

maxillæ, without exterior lobe ("galea") or palpus; and, as to internal organization, above all, by the want of Malpighian vessels.

Nicoletia terrestris, L. (sp. *Lepisma*) may be a connecting link, resembling *Campodea* in the form of body, equally scaleless and bleached, and having the internal lobe of the maxilla pectinated somewhat alike; but, in this view, the internal anatomy of *Nicoletia* remains to be investigated. From Poduridæ the proposed family differs no less by the oral organs, than by the essentially many-jointed antennæ, the full normal number of abdominal segments developed, the consequent direction of the terminal appendages, and the elongated tarsus, armed with a pair of equal unguiculi.

On Animal Individuality from an Entozoological point of view.

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[Read June 1, 1865.]

WHEN Dr. Carpenter in the first instance, and Professor Huxley subsequently, promulgated their original and philosophic views respecting the question of animal individuality, they virtually established a general proposition regarding the constitution of the "zoological individual," which forms an admirable stand-point by whose aid we may interpret the significance and relations of a series of life-phenomena which must otherwise have long remained misunderstood and, consequently, also undervalued.

The general proposition here referred to was formally embodied in the announcement that the "zoological individual" comprises the sum-total of the phenomena displayed by all the products of a single ovum, or, to employ Prof. Huxley's own words, "the *individual* animal is the sum of the phenomena presented by a single life."

Physiologists have long since maintained that the human frame, during its life-period, is represented by several epochs, each of which is absolutely distinctive and separable in so far as actual matter or tissue is concerned, but inseparable and almost indistinctive as regards mere appearances, whether external or internal. In other words, during man's growth we have a definite succession of life-phases which are analogous to, if not in any sense homologically identical with, the distinctive and peculiar temporary forms of life so notably characteristic of certain of the lower animal types.

Taking, as it were, a bird's-eye view of the whole zoological

series, these temporary life-phases display every degree of distinctiveness from the almost imperceptible up to the separable, free, individual-like being for the designation of which Prof. Huxley has felicitously proposed the term "zoöid." All these phases are now known to be phenomena of growth, metamorphosis, and gemmation, there being no such thing as "alternate generation" in the truest sense of this phrase*.

Applying these principles to the interpretation of the phenomena of entozootic life, some very curious results appear to be attainable when we come to deal with the more complicated forms. Starting, however, with a species where the individual is represented by simple, non-metamorphosed life-phases, we necessarily encounter the almost indistinctive conditions of ordinary growth. Thus I select, in the first instance, the so-called *Trichina spiralis*, whose life-phenomena (according to the synoptical method initiated in my work on Entozoa) may be tabulated as follows:—

ZOOLOGICAL INDIVIDUAL (*Trichina spiralis*).

- a. Ovum in all stages.
- b. Intra-uterine embryo.
- c. Free embryo or migrating larva.
- d. Resting or sexually immature larva.
- e. Expectant or sexually distinctive *Trichina* (often encysted).
- f. Free, sexually mature intestinal *Trichina*.

Now, although the various larval stages above indicated bear a general resemblance to the adult *Trichina*, we have, even here, some faint traces of "epochs" which, were they only rather more strongly pronounced, would enable us to draw lines of demarcation. In some instances the life-epoch may be homologically identical with a temporary bud, but it may also comprise a multitude of *gemmæ*. Each such successive life-epoch, whether distinctive or indistinctive, separable or inseparable, I propose to call a *biotome*; and when two or more such life-divisions are recognizable, I propose to call them "secondary" or "tertiary" biotomes, as the case may be. I would observe that the term "biotome" is not designed to supersede the term "zoöid," but rather to limit the

* Since this passage was written, I have received an important communication from Professor Leuckart, in which he states that he has reared sexually mature free Nematoids, of the genus *Rhabditis*, from *Ascaris nigrovenosa*. If this be the case, we have here, for the first time, a true alternation of generation, or, to say the least, a true sexual dimorphism in animals (Nachrichten von der Königl. Gesellschaft der Wissensch. zu Göttingen, No. 8, April 19, 1865, p. 227).

