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XLIX.—On the Calcispongiae, their position in the animal kingdom, and their relation to the theory of descendance

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Synop. Frams. af Sveriges Oniscider (1858), p. 10; Zaddach, Synop. Crust. Prussic. Prod. p. 17; Frič, Die Krustenthier e Böhmens (1872), p. 256.
Zia agilis, Koch, Deutschl. Crust. xxxiv. f. 22, 23.
Ligidium {hypnorum}, Rudde-Lund, Naturhistorisk Tidsskrift, 1871, p. 226.
Zia Saundersii, Stebbing, Ann. & Mag. Nat. Hist. 1873, ser. 4. vol. xi. p. 286.

Ligidium agile has a wide European distribution, and has been found in Sweden, Denmark, Prussia, Bohemia, and France. It might therefore have been expected to be found in Great Britain, especially as Latreille's specimens had been received from the shores of the British Channel ("Habitat in littoribus Oceani Britannici, ab entomologo Brébisson mihi transmissus").

The relationship of the species to *Ligia* rather than to *Oniscus* was first pointed out by Fabricius, who, in his 'Suppl. Entom. Syst.,' though he assigns it to *Oniscus*, asks "An potius *Ligia*?"

As has been already mentioned, Koch described two other species, which, however, are perhaps mere varieties of *L. agile*. More recently Schöbel has described a form, under the name of *Ligidium amethystinum*, as distinct from *L. agile*. Perhaps this species also is destined hereafter to reward the careful search of some British carcinologist. Very little has as yet been done among our *land* Crustacea, my lamented friend Dr. Kinahan being the only British naturalist who has paid any attention to the Isopoda Aërospirantia.

XLIX.—*On the Calcispongïæ, their Position in the Animal Kingdom, and their Relation to the Theory of Descendence.*
 By Professor ERNST HÆCKEL.

[Continued from p. 262.]

II. THE CALCISPONGIÆ AND THE THEORY OF DESCENDENCE.

1. Principles of Classification.

The task which we had set before us as the primary object in this monograph of the Calcispongïæ, *the analytical solution of the problem of the origin of species*, has been followed out in different ways in the first and second volumes. In the first volume, and especially in its second section, the "Morphology of the Calcispongïæ," I have endeavoured to describe all the

characters of form occurring in this group in their general connexion, and to explain the perfect "unity of their plan of structure" by the *common descent of all Calcispongiæ from the Olynthus*. In the second volume, on the other hand, I have sought to demonstrate the stock-relationship of all the forms of this group by subjecting the species of Calcispongiæ to the most exact anatomical analysis; in doing which I found myself compelled, in opposition to the existing rules of classification, to set side by side two perfectly different systems, a natural and an artificial one.

The principles of classification which I have followed will manifest themselves to the thoughtful reader from a comparative study of the two systems. The *natural system* is "carried out in accordance with the phylogenetic principles of the theory of descendance, with an average extension of the idea of species." It contains 21 genera with 111 species. The *artificial system* is "carried out in accordance with the principles hitherto followed in the classification of the sponges, with an average extension of the idea of species." It includes 39 genera with 289 species.

The logical principles upon which the artificial system is founded are quite different from the genealogical principles upon which the natural system rests. The former takes into consideration especially the products of *adaptation*, the latter the constancy of *inheritance*. The artificial system furnishes as definite a distinction as possible, and a summary arrangement of the various forms founded on those characters which strike one as specific characters on a logical comparison merely directed to the *external* morphological connexion of the forms. The natural system, on the contrary, strives after the more profound recognition of their *internal* morphological connexion, and seeks, in accordance with this, to approach the genealogical tree of the species. As a matter of course, this object will never be completely attained among the sponges, any more than with other organisms, for the simple reason that the three great documents of the natural history of Creation (Comparative Anatomy, Ontogeny, and Palæontology) are accessible to us only in imperfect fragments. Nevertheless, by continued phylogenetic attempts, the natural system will gradually approach more and more to the true genealogical tree.

How far this approximation has been successful in the natural system of the Calcispongiæ, the thoughtful reader will best see by the study of the second volume, and especially from the estimation of the generic and specific, connective and transitory varieties. The approximation to the true genealogical tree is more possible than with other groups of organisms, because

the conditions of *inheritance* and *adaptation* may be unusually clearly reviewed in the Calcispongiæ. The part taken by these two formative functions in the production of the individual form may be here determined more accurately and certainly than is usually the case.

