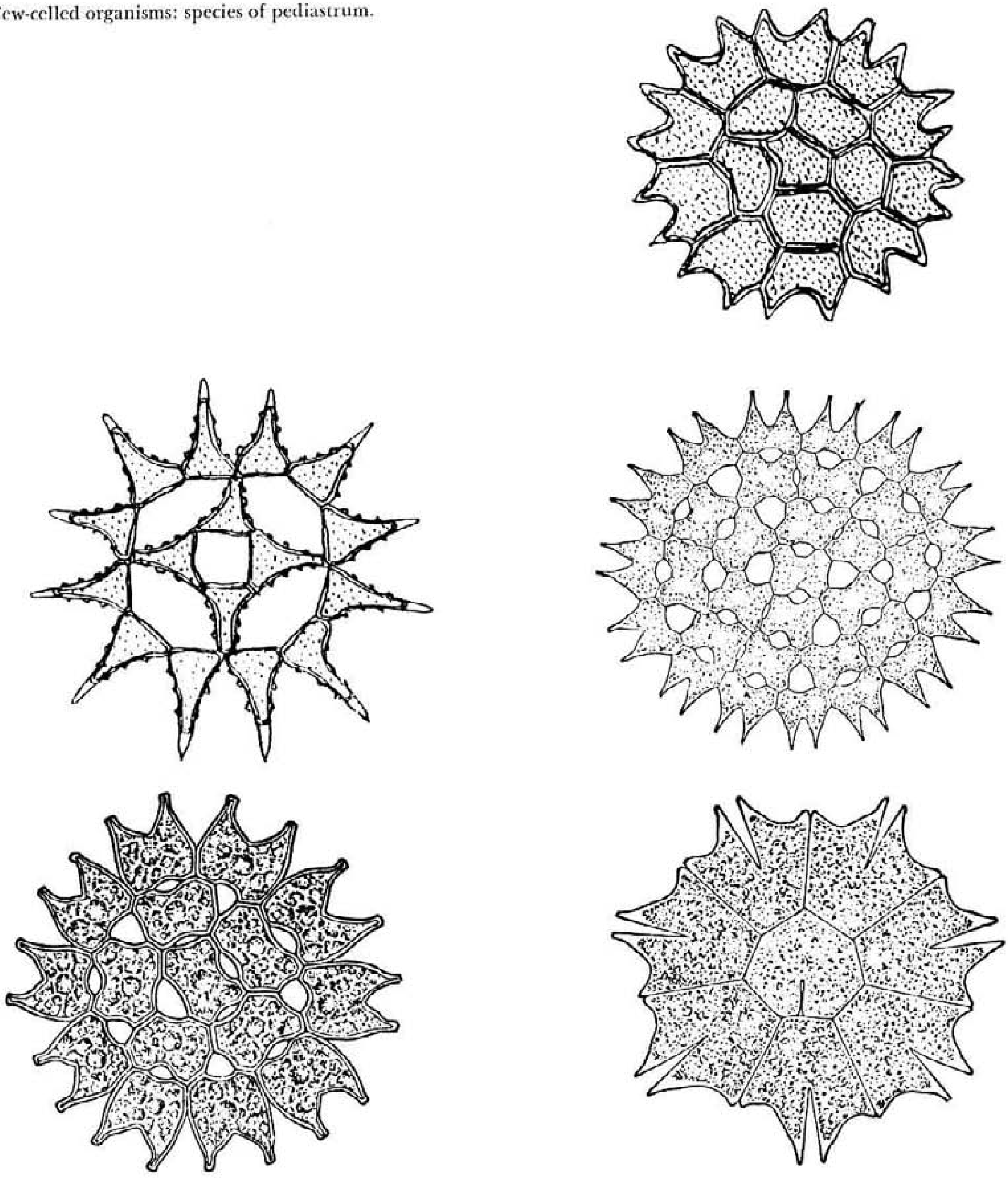
THE MODULAR PRINCIPLE AND BIOLOGICAL FORM

The term "module" is not commonly used in biology, and a biologist who undertakes to discuss the application of the modular principle to biological forms should, perhaps, begin by stating what he takes that principle to be. As I understand it, the idea of the module covers two related notions: firstly, using some standard unit of length or volume as the basis for a whole design; and secondly, adopting throughout the design a single definite series of proportional relations. I am taking Le Corbusier's Modulor as a classical formulation of the principles, allowing, however, that the set of proportions that he worked out in his book, *The Modulor,* are only one particular example, and that many other schemes of proportion would agree equally well with the general principle.

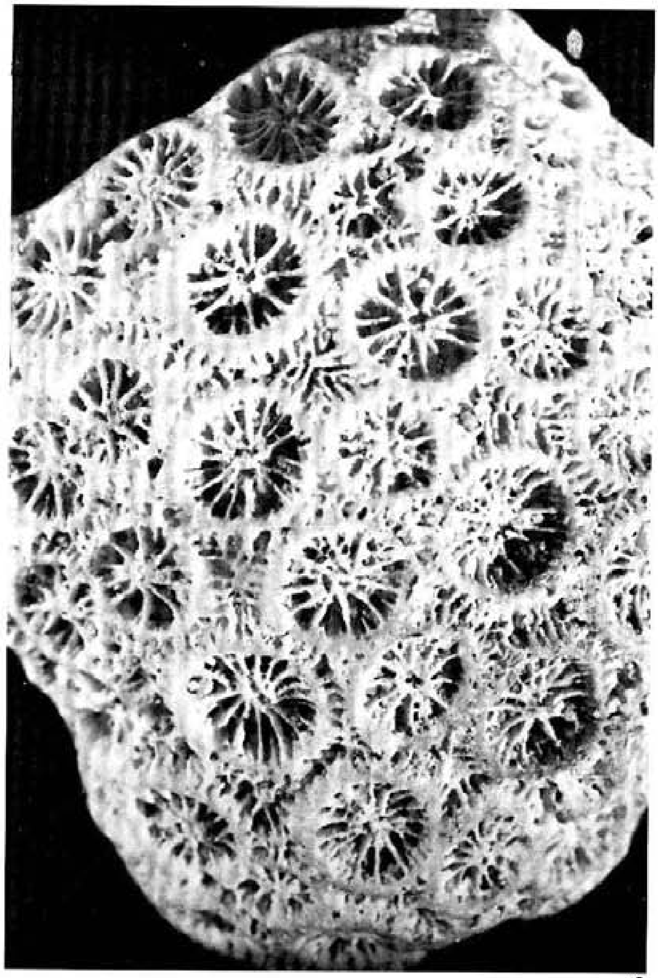
Now the first point to be made—if only to get it registered, since it will lie in the background even when it is not in the foreground of all the following discussion—is that, in the most profound sense, biological forms can never be modular in the sense in which an architectural or pictorial design may be. It is of the essence of biological structures that they are involved in processes of growth and development. Even when we can, for some purposes, identify a basic unit, fundamentally it is not constant but changes (usually increases) as time passes. Similarly, as we shall see, the system of proportions usually alters as development proceeds. The only reason why it is not completely beside the point to discuss modular theory in connection with biological forms is that in many organisms, including the one the artists are most interested in, man himself, there is an extensive period in life—adulthood—during which developmental changes are relatively slight. They can therefore be neglected, if we are willing to remain at a level of discussion which is humanistically important even if it is biologically superficial. However, one must always be ready to find that, in a particular context, such neglect ceases to be justified if we wish to make comparisons which are really illuminating and not merely rhetorical.