latter to an individualized, free, constituent portion of the "biotome." The propriety of this arrangement will, I think, appear in the sequel. Let us, therefore, in the next place, glance at the life-phases of one of the cestodes. Those of *Tænia serrata* may be tabulated thus:—

ZOOLOGICAL INDIVIDUAL (*Tænia serrata*).

a. Ovum in all stages	} Primary "biotome."
b. Six-hooked embryo, boring larva, or prosclex	
c. Resting larva, scolex, or <i>Cysticercus pisiformis</i>	
d. Sexually immature tapeworm in all stages ...	} Secondary "biotome."
e. Mature tapeworm-colony, strobile, or <i>Tænia</i> ...	
f. Segment, free-joint, or <i>proglottis</i> (zooid)	

According to Prof. Huxley's views, in the above "individual" the stages *a*, *b*, *c*, *d* would collectively represent the first life-phase or "protozooid," whilst the final phase, *f*, would be the "deuterozooid." I have, indeed, with Professor Huxley's approval, so represented them in my introductory treatise on Entozoa; but, recently, I have not been able to satisfy myself that the nomenclature in question meets all the requirements of the case. In my view, the six-hooked embryo is as much an individualized form as the *Cysticercus*-stage, whilst the latter is as much a life-phase as the *proglottis* itself. Why therefore may we not here recognize three zooids (proto- deutero- trito-zooids), instead of two only, after the manner suggested by Prof. Huxley? If this view be accepted, our *Tænia serrata*, in its full zoological individuality, would be represented by two biotomes, the primary one comprising two individualized phases (the prosclex and scolex, or protozooid and deuterozooid), and the secondary one comprising a practically indefinite number of individualized forms or tritozooids. In the one case the independent life-phases are the result of metamorphosis, but in the other they are the product of gemmation. Let us next see how the matter stands in regard to one of the Trematodes, say, for example, the common liver-fluke (*Fasciola hepatica*), which may be tabulated as follows:—

ZOOLOGICAL INDIVIDUAL (*Fasciola hepatica*).

a. Ovum in all stages	} First "biotome."
b. Ciliated free-swimming embryo	
c. Non-ciliated larva (nurse, germ-sac, sporocyst, <i>redia</i>) ...	} Second "biotome."
d. Active, migrating, tailed larva (<i>cercaria</i>)	
e. Encysted, resting larva (<i>pupa</i>)	} Third "biotome."
f. Sexually mature fluke (<i>fasciola</i>)	

This is probably a fair representation of the ordinary fluke individual (*Fasciola hepatica*), in which species the entire life-phases have not as yet been thoroughly identified. It is quite certain that the life-phases are never less numerous or complicated than is here indicated; whilst Pagenstecher's researches tend to prove that, under certain climatal conditions, the number of larval forms may vary considerably. In other words, the fluke individual does not comprise any definite number of "zooids," although the kinds of zooids are limited. In the present case I recognize three "biotomes." The first includes only one temporary, independent life-phase; this is the ciliated animalcule, which, in my view, possesses sufficient individualized life to entitle it to be recognized as a "protozoid." The second "biotome" may in some cases comprise only a solitary, simple sporocyst or germ-sac (deuterozoid); but an almost indefinite multiplication of new and independent germ-sacs, as well as other more highly organized "nurse-formations," may also be developed from the primary sporocyst (secondary and tertiary "deuterozooids"). This reminds us of the practically indefinite number of zooids (proglottides) which the second "biotome" of the Cestode gives rise to; but here there is analogy, and not homology. The third "biotome" embraces a large but variable number of "tritozooids" (*cercariæ*), an equal number (whatever that may be) of "tetartozooids" (*pupæ*), and therefore, also, a similar number of "pemp-tozooids" (flukes).