• 2. *Idea and Descent of Species.*

The idea of the species is the central point of attack of the theory of descent, and the true nucleus of all discussions on "development or creation." To investigate this idea again here would be completely superfluous. I have explained my views upon it in such detail in my criticism of the morphological, physiological, and genealogical idea of species in my 'General Morphology' (Bd. ii. pp. 323-364) that I should merely have to repeat what I have there said. All attempts up to this time to give the idea of the species a decided limit and contents have failed, and by this negative result itself have led to the conviction that the positive idea sought for cannot be defined. The genealogical definition of the idea attempted by me is just as unsatisfactory and untenable as all the rest. This lies in the nature of the thing. The species is just as arbitrary an *abstraction* produced by the subjective contemplation of the author, just as much a category of only relative significance, as the ideas of the variety, genus, family, &c. All these categories have their value only in their reciprocal relations to one another, and owe their origin to the *subjective law of specification* (l. c. p. 331).

Moreover we have only to glance at the practice in zoological and botanical classification to be convinced that the *practical distinction of species has nothing at all to do with all these theoretical definitions of the idea of species*. On the contrary there prevails in that distinction the greatest subjective arbitrariness, and hence an endless dispute between the various systematists. No two systematists, who have thoroughly worked upon the same group of forms, have ever yet agreed perfectly as to the number and limitation of the species united in it.

In the Calcispongiæ the practical distinction of species is subject to much greater difficulties than in most other groups of animals. According as the systematist conceives the idea of the species in a wider or narrower form, according as he estimates most highly the principles of the artificial or the natural system, he may considerably increase or diminish the number of 21 genera and 111 species of the natural system which are described in the first section of my second volume. The *natural system* might, for example, be founded upon any one of the following six conceptions:—A. 1 genus with 1

species; B. 1 genus with 3 species; C. 3 genera with 21 species; D. 21 genera with 111 species; E. 43 genera with 181 species; F. 43 genera with 289 species. On the other hand the *artificial system* might experience the following six arrangements:—G. 1 genus with 7 species; H. 2 genera with 19 species; I. 7 genera with 39 species; K. 19 genera with 181 species; L. 39 genera with 289 species; M. 113 genera with 591 species. Every one of these twelve systems might cite in its support arguments such as every systematist brings forward in favour of his subjective conception. None of them, however, could ever be demonstrated as the absolutely true system. This circumstance shows most clearly that no absolute species exists, and that species and variety cannot be sharply separated*.

3. *Generic and Specific, Connective and Transitory Varieties.*

The different forms which I have cited in the system of the Calcispongiae as generic and specific, connective and transitory

* The twelve systems here cited as examples (in which, moreover, the external form is not taken into consideration) would be as follows:—

A. I. Natural system with the widest conception of the idea of species (in the first degree): a single genus with one species, *Calcispongia grantia*.

B. II. Natural system with a very wide extension of the idea of species (in the second degree): a single genus with three species: 1. *Calcispongia ascon*, 2. *C. leucon*, 3. *C. sycon*.

C. III. Natural system with a narrower conception of the idea of species (in the third degree): 3 genera (*Ascon*, *Leucon*, *Sycon*) with 21 species. Here the 21 groups of forms which the next system accepts as genera (*Ascetta*, *Leucetta*, *Sycetta*, &c.) are reckoned as species.

D. IV. Natural system with average extension of the idea of species (in the fourth degree): three families (*Ascones*, *Leucones*, *Sycones*) with 21 genera and 111 species.

E. V. Natural system with a narrower extension of the idea of species (in the fifth degree): 3 families with 43 genera and 181 species. This system is attained when the subgenera cited in the natural system in the second volume are accepted as "good genera," and the "specific varieties" or incipient species as "good species." Their characters are sufficiently sharply marked and relatively constant.

F. VI. Natural system with a very narrow extension of the idea of species (in the sixth degree): 3 orders, with 21 families, 43 genera, and 289 species. This system is attained by a further analytical specification of the fifth system, the "generic varieties" of the latter being raised to the value of distinct species.

G. VII. Artificial system with the widest conception of the idea of species (in the first degree): all Calcispongiae form a single genus, *Grantia* (Fleming, 1828), or *Leucalia* (Grant, 1829), or *Calcispongia* (Blainville, 1834). We may then distinguish the following as seven species:—1. *Culeispongia dorograntia*; 2. *C. cystograntia*; 3. *C. cormograntia*; 4. *C. cœnograntia*; 5. *C. tarrogantia*; 6. *C. cophograntia*; 7. *C. metrograntia*.

varieties, are of the greatest importance to the theory of descent and the object of this monograph, namely to ascertain analytically the origin of species as exemplified by a single group. The thoughtful and unprejudiced systematist, who has followed carefully the method of classification followed by me in the second volume, will comprehend without further explanation the extraordinary phylogenetic importance of these four different varieties. I may, however briefly sum up the most important points connected with them.