With this point in the open, let us begin by considering the application to biology of the simplest aspect of modular theory, the use of a basic unit. At first sight one might think that biological forms are definitely modular in this sense, since they are built of elementary units, namely cells. However, it is only in very simple and small organisms that the cells play the part of a modular unit. Usually they are far too small in proportion to the total size; their relation to the whole form is more like that of the bricks in a skyscraper than of the units of the design. Moreover, in the small organisms in which the cells are few enough to function as the module, it is only exceptionally that the design is based on arrangements of an unmodified module. Usually, even in groups of only a few cells, there is some differentiation of these units into slightly different kinds, and the form is achieved by an orderly arrangement of these different units. A few examples of such simple few-celled organisms can be seen in Fig. 1.

Fig. 1. Few-celled organisms: species of pediastrum.



There are, of course, also many biological forms which are built up of units, in which these units are much larger than cells, being in fact composed of large numbers of cells just as the modular unit in a building may be constructed of numerous bricks. How far can modular principles be said to apply to these more complex biological structures? There is—and this is one of the main points to be made about biological forms in general—a whole range of different situations. At one extreme there are structures in which the units are very similar to one another and are arranged into quite regular patterns. The best known example is perhaps the honeycomb, in which the symmetry is so pronounced as to be nearer to the crystalline than the modular. Fig. 2 shows another form, a lump of coral, which is similar in that it is also made of a number of tubular elements assembled into a compact mass; but here the tubules are further apart and their arrangement is less regular, although there is still a hint of the formation of ordered rows. Fig. 3 shows the bony plates covering part of the back of an armadillo. Its pattern is considerably more orderly than that of the coral, although still far from the perfect regularity of the honeycomb. For one thing, it includes elements of at least two main orders of size: one small and squarish, the other larger and rectangular. Also, there is an orderly increase from the top to the bottom area in the length of the rectangular units. Finally, neither these elements themselves nor their arrangement is precisely geometrical.



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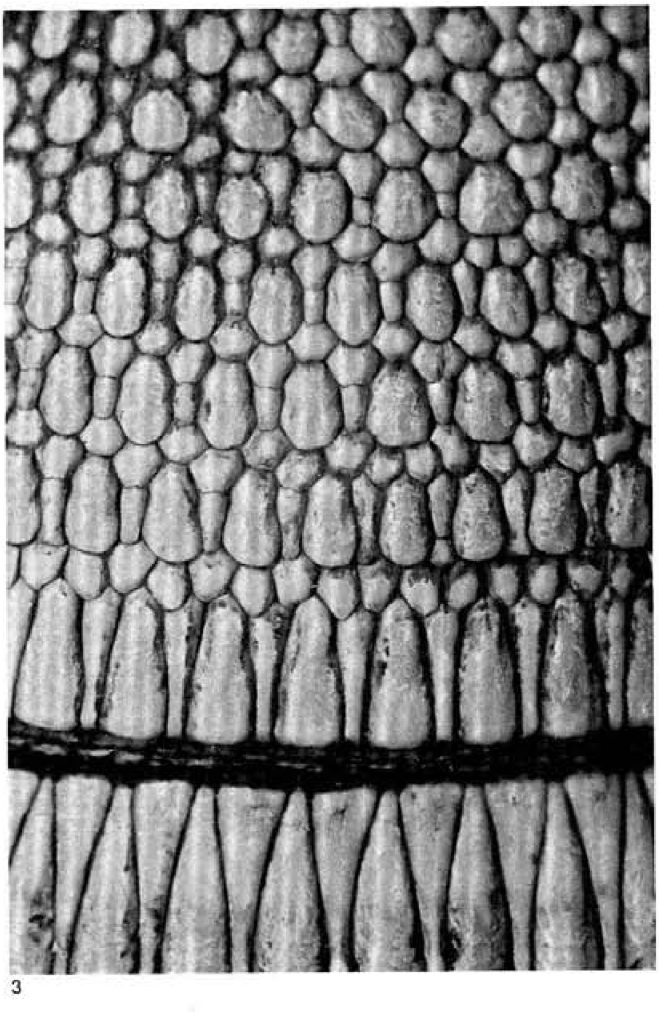

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These two examples show rather well one of the characteristic features of those biological forms which involve the repetition of a basic unit. Both the patterns are rhythmical, the coral more loosely, the armadillo's skin in a more definite way. By a rhythm I mean, roughly speaking, something which is almost a regular periodicity but not quite. As Alfred North Whitehead defined it in the *Principles of Natural Knowledge:* "The essence of rhythm is the fusion of sameness and novelty; so that the whole never loses the essential unity of the pattern, while the parts exhibit the contrast arising from the novelty of their detail. A mere recurrence kills rhythm as surely as does a mere confusion of differences. A crystal lacks rhythm from excessive pattern, while a fog is unrhythmic in that it exhibits a patternless confusion of detail." Whitehead held that rhythms were characteristic of life in some ultimate philosophical sense. Without attempting to follow him into such deep water, I think that there is no doubt that rhythms are very characteristic of many of the objects made by living things.

Fig. 2. A lump of coral.

Fig. 3. Bony plates of the back of an armadillo.

It is instructive to compare these rhythmic biological structures with other patterns in which rhythm is absent or very weak. Figs. 4 and 5 are two other examples of patterns based on the repetition of circular elements. Fig. 4 is a biological specimen, a pattern formed on the upper surface of a cowrie shell. Here the arrangement of the dark-colored rings is too irregular to exhibit much rhythm, although there is some in the disposition of the large irregularly shaped black patches. Fig. 5 is not biological, but is an unsophisticated human pattern, a Nigerian dyed cotton cloth. Here again we are not dealing with a precise periodicity, yet I have the feeling that the divergences from precision are of a kind which do not engender a feeling of well-marked rhythm. Possibly this is because all the elements of the pattern seem to be out of place by about the same absolute amount. The divergence of the main straight lines from perfect straightness is not much greater than aberrations of the smaller circles from perfect circularness. In a rhythmic pattern the differences from perfect periodicity are more closely related to the magnitude of periodicity in question.

