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I. Wissenschaftliche Mitteilungen.

1. The Classification of the Copepods.

By C. B. Wilson, Westfield, Mass.

eingeg. 4. Februar 1910.

Everyone who has studied the Copepods, whether free-swimming or parasitic, must have been impressed with the great diversity of opinion which has prevailed among investigators in regard to their classification. On examining the different schemes proposed we find that not only has every portion of the Copepod's body been used by one systematist or another as a basis of classification, but even their habits, their mode of life, and their method of reproduction have been called into service.

And the men whose names we find attached to these various schemes take rank among the foremost scientists of their time.

We find *Linnaeus* (1735), for example, including the Copepods (with other Crustacea) among the wingless insects, and dividing them according to the number of appendages and the fusion of the head and thorax. *Fabricius* (1775) in his revised editions of the *Entomologia*

Systematica used the structure and position of the mouth-parts as a basis of classification. Latreille (1796) selected the fusion of the head and thorax, together with the structure of the thoracic appendages, and in his later editions does not even mention the mouth-parts. Lamarck (1801) preferred the form of the gills, and the form and structure of the thoracic appendages. Desmarest (1825) used the mouth-tube and the number and structure of the thoracic appendages. Burmeister (1833) selected the antennae and the structure and arrangement of the mouth-parts. H. Milne-Edwards (1840) united the parasitic Copepods with the Pycnogonids and created out of the two a separate sub-class (Des Crustacés suceurs) of the Crustacea. The former were then divided according to the jointing of the thorax and the development of the swimming legs, the second antennae, and the maxillipeds. Steenstrup and Lütken (1861) made their division according to the kind of egg-sacks and the arrangement of the eggs within them, thus shutting out the male sex entirely. These two authors and Thorell (1861) were the first to include parasitic forms along with the free-swimming species, and to divide the entire group on a common basis. Thorell used for this purpose the mouth-tube and mandibles, and the structure and arrangement of the maxillae. Unfortunately he made a serious mistake in denying the existence of mandibles in his second division, the Poecilostoma. Claus corrected this mistake in 1862, adopting the first (Gnathostoma) and third (Siphonostoma) of Thorell's divisions; he then included the families which had been placed in the second under the one or the other of them according to the structure of the mouth-parts.

Gerstaecker in Bronn's Tierreich (1881) adopted Claus' classification with a few minor changes. Canu in »Les Copépodes du Boulonnais« (1892) proposed the number of sexual openings in the female as a primary basis of division, thus again excluding the male sex entirely. Giesbrecht (1892), including only pelagic forms, separated them first according to the articulation between the fore and hind body and the structure of the fifth thoracic legs. His second division was based on the structure of the first antennae.

G. O. Sars (1901—3) in his extensive work on the Crustacea of Norway, divides the order Copepoda into seven suborders, each named from the type genus which represents it, the Calanoida, Harpacticoida, Cyclopoida, Notodelphyoida, Monstrilloida, Caligoida, and Lernaecoida. No one thing is taken as the basis of this classification, but rather a combination of all the differences which characterize these respective types. For his division of these suborders he has adopted Giesbrecht's basis of the structure of the first antennae in the Calanoida and uses

the mouth-parts in the Harpacticoida, the only two thus far published. The most recent works on the Crustacea, that in the Cambridge Natural History by Geoffrey Smith, and that in Lankester's Treatise on Zoology by W. T. Calman, both bearing the date of 1909, adopt Giesbrecht's classification. Smith says "Although much detail remains to be worked out and the position of some families is doubtful, Giesbrecht's scheme is the most satisfactory that has hitherto been suggested." (p. 57.)

Calman, after noting that Giesbrecht makes no attempt to define the position of many of the parasitic forms, says "The system is therefore incomplete and can only be adopted as a temporary expedient pending further investigation." (p. 101.)

It requires about as thorough a knowledge of the Copepods to select intelligently from these various schemes, backed as they are by competent authority, as it would to construct an original scheme. Indeed most authors have apparently found the latter the easier, since each has propounded a scheme of his own. In the face of such perplexity and disagreement we may well ask a few pertinent questions.