1. The *generic varieties* of the natural system are the *genera of the artificial system*. Within one and the same natural species many different forms may be developed by multifarious stock-formation and mouth-formation; and these the artificial system (having no knowledge of their close genealogical connexion) must regard unconditionally as representatives not only of distinct species but even of distinct genera. Thus, for example, *Ascandra variabilis* includes forms which the artificial system would divide among eleven different genera;

H. VIII. Artificial system with a very wide extension of the idea of species (in the second degree): 2 genera with 19 species, namely:— I. MONOGRANTIA, with 6 solitary species: 1. *M. olynthus*; 2. *M. disycus*; 3. *M. sycurus*; 4. *M. clistolythus*; 5. *M. lipostomella*; 6. *M. sycocystis*: II. POLYGRANTIA, with 13 social species, namely: 1. *P. soleniscus*; 2. *P. amphoriscus*; 3. *P. sycothamnus*; 4. *P. nardosus*; 5. *P. cœnostomus*; 6. *P. tarrus*; 7. *P. artynas*; 8. *P. auloplegma*; 9. *P. aphroceras*; 10. *P. sycophyllum*; 11. *P. ascometra*; 12. *P. leucometra*; 13. *P. sycometra*.

I. IX. Artificial system with a narrower extension of the idea of species (in the third degree): 7 genera with 39 species. The genera would be:— 1. *Dorograntia*; 2. *Cystograntia*; 3. *Cormograntia*; 4. *Cœnograntia*; 5. *Tarroggrantia*; 6. *Cophograntia*; 7. *Metrograntia*. The 39 species would be represented by the 39 forms which are cited as genera in the artificial system in the second volume. Thus, for example, the second genus (*Cystograntia*) would contain three species:—1. *C. clistolythus*; 2. *C. lipostomella*; and 3. *C. sycocystis*.

K. X. Artificial system with a still narrower extension of the idea of species (in the fourth degree): 7 families, with 19 genera and 181 species. The 7 genera of the ninth system are here raised to the rank of families, and the 19 species of the eighth system to that of genera; and the 181 species are the same that in the fifth system were divided into 43 essentially distinct genera.

L. XI. Artificial system with an average extension of the idea of species (in the fifth degree): 7 orders, with 19 families, 39 genera, and 289 species. This system is carried out in the second section of the second volume on the principles hitherto followed in the classification of sponges.

M. XII. Artificial system with a very narrow extension of the idea of species (in the sixth degree): 7 orders, with 19 families, 113 genera, and 591 species. Here those groups of forms are regarded as genera which in the eleventh system had only the rank of subgenera (*Olynthettus*, *Dys-sycettus*, *Sycurettus*, &c.), and as species those forms which figure in the eleventh system as subspecies.

Leucetta primigenia represents seven different genera of the artificial system; and *Sycandra compressa* furnishes the artificial system with no fewer than nine distinct genera.

2. The *specific varieties* of the natural system are *incipient species of the natural system* in the sense of the theory of descendance. By further development and increasing constancy of the characters by which the specific varieties of a natural species are distinguished they would raise themselves to the rank of "*bonæ species*." An analytical system that takes a very narrow conception of the idea of species might already recognize them as species. Thus, for example: *Ascandra variabilis* would divide into four natural species (*A. cervicornis*, *confervicola*, *arachnoides*, and *hispidissima*); *Leucetta primigenia* would form three good species (*L. isoraphis*, *micro-raphis*, and *megaraphis*); and *Sycandra compressa* would even break up into six natural species (*S. foliacea*, *pennigera*, *clavigera*, *rhopalodes*, *lobata*, and *polymorpha*). Many of these specific varieties have, in fact, already been described as species.

3. The *connective varieties* of the natural system are *direct transition forms between the genera of the natural system*. The foundations of a new natural genus are laid by very trifling changes in the constitution of the skeleton. Thus, when certain triradiate spicules of the skeleton of *Ascetta* (*Leucetta* or *Sycetta*), which is composed only of triradiate spicules, develop a fourth ray, this genus passes into *Ascallis* (*Leucaltis* or *Sycaltis*). For example:—*Ascandra variabilis* furnishes transition forms to four natural genera (*Ascallis*, *Ascortis*, *Asculinus*, *Ascyssa*); *Leucetta primigenia* produces connective forms towards three genera of the natural system (*Leucaltis*, *Leucortis*, *Leucandra*); and *Sycandra compressa* passes into *Sycortis*.