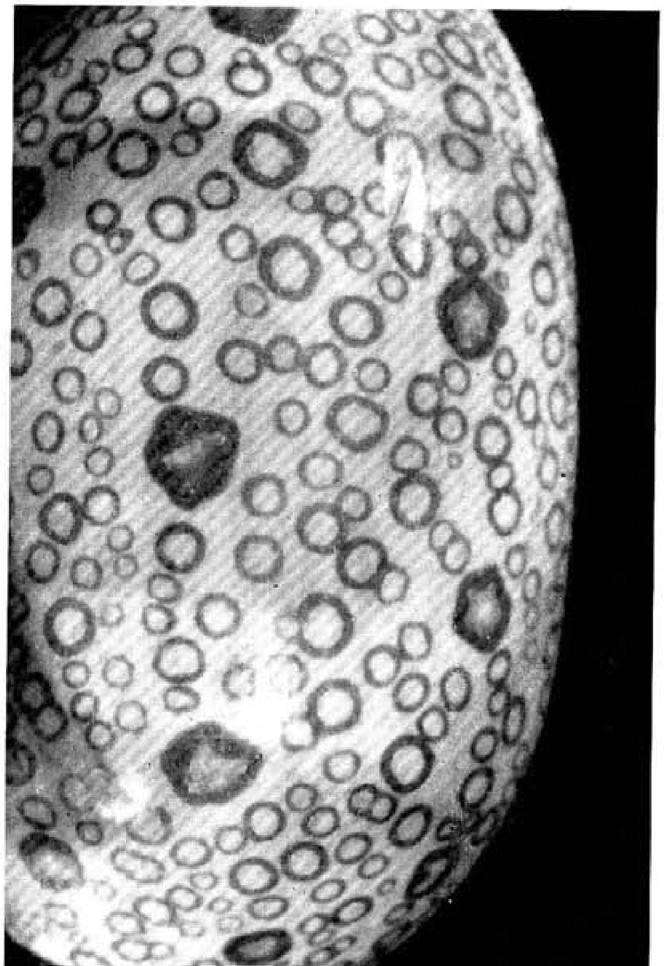
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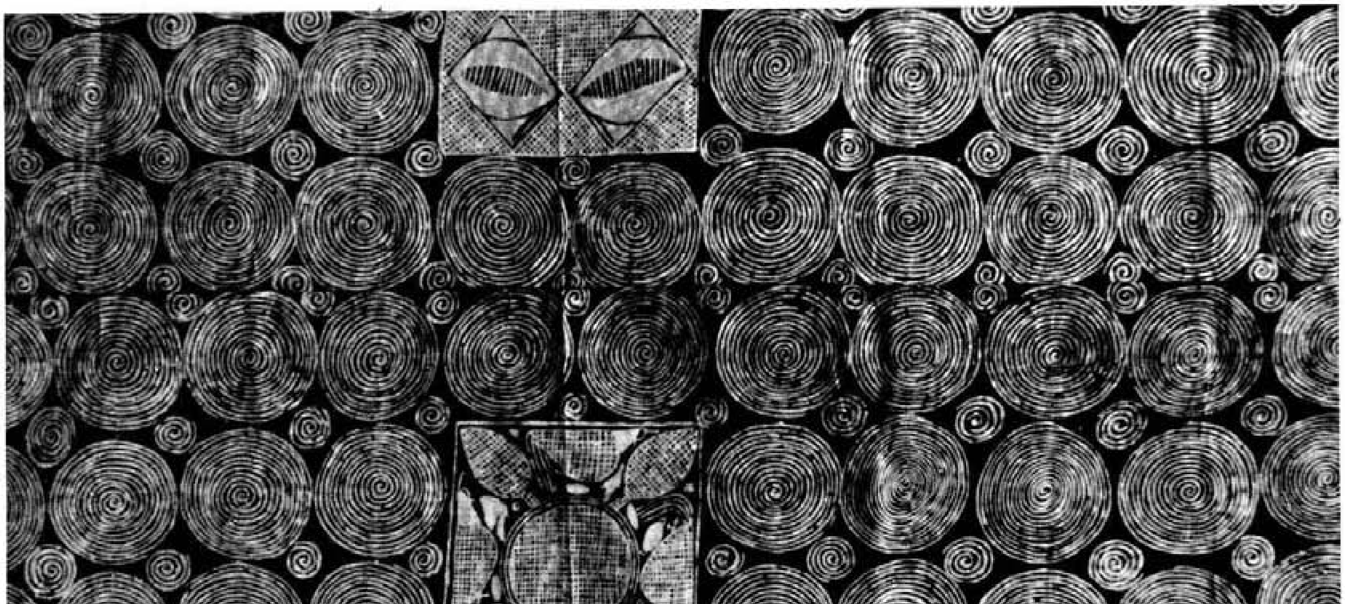
Fig. 4. Pattern on the upper surface of a cowrie shell.

Fig. 5. Nigerian dyed cotton cloth.



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To compare with these non-rhythms, we provide the following four typical biological examples. The mouth of the cowrie (Fig. 6) shows on its lips two examples of linear rhythms. The solitary coral (Fig. 7) is an example of a basically radial symmetry somewhat affected by bilaterality. The pattern on another type of cowrie shell (Fig. 8) and the skeleton of a type of coral known as "sea-fan" or gorgonian (Fig. 9) are instances of all-over patterns. All of these examples are typical of the degree to which biological repetitive patterns are modular. It is a rather slight degree; in general the repeated units vary more or less considerably, and their arrangement is usually quite far from a regular geometrical pattern.

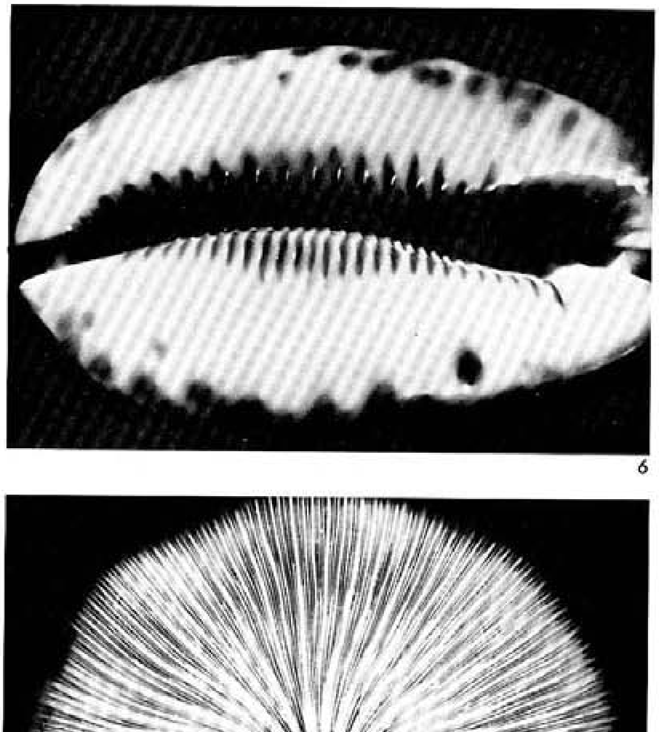

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Fig. 6. The lips of a cowrie shell.

Fig. 7. A solitary coral.