I. Are there objections which, when impartially considered, are of sufficient weight to warrant the elimination of any of these schemes?

a. The methods of classification used by the early writers, according to which the Copepods were placed now among the insects, and again with the mollusks or worms, are of course not to be thought of at the present day, however useful they may have been as stepping-stones of progress. This objection removes all the schemes proposed prior to the time of Milne-Edwards (1840).

b. It seems perfectly obvious that any truly scientific classification must include all the Copepods, free-swimmers, semi-parasites and parasites. The transitions in body-form, in the structure of the appendages, in habits and mode of life, and in the method of reproduction are so gradual that no classification can claim to be complete which does not include the whole group. Milne-Edwards entirely separated the free-swimmers from the parasites, placing them even in different subclasses of the great class Crustacea. Brady's fine monograph (1878—80) included only the free and semi-parasitic species, and made no provision for the true parasites. And Giesbrecht really included only the pelagic species which he had examined. These three systems, therefore, must be regarded as partial and incomplete.

c. Finally to confine the basis of division to the female sex is as pernicious here as it would be among the birds; for many of the most striking characteristics are to be found only in the males. This is particularly true of the parasitic forms where the female often becomes so

degenerate as to lose all distinctive characters while the male retains them. For this reason the classifications of Steenstrup and Lütken and Canu cannot be accepted. The former is also open to the further objection that it includes only the true parasites and leaves out of account the free and semi-parasitic species.

We have thus by elimination practically brought our choice down to two systems, the one originally proposed by Thorell, and afterward adopted and corrected by Claus and Gerstaecker, and the other put forward by Giesbrecht and subsequently modified by Sars. And we may propose a second practical question.

II. Is there anything aside from inherent excellence and the authority and experience of the propounder that will guide us in selecting between these two schemes?

a. Thorell's well known division received much credit when proposed, but we have already shown that in the very next year it was found that many of the genera in the second division really did possess mandibles. Claus and Gerstaecker tried to correct this and other errors, and still preserve Thorell's scheme. But the original basis having proved false, the corrected schemes are necessarily patched up affairs, and for that reason not satisfactory. In the final correction by Claus, for example, the first suborder is called Gnathostoma from the structure of the mouth-parts, while the second sub-order is known as the Parasita from the habits of its members. The Parasita are then divided into those with a beak or siphon (Siphonostoma) and those which have none. The first suborder thus corresponds to one of the divisions under the second one.

b. This scheme does not readily include all the known forms, either free or parasitic. Gerstaecker acknowledged (Tierreich, pp. 716 bis 730) seven genera of doubtful position, and there are fifty others which he enumerated under the several families but could not place definitely. This is more than 25% of all in the entire group, far too large a proportion to be omitted in any valid classification.

c. Finally this scheme mixes up the genera badly, so that forms otherwise closely allied are widely separated by some habit or anatomical detail. Giesbrecht has well shown that forms with biting (Gnathostoma) and others with suctorial (Siphonostoma) mouth-parts may occur even in the same family. Again the females of the genus *Ergasilus* are true parasites while the males are free-swimmers all their lives. To separate the members of such families or the sexes of such genera in a scheme of classification is manifestly as unscientific as it is unnatural.

After such an accumulation of adverse criticism of the one system a third question naturally suggests itself.

III. Is the remaining system to stand solely because it is the only one left, or can we find positive recommendations for it?

Is this a case of simply selecting the "most satisfactory hitherto suggested", or is there some standard, reliable as well as impartial, which will testify to absolute rather than relative merit? There are two such standards, of differing values, the one universally acknowledged, the other presented here for the first time within the writer's knowledge.

a. The former is found in the life-history of the various species, and its testimony, when once accurately presented, is received as final.

It needed but a partial knowledge of the development of *Lernaea* to remove it forever from among the worms (Vermes mollusca) where it was first placed. The complete life-history we now possess will locate it just as definitely among the Copepoda.