Whether the views here promulgated be accepted or not, I have, I trust, made it sufficiently clear that the fluke-individual may comprise, in its life-cycle, a great and varying number of life-phases, each of which may or may not possess equivalent (and, necessarily, very limited) zoological value. The variability of the character of these life-phases is shown by the sporocysts (deuterozooids), which are not only unequal to one another in bulk, but also in organization, the higher forms (*redia*) developing a rudimentary digestive apparatus. Apparently the *redia* is not, in all cases, an essential feature of Trematode larval life. Putting together the whole possible and independent life-phases, and placing their numerical development within the lowest limits, our ordinary fluke-individual would, I reckon, comprise about 370 "zooid" formations, those of the second "biotome" being produced by the well-known process of internal gemmation, whilst those of the third "biotome" are the result of a simple yet prolonged metamorphosis.

I conceive that Dr. Pagenstecher's apparently well-established proposition (that "only such Trematode larvæ as are capable of arriving at sexual maturity are furnished with special appendages") gives strength to my views regarding the recognizable epochs in the fluke-individual's life, and points to the line of origin, continuity, and definiteness of the third "biotome" which I have recognized on totally independent grounds. There is about the same relative amount of individualized being in the caterpillar, pupa, and imago states of the Insect as there is in the cercaria, pupa, and fluke conditions of the Trematode; but the "epoch" of the one embraces the whole life of the "zoological individual," whilst in the other it represents only a section or "biotome" of the life-cycle. If the term "zooid" be not allowable for the separate metamorphosed life-phases, as well as for true gemmæ, some other distinctive nomenclature must be substituted. I would like to see it retained to designate the semi-individualized, separable life-phase, without regard to its mode of genesis.

Practically, other curious results arise out of the foregoing considerations. For example, a single sheep may harbour 1000 flukes. Each fluke carries, I believe, at least 10,000 eggs. Each egg may give rise to 370 zooids. It thus appears that, if all the conditions were favourable, a single fluke might originate between three and four millions of individualized life-forms; whilst the solitary sheep itself would, under the same circumstances, be the means of producing at least 3,000,000,000 fluke-zooids! Happily no such result as this can possibly occur in nature, since a multitude of "interfering agencies" places the "favourable conditions" in a comparatively insignificant minority. However, the balance of parasitic forms from all cattle-sources is sufficient to destroy thousands of sheep annually, to say nothing of the wounds inflicted on millions of small mollusks, into whose bodies the "zooids" penetrate.

Reverting to the Cestodes, the results attainable from particular species are, in some respects, still more striking. Let us separately examine the "zoological individuals" of *Tænia cœnurus* and *Tænia echinococcus*. The life-phases of the former may be tabulated as follows:—

ZOOLOGICAL INDIVIDUAL (*Tænia cœnurus*).

- | | |
|---|--------------------|
| a. Ovum in all stages | } First "biotome." |
| b. Six-hooked embryo, boring larva, or <i>proscœlex</i> ... | |
| c. Resting, polycephalous larva (<i>Cœnurus cerebralis</i>) | |

- | | |
|--|---------------------|
| d. Sexually immature tapeworm | } Second "biotome." |
| e. Mature tapeworm-colony, or strobile | |
| f. Segment, free-joint, or <i>proglottis</i> | |