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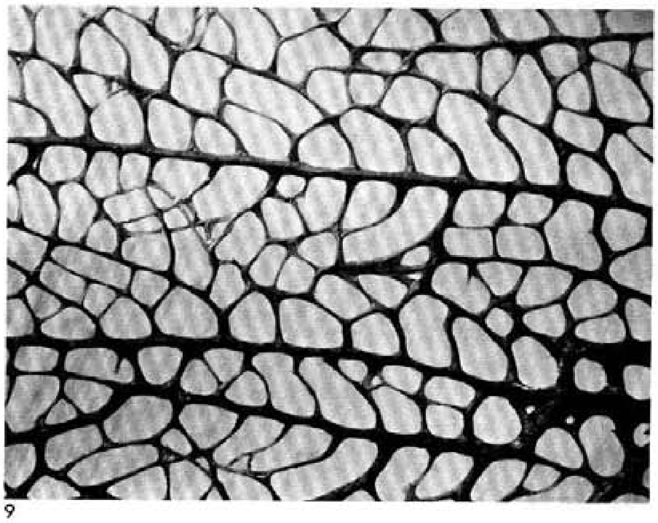
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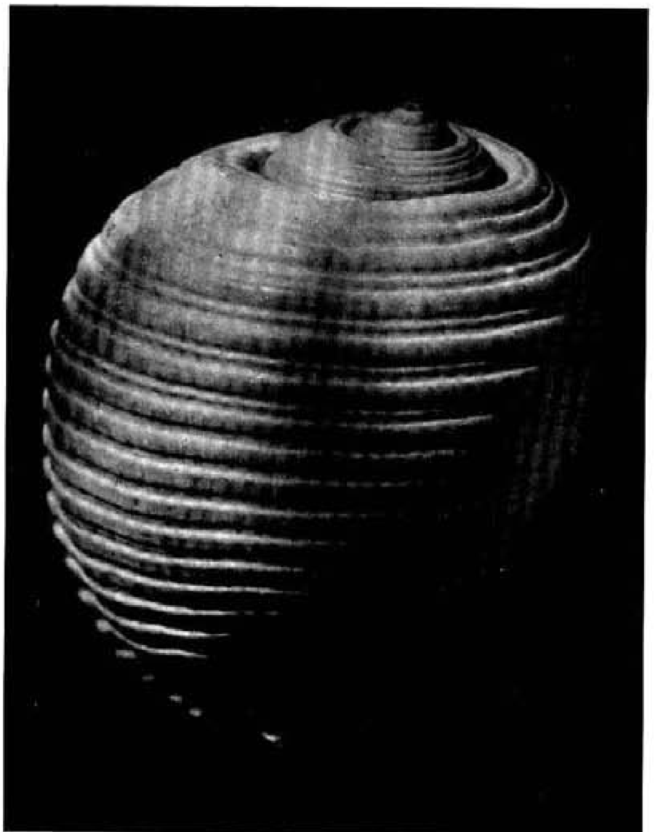
Fig. 8. Pattern on another type of cowrie shell.

Fig. 9. Skeleton of a type of coral ("sea-fan" or gorgonian).

Figs. 10–13. Various types of sea snails.

In many biological patterns the variation of the units is not random, but follows regular rules. One example of this has been shown in the armadillo's skin, but the other patterns have been selected so that this factor had little importance in them. It raises another aspect of the modular principles, that of proportion. In this connection also we can find a vast range of different conditions among biological entities, just as we did in connection with patterns depending on the repetition of units. But probably the dominant characteristic of biological proportions is that any given form usually exhibits the simultaneous operation of several rules of proportion, rather than of only one. And in discussing these proportions it becomes extremely superficial to omit the time factor, since in the great majority of instances the proportions of a biological form change as it grows and develops. This is not quite always the case. For instance, Fig. 10 shows a shell which owes its beauty to the regularity of its shape, which arises from the constancy of the proportions of the spiral tube and of the angle at which it is coiled. Many snails, however, are not so modest, and their shells, even when based on a spiral of regular proportions, are ornamented with all sorts of excrescences, giving rise to forms which vary from the flowingly rhythmic (Fig. 13) to the baroque or the rococo (Figs. 11, 12).



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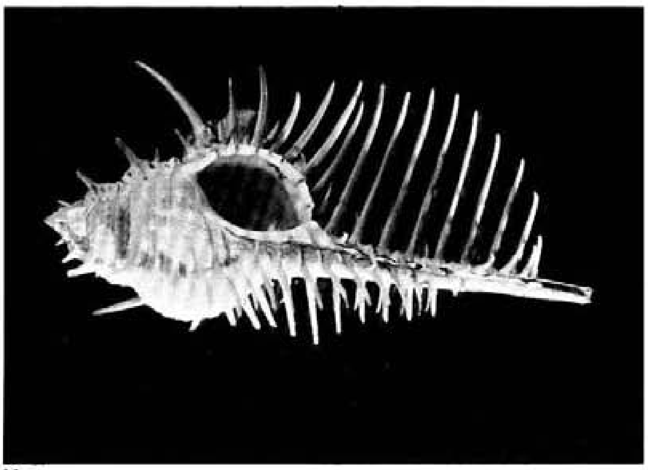
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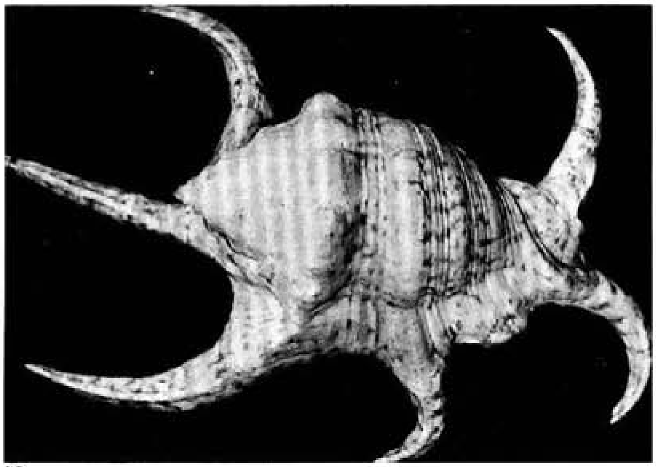
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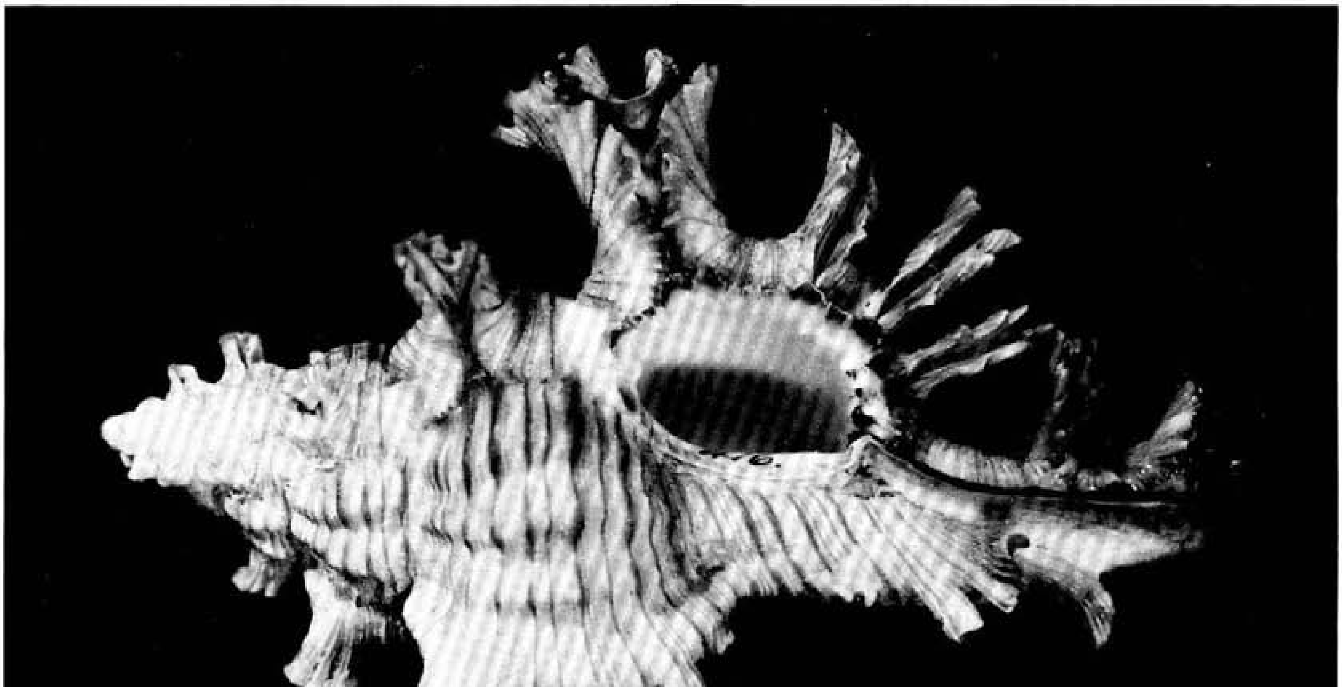
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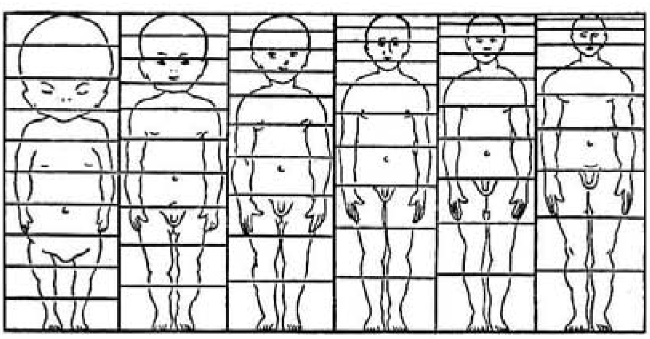
Change of proportions during growth is, however, the more usual situation. It is, of course, characteristic of man's own body. In the cold eye of science the proportions of the average human figure, from before birth to maturity, appear as shown here in this diagram from P. B. Medawar, *Essays on Growth and Form* (Oxford University Press, 1945):