4. The *transitory varieties* of the natural system are *direct transition forms between the species of the natural system*. They are the "transitions from one good species to another" which horrify the opponents of the theory of descendance. Such intermediate forms, the existence of which is denied by dogmatic species-makers, occur in abundance among the Calcispongiæ. Thus we have transitions from *Ascandra variabilis* to *A. pinus*, *A. Lieberkühnii*, and *A. complicata*; transitory intermediate forms between *Leucetta primigenia* and *L. pandora* and *sagittata*; and direct transitions from *Sycandra compressa* to *S. utriculus* and *lingua*.

4. Polymorphosis and Polymorphism.

One of the most remarkable peculiarities of the Calcispongiæ,

by which they are most strikingly distinguished from most other organisms, is *the extraordinary instability of the outer form of the body*. It is this that renders their study so instructive in connexion with the problem of species. Every systematist knows how great and decisive is the significance of the external form in the distinction of species in almost every class of animals; indeed the great majority of species are distinguished merely by more or less important differences in the details of the external form. In complete opposition to this, the external form in the Sponges, and especially in the Calcispongiæ, is so variable that it cannot be employed at all for characterizing species, either in the natural or the artificial system. What I have observed in this respect among the Calcispongiæ exceeds all previous conceptions, and goes much further than the wonderful variability of the external form in the Fibrospongiæ, which have been indicated as quite extraordinary by all recent spongologists, especially Oscar Schmidt. A systematist who should adopt the external form alone as a specific character in the case of *Ascandra variabilis*, *Leucetta primigenia*, or *Sycandra compressa* might at his pleasure distinguish among the individuals of any one of these extremely variable species from a single locality ten, twenty, or more than a hundred species.

It may perhaps seem still more remarkable that this excessive instability affects even the most important organs, such as the stomachal cavity and the mouth. In very many natural species we find side by side individuals with and without a mouth. Among the Fibrospongiæ also the loss of both mouth and stomach appears to be very frequent. This singular phenomenon is probably to be explained by the fact that in the Sponges (as in the parasitic worms, Crustacea, &c.) the mouth-opening does not possess the same physiological importance as in the higher animals. It becomes rudimentary and is finally lost (Cestodea, Rhizocephala, lipogastric Sponges). The quadruply different nature of the mouth in the Calcispongiæ is also very variable.

I have particularly described this remarkable multiformity of the species of Calcispongiæ in the second volume, and elucidated it by many figures. In the explanation of the plates it is called *polymorphosis*, in contradistinction to the well-known *polymorphism* of the Siphonophora and of many of the higher animals. The latter is well known to be a product of physiological division of labour. *Polymorphosis*, on the contrary, is a *polymorphism without division of labour*; its cause is to be sought merely in adaptations to external conditions of existence of quite subordinate importance.

The most remarkable form of polymorphosis among the Calcispongiæ is *the union of polymorphotic persons upon one stock*, which I have called *metrocomism*. In the artificial system these *metrocomotic Calcispongiæ* form the order of the Metrograntiæ (*Ascometra*, *Leucometra*, *Sycometra*). Forms which the artificial system regards as representatives of different genera and species here grow united upon a single stock. This fact is quite irreconcilable with the species-dogma.

5. Causes of the Production of Form.

Besides the great interest which the biology of the Calcispongiæ possesses in connexion with the theory of descendance and the critical conception of the organic species, it is also of extraordinary general significance, because in this small and simply constructed group of animals *the true causes of biological phenomena*, and especially the causes of the production of form, may be reviewed with particular clearness and recognized with particular certainty. These causes prove throughout to be *purely mechanical unintelligent causes* (*causæ efficientes*), while we seek in vain for any *designedly active intelligent causes* (*causæ finales*).

If we briefly sum up the most essential points relating to this matter, we arrive at the following results:—

1. *The general external form of the Calcispongiæ, both that of the social stocks and that of the individual persons, is a product of growth* which is principally governed by *adaptation to the external conditions of existence* of the locality and surroundings; the mode of growth is only to the smallest extent inherited within the species. The same applies to the *quadruply different formation of the mouth* in the persons.

2. The *triply different structure of the wall of the stomach* by which the three natural families are distinguished is in part a product of *inheritance* and in part of *adaptation*. The original structure of the wall of the stomach, as it occurs in the *Ascones*, is inherited from *Olynthus*, the stock-form of all Calcispongiæ: *Olynthus*, however, inherited it from the *Archispongia*, the latter from the *Protascus*, and this from the *Gastræa*. The structure of the wall of the stomach in the *Leucones* has been produced from that of *Olynthus* by growth of the exoderm and stabilization and ramification of the inconstant pores, and the structure in the *Sycones* by strobiloid budding.