But unfortunately our knowledge of the life histories of the Copepods, especially the parasitic forms, is at present extremely limited. Moreover every investigator who has made the attempt to secure one of these life-histories realizes the extreme difficulty of the task. In a recent number of the *Zoologischer Anzeiger* (March 16, 1909) Dr. Otto Pesta has called attention to this very fact. He first quotes from Giesbrecht (1892). "Für eine natürliche Systematik der Parasiten wird es nach meiner Meinung vor allem richtig sein, festzustellen, welche Gruppe der Podoplea die Parasiten sich ausschließen, dann in welchem Cyclopoïd Stadium bei den einzelnen Arten sich der Beginn des Parasitismus nachweisen läßt . . . von weiterer Bedeutung für die Gestalt, die der Parasit schließlich annimmt, wird es auch sein, welcher Art die Existenzbedingungen sind, die er an dem Wirte vorfindet" (p. 151). After noting that these suggestions of Giesbrecht's involve difficult and long-continued study, he offers some consolation in the fact that it is not necessary to know the development of every parasitic species in order to lay the foundation of a good classification; it would be sufficient to investigate only the more typical members of the various families. He adds at the close that only when Giesbrecht's proposed investigations have become actualities will there be hope of establishing a system that will correspond to the natural relationships. But these facts come slowly. Among the true parasites we do not at present know the life-history of any genus belonging to the families Ergasilidae, Chondracanthidae, Dichelestiidae and Antheacheridae. We need at least one from each of these; let it be hoped that such an imperative demand will furnish the requisite incentive to some investigator in the near future.

b. A second standard may be found in a study of the degeneration produced by parasitism, and its testimony is much more easily and

quickly available. One of the most common results of parasitism is that an organ ceases to be used, and in consequence first loses its function, then its size and shape, and finally may altogether disappear. A careful study of the comparative anatomy of these parasites shows that in them degeneration is almost an exact reversal of development. They plainly demonstrate the truth of the three principles originally proposed by Vøgt in 1878. Parasitism exerts its first influence upon the size and external shape of the body. In the second place it works upon the jointed appendages, beginning with the swimming legs and ending with the appendages of the head. And finally the appendages yield to adaptation in an inverse order to that in which they made their appearance during larval development, the first antennae being the last pair to suffer serious modification. From these facts certain conclusions may legitimately be drawn.

1) Degeneration may be made a valuable factor in determining the classification of parasitic forms. Being the reverse of development it may be used to corroborate the latter on doubtful points, or may furnish timely suggestions where for any reason the life history is not available.

2) If the body form offers least resistance to parasitism, it will as readily yield to other transforming influences, and its systematic rating should be correspondingly low. To distinguish a sub-group, or even a family like the Lernaeidae, chiefly by the fact that they possess an unsegmented and highly degenerate body, will be sure to result, as was actually the case, in bringing together degenerate forms belonging to several families, which subsequent investigation must sort over and rearrange. But to distinguish the genus *Lernaea* from the genus *Penella*, both of them highly degenerate, or to separate one species of *Caligus* from another nearly like it, by their general body form, proves to be scientific, logical and satisfactory.

3) The testimony derived from body form must always give way to that derived from any of the appendages, whenever there is a conflict between the two. Krøyer located the genus *Echetus* in the family Lernaeidae on the basis of its body form, not having the opportunity to examine its appendages. As soon as the latter were determined it was transferred from this most degenerate of the Copepod families to one of the least degenerate, the Caligidae, and yet its body form was totally unlike that of any known Caligid.

4) Among the appendages themselves degeneration emphasizes the testimony of development, that their systematic value varies directly with their appearance during development and indirectly with their disappearance during degeneration.

The three nauplius appendages should possess higher systematic

value than the remainder of the mouth-parts, and the latter in turn should outrank the swimming legs. To base the primary divisions of the Copepoda upon the form of one or more of the swimming legs, and to follow this with subordinate divisions derived from the structure of the first antennae, may seem convenient, but it will not prove to be scientific or satisfactory. In proof of this statement see the discussion under 6.