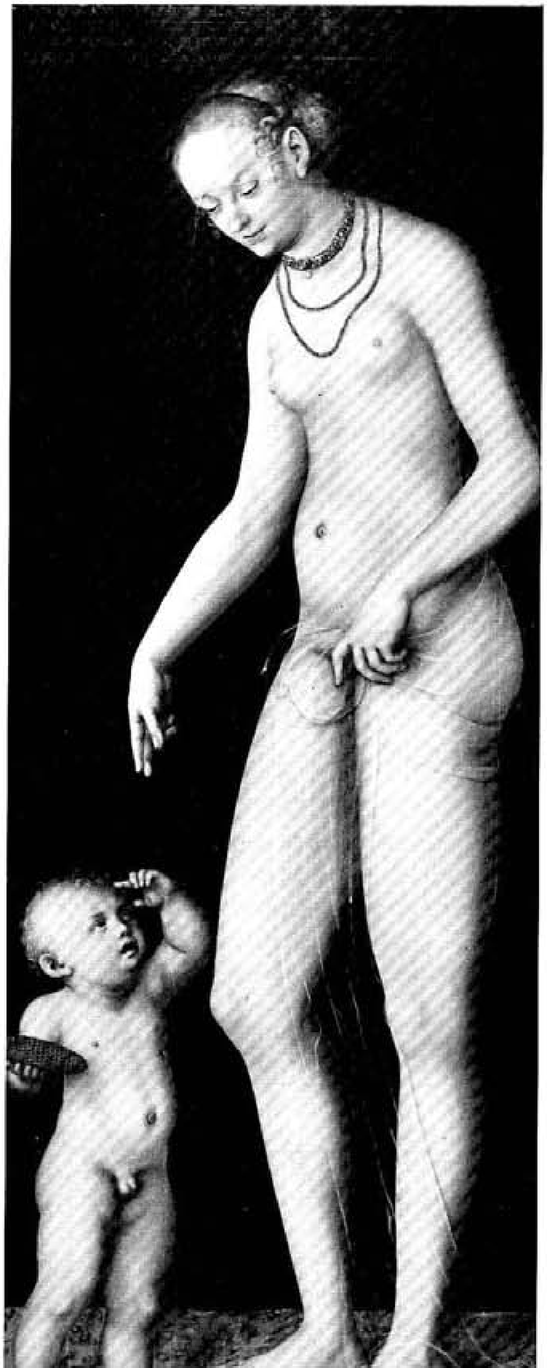


There is, clearly enough, a tendency for the head to become proportionately smaller, and the limbs proportionately longer, as growth proceeds. And these diagrams show only the general average. In particular individuals there may be variation in the relative rates at which the lengthening of the limbs or the slowing-up of head growth proceeds; and some individuals may go further along the general path than others.

As a reminder of the variability of biological proportions within one and the same species, it is amusing to compare a nude by Cranach (Fig. 14), exaggeratedly "adult" in its proportion of limb to body, with the more succulent but equally life-like version of the same form produced by an Indian sculptor on a Buddhist temple. (Fig. 15).

Fig. 14. Lucas Cranach, the elder. *Venus and Amor.* Kröller-Müller Museum, Otterlo, Holland.

Fig. 15. Female figure from doorway of the Buddhist temple at Karli, near Bombay, India.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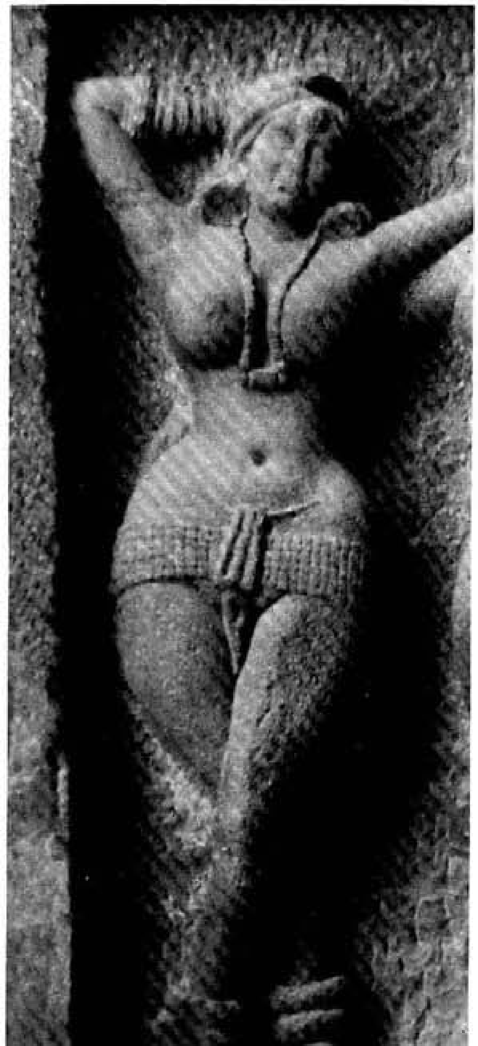
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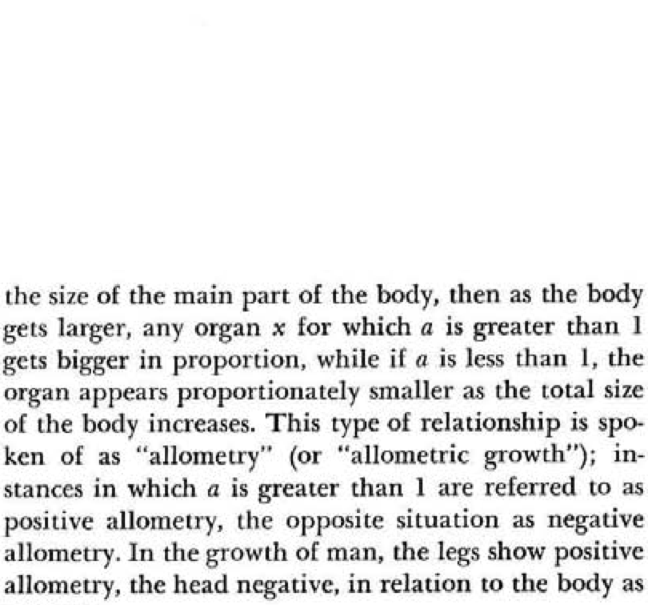
Although the most famous exposition of modular theory, in Le Corbusier's book, *The Modulor,* is plentifully illustrated with a little drawing of a man, with the implication that the system of proportion worked out there is based on relations within the human body, it is actually clear that man's frame contributed nothing to the system except a general order of magnitude. The basic module has a length based on a man standing with his arm raised an arbitrary height above his head, but the division of this length into segments, which gives rise to the whole modular system of proportions, is arrived at by a peculiar mathematical procedure which has nothing to do with any sort of biology, human or other.