At first sight, this representation appears to be the same as that of the *Tænia serrata*, already given. It is, in truth, zoologically equivalent, but the component life-phases are both structurally and numerically different. The "resting larva" of *Tænia serrata* consists of a single free scolex, whilst the resting larva of *T. cænurus* comprises a multitude of conjoined, inseparable *scolices*. In the one case the scolex is a true "zooid," in the other it is the merest fraction of a "zooid." In the case of *Tænia serrata* one single egg, under the most favourable conditions, can only lead to the development of one tapeworm; but, under like circumstances, the single egg of *Tænia cænurus* may lead to the formation of at least 300 tapeworms. This is accomplished when the *Cænurus* of the sheep's brain is transferred to the stomach of the dog, and all the scolex-heads with which it is furnished become developed into tapeworms. If we call to our aid an estimate of the "zooids," the result is much more markedly significant. On the plan of interpretation previously adopted, the "zoological individual" of *Tænia serrata* (allowing 500 proglottides for the strobile) would only yield us 503 "zooids" (as I have defined them); but in the case of *Tænia cænurus* this representation would certainly give us as many as 1,500,000 "zooids." Then, as regards the total number of eggs produced by all the final "zooids" collectively, we should, in the case of *Tænia serrata* (allowing each proglottis to contain 5000 ova), obtain the comparatively small total of 2,500,000 eggs; whilst in the case of *Tænia cænurus*, the progeny of a single germ would collectively give out no less than 7,500,000,000 ova! Lastly, let us glance at the possible results derivable from a consideration of the "zoological individual" of *Tænia echinococcus*, which may be tabulated after the same fashion:—

ZOOLOGICAL INDIVIDUAL (*Tænia echinococcus*).

- | | |
|--|---------------------|
| a. Ovum in all stages | } First "biotome." |
| b. Six-hooked embryo, boring larva, or proscœlex ... | |
| c. Resting, acephalocystic larva (hydatid) | |
| d. Sexually immature tapeworm | } Second "biotome." |
| e. Mature tapeworm-colony, or strobile | |
| f. Segment, <i>proglottis</i> , or free-joint..... | |

Here, again, the representation is as simple as obtained either in the case of *Tænia serrata* or in *Tænia cænurus*; but, in point of numerical and structural detail, the life-phases are remarkably different. In this case the "resting larva," as in *Cænurus*, is

furnished with a multitude of "heads," the latter being the so-called echinococci or scolices developed in a rather more complete form than obtains in the case of *Cœnurus cerebralis*. In fact, the so-called "heads" are almost separable "phases," being attached to the maternal larva by slender pedicles only. They are, indeed, frequently found detached; but then it is questionable if they have not already parted with their vitality. In this view I cannot call them "zooids"; but the daughter-hydatid formations, which are developed within or without the original maternal hydatid, are quite deserving of such distinction. The latter are separable, organized life-phases, each of which, like its parent, may develop a multitude of echinococci; so that, under favourable conditions, there is practically no limit to the number of "heads" which may be generated by a proliferating hydatid; consequently, also, there is practically no limit to the number of tapeworms liable to be developed from the same source. The tapeworms in this case, however, have only three joints capable of arriving at sexual maturity, and only one of these is mature at one and the same time. Whether or no these *Tæniæ* are susceptible of indefinite proglottis-multiplication, after the fashion of ordinary tapeworms, is a point on which I am, at present, uninformed; it is probable, however, that the joints follow the ordinary law of successional development. In either case our computation of the number of zooids and eggs capable of arising from a single germ needs not be affected by this consideration. Taking an average case of hydatid development, and assuming the existence of conditions favourable to the complete development of the entire progeny, a single germ of *Tænia echinococcus* might, without any exaggeration, give us between five and six million separate life-phases or "zooids," from which, under like circumstances, there would result not less than 150,000,000,000 ova! In this calculation I do not take into account the probability of any one tapeworm developing more than three successive sexually mature segments, and I allow for each proglottis (tetartozooid) 10,000 eggs. For each hydatid I allow 10,000 scolices, though one large acephalocyst may develop ten times that number. As many as a thousand hydatids, or more, may be developed in a single "host"; but echinococcus-heads are not usually present in more than a limited number of the daughter vesicles. Were they less "cribbed, cabined, and confined" than is usually the case, no doubt their power of developing the so-called "heads" would be correspondingly increased. As it is, we may truly say, "*Quantitas sufficit.*"



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