5) Degeneration may go a step farther and indicate for us which of the appendages in the various groups is likely to possess the higher systematic value. The three nauplius appendages appear simultaneously and development does not enable us to make any selection among them. But in degeneration they disappear one at a time, and the first antenna remains the longest. Consequently the marked differences, for example, in the structure of the first and second antennae ought to outweigh the similarity of the mandibles, in deciding whether the two genera *Thersitina* and *Ergasilus* are to be fused or kept distinct. Among the other (i. e. beside the mandibles) mouth-parts the maxillipeds disappear first, but the second maxillae are not as easily modified as the first pair. The swimming legs degenerate in exactly the reverse order of their development, the posterior pair disappearing first. These relative values of the various appendages may well furnish useful suggestions in deciding such systematic questions as the one just referred to.

6) The parasites and semi-parasites comprise more than three-fifths of the entire group of Copepods. No classification of this group, therefore, can afford to neglect the testimony and the suggestions derived from degeneration. Let us examine the Giesbrecht-Sars system on this basis. We have already stated that Sars adopted Giesbrecht's secondary basis of division; the vital question therefore is with reference to the primary division. Giesbrecht used as the basis of his first division the location of the boundary between the fore and hind body and the structure of the fifth (posterior) pair of swimming legs.

These are two of the things which possess the very lowest systematic value according to the testimony of degeneration, useful for distinguishing genera and species, but not stable enough for separating sub-orders and tribes.

No better proof of the truth of this testimony could be asked for than that which is furnished by the attempted application of such a primary basis in the hands of three as able workers as Giesbrecht, Smith and Calman. What measure of success has attended their efforts?

a. Objection has already been made that the resulting system is only a partial and incomplete division of the group. It is worth while

to emphasize this incompleteness more fully. Giesbrecht himself in his latest word on the subject, "Die Asterocheriden des Golfes von Neapel" (Fauna and Flora, Gulf of Naples, Monograph 25, 1899), enumerates fifteen families which he says "can be assigned with certainty" to the Podoplea (p. 57), three of them being fish parasites. But he makes no attempt to even mention the doubtful families, and hence we cannot judge how many of these there are in his estimation.

Smith, on the other hand, comes out boldly and places all of the parasites and semi-parasites under the Podoplea, but acknowledges that the position of some of them is doubtful. He enumerates in all twenty-four families, four in the Gymnoplea and twenty in the Podoplea. After finishing his remarks on the seventh family, he says "The rest (namely, the other seventeen families) are either true parasites or else spend a part of their lives as such" (p. 63). Of these only half can be definitely located, leaving seven families or 30 % of the whole group still in doubt.

Calman is more conservative; after locating twenty-one families more or less definitely, he adds "The position of the remaining families (consisting wholly of parasitic forms) with respect to this system of classification is not yet determined" (p. 103).

He mentions six of the "most usually accepted" of these "remaining families" but omits the Antheacheridae (Philichthyidae) which is fully as well known as any of the others, and which is included by Smith. This makes seven families undetermined and twenty-one determined or exactly 25 % and 75 % respectively.

But even these figures do not give us a correct idea, for the great majority of the determined families contain but a few genera, while these undetermined ones are among the latest in the group and together contain more than two-fifths of all the Copepod genera. Cannot such a division be justly called incomplete? And does not the failure to definitely locate from 40 % to 45 % of the group under consideration substantiate the testimony of degeneration that the basis of primary division which has been used possesses a low systematic value?

b. Nor is this due to a lack of definite information, we already know the morphology of these "remaining families" in detail, as well as the complete life history of one or two type genera in at least four of them.

And there is apparently no hope that we shall ever be able to locate some of them according to this system. Giesbrecht has stated in clear and unmistakable terms the diagnostic character which forms his primary basis of division. The body segment carrying the fifth legs belongs in the Gymnoplea to the fore body, its legs are normal in the female, modified into copulatory organs in the male, so that in this sub-

order the first segment of the hind body is the genital segment, which is always without legs. In the Podoplea the fifth segment belongs to the hind body, its legs are always rudimentary and never modified into copulatory organs, so that in this suborder the first segment of the hind body is the fifth, and it, together with the genital segment, carries rudimentary legs (Die Asterocheriden, p. 48). Such a diagnostic character may serve very well for the free Copepods, but in quite a large proportion of the fish parasites there is no body segment carrying a fifth pair of legs either in the adult male or female, or in any stage of their development. *Achtheres* and *Lernaea* are excellent examples from two of the families.