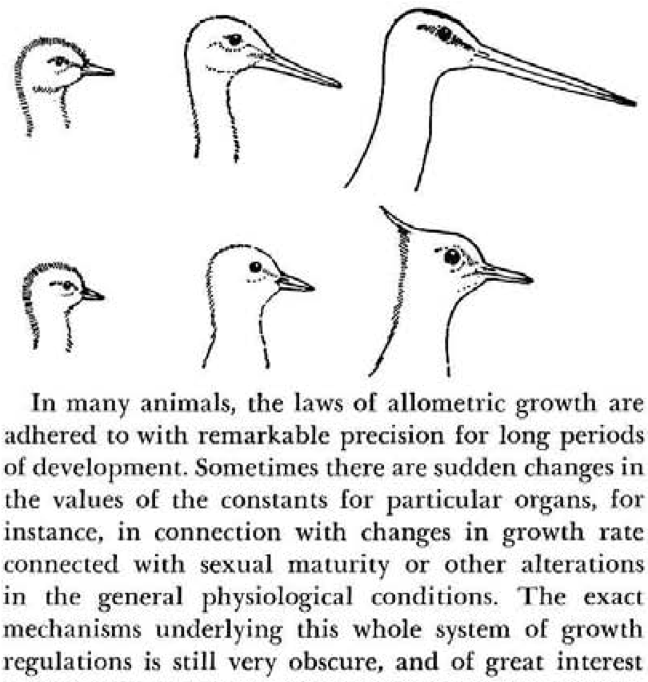
The change of proportions of a biological organism during its development is brought about by differences in the growth rates of the various parts, some of which grow faster than others. There is very often a simple relation between the growth rates of well-defined parts, such as the limbs, head, and so on. This relation—which is certainly not universal, but is very common—is a simple constant proportionality, which exists not between the sizes of the parts, but between their rates of growth. In mathematical terms, if x and y are two parts of an animal (*e.g.,* x the head and y the rest of the body, or the arms) then the relation is that the rate of increase of x is a constant multiple of the rate of change of y: *i.e.,* $dx/dt = a\ dy/dt$. From this one can deduce the relation between the sizes of the two parts at any particular time of development. It will be of the form $x = b\ y^a$. It is clear from this that if the constant a is larger than 1, then x will be increasing faster than y; for instance, if the y in the formula is the size of the main part of the body, then as the body gets larger, any organ x for which a is greater than 1 gets bigger in proportion, while if a is less than 1, the organ appears proportionately smaller as the total size of the body increases. This type of relationship is spoken of as "allometry" (or "allometric growth"); instances in which a is greater than 1 are referred to as positive allometry, the opposite situation as negative allometry. In the growth of man, the legs show positive allometry, the head negative, in relation to the body as a whole.

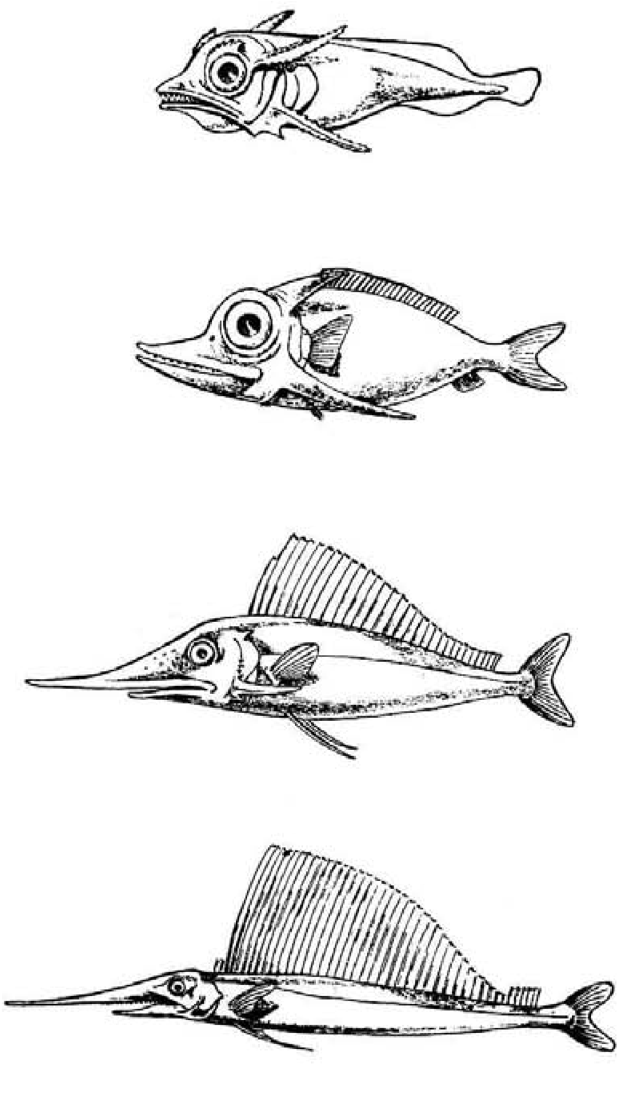


From Le Corbusier, *The Modulor,* Cambridge, Mass., Harvard University Press, 1954.