3. The multifarious other characters of the *gastro-canal system* are mere products of special adaptations, in which the *flow of water* is especially effective; this, again, is dependent on the movement of the flagella of the cells of the entoderm.

4. The extremely remarkable conditions of the *intercanal system* are brought about merely by *concrecence*. By this purely mechanical process of growth very complicated and characteristic stock-forms and personal forms are produced, in which *enclosed portions of the sea become constituent organs of the organism*.

5. The exceedingly characteristic primary *form of the calcareous spicula* is a purely mechanical product of two co-operating factors, the *capacity for crystallization of calc-spar* and the *secretory activity of the sarcodine*. In the production of the secondary forms of spicules the formative current of water and adaptation to other, more subordinate, external conditions of existence are effective.

6. The orderly, often very regular, elegant, and apparently artificial *constitution of the skeletal system* is for the most part a *direct product of the current of water*; the characteristic position of the spicules is produced by the constant direction of the current of water; to a very small extent it is the consequence of adaptations to subordinate external conditions of existence.

7. *All other characters of form* which might come into consideration here may be referred to the formative activity of the *cells* of which the two constituent lamellæ of the sponge-body, the *entoderm* and the *exoderm*, are composed; but these are inherited from the *Protascus*, and further from the *Gastræa*. The *motile phenomena* of these cells are particularly efficacious in this respect—on the one hand the *amœboid movement*, and on the other the *flagellar movement*, which is to be referred to the latter.

8. The special properties of these cells in the *Calcispongiæ* are due to the *chemical composition* of their body—of the *protoplasm* on the one hand and of the *nucleus* on the other. Of these two constituents of the cell, the *protoplasm* is especially to be regarded as the *biorgan of adaptation*, and the *nucleus* as the *biorgan of inheritance*.

9. The (chemical) properties of the two albuminoid compounds which form the *protoplasm* and the *nucleus* are to be referred to the *peculiar affinities of carbon*. Originally they were active in the simplest manner in the constitution of the *plasson* which formed the entire body of the simplest *Moneron*. From this was produced, only by *adaptation* (differentiation of the *plasson* into *nucleus* and *protoplasm*), the first cell, an *Amœba*. This is recapitulated, in accordance with the biogenetic fundamental law, by the *ovicell*. The specific properties which the *ovicell* of the *Calcispongiæ* possesses were acquired by it *by inheritance* from the most ancient *Olynthus*.

6. *The Calcispongiæ and Monism.*

The most general results furnished by the present monograph of the Calcispongiæ are of a purely philosophical nature, and may be summed up in the statement that *the biogeny of the Calcispongiæ is a coherent proof of the truth of monism*. In my 'General Morphology' I sought to demonstrate synthetically that all the phenomena of the organic world of forms can be explained and understood only by the monistic philosophy; and now this demonstration is furnished *analytically* by the morphology of the Calcispongiæ. The great contradictions of the philosophical conceptions of the world, or between *monism* or the *mechanical* and *dualism* or the *teleological* conception of nature, which are rendered evident by every consistent reflection, may be tested in detail in the biology of the Calcispongiæ; and every examination turns out favourable to the former and disadvantageous to the latter.

All the phenomena met with in the morphology of the Calcispongiæ may be completely explained by the reciprocal action of two physiological functions, *inheritance* and *adaptation*; and we need no other causes to comprehend their production. All the causes which are found to be effective in the morphology and physiology of the Calcispongiæ are unintelligent mechanical causes (*causæ efficientes*); and nowhere do we meet with intelligent designedly active causes (*causæ finales*). Everywhere we can detect the prevalence of unalterable natural laws, nowhere the interposition of a preconceived plan of creation.

It might appear that in the form-production of the Calcispongiæ *every thing depended upon chance*. But *chance* no more exists in nature than *design* or *freedom*. All processes are performed with absolute necessity, as the complex result of the coincidence of numerous causes, each of which is of purely mechanical nature, and itself again conditioned by more distant *causæ efficientes*. What we call *chance* is merely the coincidence, unexpected by us, of circumstances each of which is finally brought about with absolute necessity by a chain of efficient causes.

As all the phenomena presented to us by the biology of the Calcispongiæ may be perfectly understood by the theory of evolution, as a matter of course all assumption of a creation is completely excluded in this department. But as the body of the Calcispongiæ in the developmental stage of the *Gastrula* already consists of the same two germ-lamellæ which compose the body of man and of all the higher animals at an early period of embryonic development, we must consistently assume the same mechanical development for man also. This indication shows in the clearest manner the high importance of the Calcispongiæ for the monistic philosophy.