The adults of both sexes are so degenerate as to give no evidence at all, and this degeneration commences at such an early stage in their life history that we shall never be able to decide with certainty whether the fifth segment belongs with the fore or hind body. *Lernaea* possesses at one stage of its development four pairs of legs but does not show even the rudiments of a fifth pair, while *Achtheres* develops only two pairs with the extreme rudiments of a third. Hence, even if we could locate the fifth body segment, there must of necessity be lacking the two pairs of rudimentary legs which characterize the first two segments of the hind body in the Podoplea.

Again in the Caligidae the arrangement of the muscles in the adult clearly demonstrates that the movable articulation is between the third and fourth thorax segments and not between the fourth and fifth, and in living specimens that is where we find flexion actually taking place. Practically therefore the fourth somite is as firmly connected with the hind body as the fifth, and the first three segments of the hind body each carry a pair of legs in some of the genera, while in others there is only the pair on the fourth segment and not even the rudiments of any on the fifth or the genital segment.

c. A third objection to Giesbrecht's system is very clearly stated by Smith. "The adoption of this classification necessitates our separating many families which superficially may seem to resemble one another, e. g., the semiparasitic families Lichomolgidae and Ascidicolidae, and the Dichelesteiidae from the other fish-parasites; it also necessitates our treating the presence of a sucking mouth as of secondary importance" (p. 63).

The presence or absence of a siphon or beak ought to be of secondary importance according to the views here stated, but not so the separation of closely related families. The resemblance between the Dichelesteiidae and some of the other fish parasites, the Caligidae for example, is far more than superficial, and to separate them entirely from all the others, as is here done, is both unscientific and unnatural.

d. The unsatisfactory nature of this final attempt by Giesbrecht, one of the ablest investigators of the pelagic copepods, following upon the failures of such men as Gerstaecker, Claus and Thorell, seems to warrant the conclusion that it will be impossible to find anyone basis of primary division in the group that will include all the forms, free-swimmers, semiparasites and parasites. It thus furnishes a very strong negative reason for accepting the scheme proposed by Sars of making the first division in the group upon the same basis as obtains in the class Crustacea as a whole.

Sars selects certain types, distinguished from one another not by any single character; nor even by two or three combined, but by an aggregation of all the diagnostic characters, morphological, ontogenetical and ecological. What has such a primary division to still further recommend it?

e. Around each of the types thus selected can be gathered its near relatives, be they free-swimmers or parasites, possessed of a gnathostome or a sucking mouth, and without reference to where in their anatomy the boundary may fall between the fore and the hind part of the body. There will thus be formed a thoroughly natural and homogeneous subgroup, and all necessity of separating close relatives will be obviated. This is but the natural outcome of a tendency that has been increasingly manifested with the growth of our knowledge respecting the copepods, particularly the semi-parasites and parasites

The genus *Ratania* was found to possess a gnathostome, and yet it was classed with the typically siphonostomatous family, Asterocheridae. Similarly the close relationship of the Ergasilidae and Chondracanthidae, which are true fish parasites, to the semiparasitic Corycaeidae and Lichomolgidae has been steadily gaining acceptance. Such an affinity can be openly expressed in Sars' system, together with many others pertinently suggested by the phylogenetic table published by Gerstaecker (1881, p. 714).

f. Sars' scheme will include every known species of Copepod from the very beginning, and there will no longer be the embarrassment of a large number of "remaining" or undetermined families. If occasion warrants, a single family may constitute a subgroup by itself until it can be more definitely located, or until new forms are discovered which may be grouped with it.

g. Furthermore if it becomes necessary, as our knowledge advances, to divide any of the subgroups or to introduce newly discovered types, this can be easily done without the necessity of wholly destroying or rearranging the previous classification. It possesses in this respect

exactly the advantages of a card catalogue, which are too well known to require further comment.

h. It must not be understood that these suggestions from degeneration are to be received as an absolute dictum from which there can be no appeal.