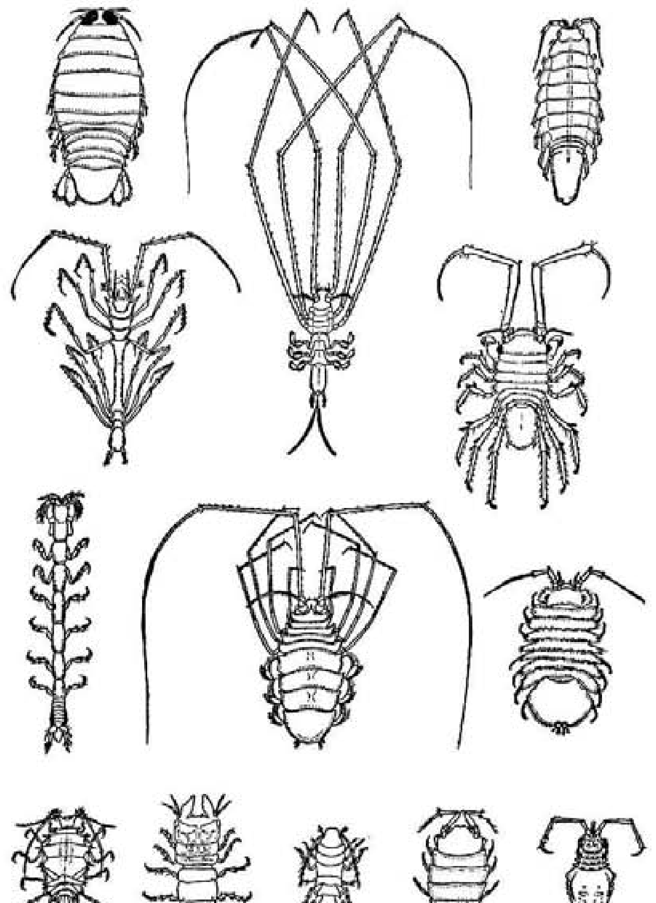
Fig. 16. Changes in proportion of the beak and head during growth, in two species of birds: black-tailed godwit, upper; lapwing, lower. From Bernard Rensch, *Evolution above the Species Level,* New York, Columbia University Press, 1960.

Fig. 17. Changes in proportion of a sailfish during growth. From J. T. Bonner, *The Ideas of Biology,* New York, Harper and Row, 1962.





In many animals, the laws of allometric growth are adhered to with remarkable precision for long periods of development. Sometimes there are sudden changes in the values of the constants for particular organs, for instance, in connection with changes in growth rate connected with sexual maturity or other alterations in the general physiological conditions. The exact mechanisms underlying this whole system of growth regulations is still very obscure, and of great interest to biologists, but the causal analysis of the phenomenon is not the point at issue in the present context. Here it is more important to note some further examples of the kind of visual images which arise from this type of growth. A very simple example is seen in Fig. 16, which compares the growth of the beak in two species of birds, the black-tailed godwit (upper) and the lapwing (lower). In the godwit there is strong positive allometry of the beak, and it is obvious that the proportions change enormously as the bird grows up. Fig. 17 shows a similar situation in a sailfish during growth. There can be no standard modular proportion in such forms.

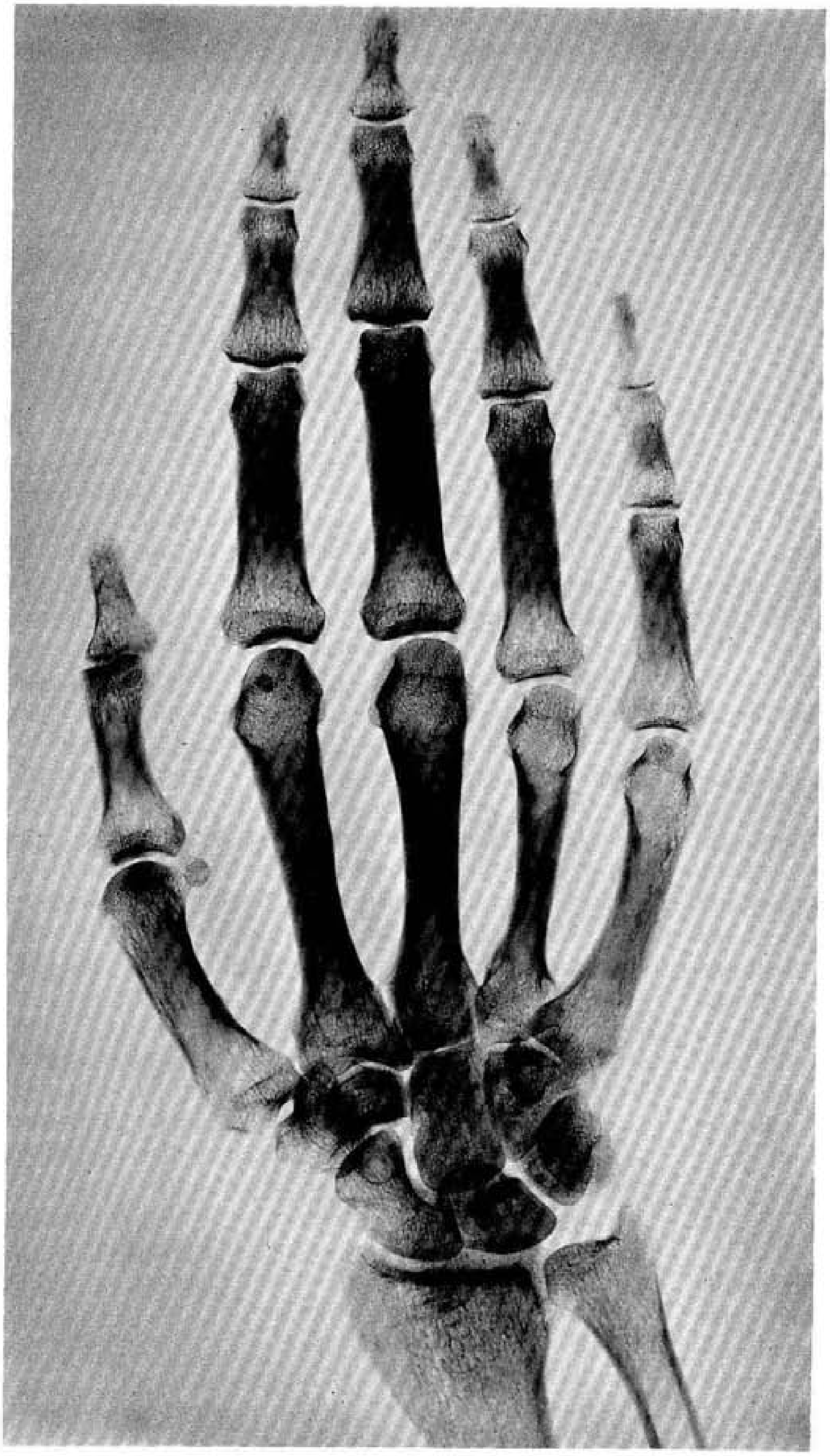


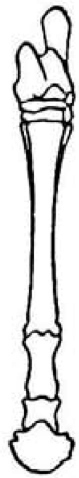
More complex alterations in proportions are brought about when growth of an allometric type occurs in biological forms consisting of many segments. Fig. 18 shows outline drawings of a number of species of marine isopods, *i.e.*, animals whose basic type is best known to most people in the form of a woodlouse. In the woodlouse, all the segments have grown at more or less equal rates, and even in the adult they are all of approximately the same size. The drawings in Fig. 18 are not growth stages of any one species, but illustrate the different types of adult which have been evolved from the woodlouse type. Their evolution has involved alterations in the growth rates of the various segments, some of which now show strong positive allometry, *e.g.*, the eight anterior ones in the third drawing from the top at left or the four posterior ones in the second from the top at center. Similarly, if one looks at the legs, it is clear that three pairs toward the front end of the animal top-center have been growing enormously faster than the rest of the body; and so on and on in all the variety of forms that have been produced. Very clearly, there is no standard system of proportions, but instead the proportions of the various regions and organs of the body can be varied almost arbitrarily.

Fig. 18. Animals related to the woodlouse.
From Bernard Rensch, *Evolution above the Species Level*, New York, Columbia University Press, 1960.

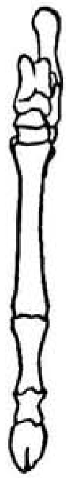
But a closer looks shows that the variations are not really arbitrary. There is an interesting type of orderliness, and one very typical of biological forms. The growth constants of neighboring segments, whether of the main body or of the legs, are nearly always closely related to each other. It is very rare to find a very long segment next to a very short one, more usually there are gradual changes in growth constants as one passes from one segment to the next. For instance, in the second animal from the top at center they increase fairly steadily from front to back, with perhaps rather a steep rise near the middle, while in the third from the top at left they remain small in the most posterior segment, then there is a considerable rise followed by a slower gradual increase with a final tailing off again in the most anterior parts. If one were to plot the growth constants along the length of the body or along the legs, they would fall on some relatively simple continuous curve instead of being scattered about in a quite arbitrary way. Such curves are known as growth gradients, and they express a type of orderliness which is very characteristic of biological form. It results in there nearly always being some recognizable relation between the neighboring parts of a biological system. For instance, a child's leg is not only shorter than an adult's in proportion to the body, but also has a different internal system of proportions between the thigh, knee, calf, ankle, etc. But both in the child and the adult the lengths of the segments form a *system* of proportions, and the legs do not give the impression of a mere assemblage of unrelated sections.

This kind of organization of the form is so important in biological organisms that it is worth looking at some further examples. The illustrations on the following pages show a situation in which not only the proportions of the elements, but also the number of elements has been varied. The hands and feet of all mammals are built on plans which are derived from a design with five digits—fingers or toes. Man retains this primitive pattern, but evolution has produced many types of animals —horses, pigs, deer, cows, and more exotic creatures—in which the numbers have been reduced, and the proportions of the various bones in a finger or toe altered. The drawings in Fig. 19 show a sample of these variations. In all of them, the "relationship of neighbors" is apparent in two ways: between the different digits, and between the bones within any one digit. The relationships may be quite different in different cases. In Myrmecophaga, for example, the central digit is enlarged and there is a gradual falling away toward the sides, whereas in Macrorhinus we see that it is the two outer digits that are largest. But whatever form the modifications have taken, whether symmetrical or asymmetrical, they always give the appearance of an over-all alteration in a general system, never of a set of changes in a number of isolated and unrelated items. Even when the elements in the pattern have no very obvious functional dependence on one another, such as the bones of a limb must have, they usually show a relatedness in form when different modifications of the pattern are compared. For instance, look at the spines and knobs on the snails illustrated earlier.

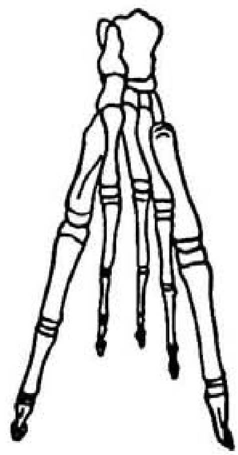




Equus

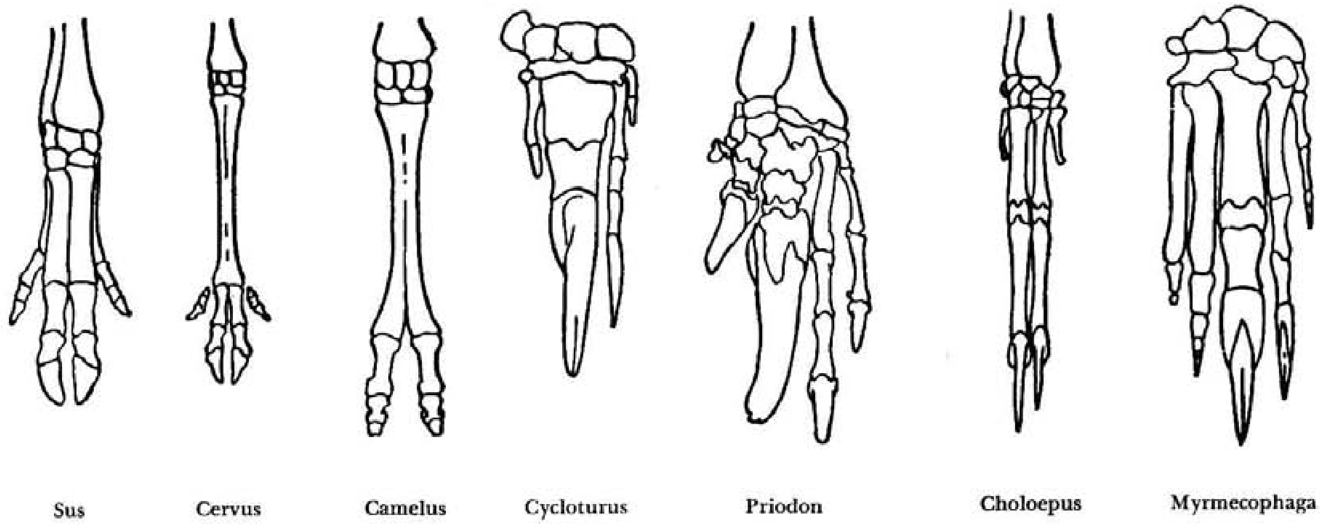


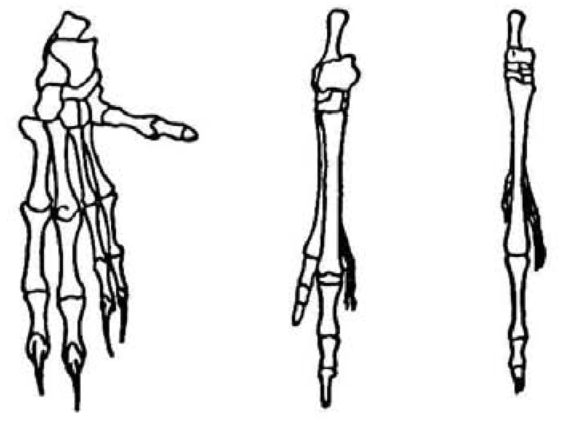
Thoatherium



Macrorhinus

Fig. 19. Hands and feet of various mammals.
Drawings from P. Tschumi, *Revue Suisse Zoologique,* 1953.





It is, in my opinion, this relatedness of contiguous parts which is particularly characteristic of biological structures. They are certainly not usually modular in the sense of being assembled by the arrangement of one or a few kinds of constant elementary units. Nor, as we have just seen, do they often employ a standard system of proportions. The Golden Mean is not an idea of a biological type. How could there be such a thing in a form which is altering the relative proportions of its parts as it grows up? On the other hand, biological forms are certainly not chaotic or arbitrary in the mutual relations of their parts, but nearly always convey a strong impression of order and organization. There are, I believe, principles which apply to the forms of the individual parts or organs of which an animal is built. These have not been discussed in this article, which is concerned with the question of the arrangement of units and with proportion, that are the province of modular theory. Within this province, I have argued that the biological rules are not those of the module, but rather of a kind which one might summarize by the phrase, "the relatedness of neighbors."