On the contrary, it may well be found that it is not feasible to use as a basis of division just that thing which possesses the highest systematic value.

In such a case the testimony of degeneration should influence us to select the highest basis available and should keep us from being satisfied with the lowest. Giesbrecht tried the structure of the first antennae as a basis for his second division and it did not prove satisfactory. Just here can be found another strong recommendation of the scheme proposed by Sars; it allows us to use a different basis in the various sub-groups as often as the conditions warrant it. Sars' sub-group Calanoida is the equivalent of Giesbrecht's Gymnoplea, but while the latter author included all the rest of the copepods in the Podoplea, or at least made the effort, and was thereby forced to divide them all on a common basis, Sars divided the same families into six sub-groups, and is thereby free to use six bases of division if necessary.

He has already shown the wisdom of this: his division of the Calanoida was made on the basis of the structure of the first antennae, than which there could be nothing of higher systematic value. But this was not found to be as feasible in the Harpacticoida, and accordingly he divided this second sub-group upon the structure of the mouth-parts, the basis next in rank, and the third subdivision was based upon the structure of the first swimming legs, again the basis next lower in value.

From these considerations it would seem as if, after often repeated changes and more than one hundred years of discussion, we have at last a solid foundation, upon which in due time there is good hope of being able to rear a permanent systematization of the copepods.

By adopting these considerations, therefore, we have the order Copepoda divided into seven suborders. 1) The Calanoida, free living and pelagic. 2) The Harpacticoida, also free living but demersal. 3) The Cyclopoida, partly free-living and freshwater species, partly commensals and messmates with other animals, partly parasitic. 4) The Notodelphyoida, semi-parasitic and living upon ascidians and similar animals. 5) The Monstrilloida partly parasitic and partly free. 6) The Caligoida, parasitic upon fishes, moderately degenerate and with some freedom of motion. 7) The Lernaeoida, fish parasites, strongly degenerate, fixed in position, and with marked sexual dimorphism.

The sub-group Calanoida has been divided into three tribes upon

the basis of the structure of the first antennae, the Amphaskandria, the Isokerandria, and the Heterarthrandria. Each of these tribes is then divided into its various families upon the basis of the family diagnoses, the families of Sars corresponding in general to the sub-families recognized by Giesbrecht.

The sub-group Harpacticoida contains two tribes, the Achirota and the Chirognatha, distinguished according to the structure of the mouth-parts with special reference to the maxillipeds. The second tribe is then separated, according to the structure of the first swimming legs, into two sub-tribes, the Pleopoda and Dactylopoda. This is as far as the work has progressed at the present time, and it would be discourteous to try here to carry it any farther. One or two suggestions, however, will be entirely in place.

It is understood that the Ergasilidae are to be included in the Cyclopoida along with the Lichomolgidae and Corycaeidae, but that the Chondracanthidae are in the last group, the Lernaeoidae. We have already pointed out the close relationship of these four families, which form a natural series from a free-swimming condition as shown in some of the Lichomolgidae, through the various stages of commensalism and semiparasitism seen in other Lichomolgidae and in the Corycaeidae, to the complete parasitism of the Ergasilidae, and the modification and degeneration shown in the Chondracanthidae.

No longer can there be any objection to placing the Chondracanthidae in the third sub-group provided their relationship warrants it, and it would seem better to keep the four families together.

Again further study is likely to emphasize the fact that the Lernaeidae, in spite of their degeneration, are more closely related to the Caligidae and Dichelesteidae than they are to the Lernaeopodidae. Here again as Gerstaecker pointed out in his phylogenetic table, we have a gradation in parasitism, from Caligidae which can still swim and move about freely (*Caligus*, *Lepeophtheirus*, *Trebius*) through various degrees of attachment to their host, with a corresponding loss of the ability to move about (*Pandarus*, *Cecrops* and *Laemargus* among the Caligidae and all of the Dichelesteidae) to the complete fixity and degeneration of the Lernaeidae.

This relationship can well be shown by transferring the Lernaeidae to the Caligoida. There will still be left for the last and most degenerate sub-group an abundance of material.

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