SPECIES CRITERIA IN OSTEOSTRACI, WITH SPECIAL REFERENCE TO THE GENUS TREMATASPIS

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ABSTRACT. An attempt is made to compare species criteria as used in the Genus *Tremataspis* with those used in establishing species in the other genera of the order *Osteostraci*. Exception is taken to Denison's use of histologic characters of the shield as an adequate basis for placing specimens which differ in other respects in the same species.

ONE of the problems which arises to plague every practicing taxonomist is that of establishing valid criteria for the delimiting of species. Few of us would admit serious doubt as to the validity of the species concept, but certainly the criteria we use in our attempt to establish the identity of the species are rather arbitrary. There is an old statement somewhere to the effect that "God made the species, man the higher categories," but if that were true it would have helped mightily if the species had been more carefully labelled. The criteria we use in setting up our taxonomic categories may not be "man-made" but they are definitely "man-selected."

One of the most realistic definitions of species which I happen to have seen is that of Tate Regan (1925), which can be paraphrased to state that a species is any group which has been so designated by a "competent taxonomist." Huxley (1942), in commenting on that definition points out that the definition of competent needs some clarification. Perhaps it would be better stated that a species is any group which has been so designated by a competent taxonomist who has worked with the group under discussion.

We find, to be sure, that there are disputes among the "competent taxonomists" working in the same group as to what shall be valid criteria, but it would seem as though such questions could be settled by following principles which the workers on that group could agree upon. Whether it will ever be possible to establish certain "grades of organization" which can be applied to species criteria throughout the animal kingdom, or even through entire classes or phyla, is questionable, although closer agreement than present schemes indicate would certainly be desirable. Probably no biologist would deny that the number of species of insects is justifiably enormous, but there would be found, I believe, a considerable number of us who would question whether the concept has exactly the same significance that it has in mammalogy.

Even within the class Mammalia the number of species recognized increases markedly as one goes from the large to the small forms. There are many more species of rodents recognized than there are of carnivores. It may be another valid question whether a "species" among rodents is the morphological equivalent of a "species" among carnivores, *i.e.* whether they recognize similar "grades of organization."

When, as in the present paper, we deal with fossil forms there are still other problems which bedevil the would-be systematizer of the systematists. On the strictly morphological level to which we are almost invariably limited in dealing with fossil forms it has been pointed out that the type of criteria used in specific distinctions when dealing with living forms are frequently unavailable when we deal with fossils. In discussing with another taxonomist the problem of separating species in the *Tremataspidae*, during the period when I had my 1938 paper on that group under preparation, he remarked that he believed one was justified, in dealing with fossils, in recognizing as distinct species any form which could be consistently recognized by the investigator. In his account of the history of land mammals, Scott (1937) wrote that he believed that what we recognize as species in fossil mammals would be more nearly equivalent to the genera of the neo-taxonomist. I would not advocate adopting that procedure. It would result in an enormous amount of confusion to do so.

Another difficulty faces the paleo-taxonomist when he attempts to correlate his work with that of the neo-taxonomist. Population genetics seems to be entering the thinking of the taxonomists, and rightly. Simpson (1943) has stressed the concept that among modern forms a species is a breeding population. How far can we go in the recognition of such populations among fossils? How great a stratigraphic range should be regarded as justifiably included in the same breeding group?

In his scholarly discussion of "Tempo and Mode in Evolution" Simpson (1944) has made an interesting attempt to bring genetics and paleontology somewhat closer together. It has occasionally been possible to recognize in fossil series what are apparently the effects of single mutations. Simpson has discussed the case of digit reduction in the horse series from that view-point and seems to have made out a good case for it. But even in neo-biology we are still far from reaching any agreement as to what degree of genetic change constitutes specific distinction. It would be very convenient if we could erect a scheme based on mutations, such that so many mutations constituted sub-specific distinction, a certain additional number differentiating species, etc.

Growth stages bring in still another problem for the paleontologist. Bashford Dean (1899) once discussed the suggestion that *Paleospondylus* might be a larval "lamprey." Among some incomplete notes left by Dr. Wm. Patten were some sketches in which he appeared to be trying to correlate the structure of the same creature with known larval forms, probably Tunicate. In 1947 Denison suggested that one species of *Tremataspis* which I had separated, *T. patteni* (Robertson, 1938), was based on what probably were juvenile specimens of *T. mammillata.* Our inability to follow through the development of these creatures leaves uncertainty as to how far we can go in identifying growth stages.

In 1945 I published a discussion of cephalaspid genera and species. The present paper is an extension of this discussion to include other *Osteostraci.* It is an attempt to see whether it is possible to set up a standard set of criteria for family, genus, and species within the entire order. It has seemed to me that the *Osteostraci* would lend themselves well to such an attempt, in that there is a rather close adherence to pattern within the order, with an apparent similarity of habitat throughout.

The more immediate stimulus to make the attempt comes from the above-mentioned paper by Denison (1947), in which he suggested certain revisions of the species of *Tremataspis.* It has seemed to me that it should devolve upon me either to acknowledge his strictures on these species as justifiable or to show to what degree I regard his criticisms as unsound. The question in this case should be settled only after analysis of the broader question of species criteria in the *Osteostraci.*

In my discussion of cephalaspid genera and species (1945) I laid emphasis on one aim of taxonomy. When we classify any group of objects we are attempting to bring order into the grouping so that when any of the terms of reference are used they will have definiteness of meaning. In other words, one of the major aims of taxonomy is specificity of reference. It is sometimes necessary to revise a classification, but it does not appear to be justifiable to change it because of slight differences in viewpoint, or on the basis of some theoretical construction which represents simply another hypothesis. In general, according to my philosophy of taxonomy, uniformity among workers with a particular group is at least a major consideration and should not be sacrificed without a very thorough consideration of the viewpoints of all workers concerned.

My present view regarding the origin of species is simply that, generally under conditions of isolation, geographic, ecologic, etc., mutations have accumulated in groups previously conspecific to such an extent that students of the group would recognize them as specifically different. In some cases environmental selection has played a definite role in the separation, especially when one group, either the parent or an off-shoot, has become extinct, and in every case selection plays a part in the ensemble of characters which constitute the distinct species, since the organisms constituting the species had to be "going concerns" in their environment, but even when selection did not influence the distinction between the species isolation would tend to result in differentiation.

There are recognized at present the following families of *Osteostraci*: *Cephalaspidae*, *Tremataspidae*, *Dartmuthiidae*, and *Oeselaspidae*. In my 1945 paper, I suggested that *Didymaspis* should perhaps be raised to family rank, adding thus a fifth family, the *Didymaspidae*. *Didymaspis* has been variously placed. Recent workers have generally listed it under the *Cephalaspidae*. Romer listed it under the *Dartmuthiidae* (1945, p. 572).

Comparison of the papers of recent workers in the taxonomy of the cephalaspids indicates that these workers in general have used the following list of criteria of species:

(1) Shape and proportions of the shield;
(2) Configuration of the rostral margin of the shield;

(3) Shape, direction, and ornamentation of the cornua of the shield;
(4) Shape and size of the "pectoral sinuses";
(5) Shape and extent of the "interzonal" region of the shield;
(6) Size and shape of the orbital openings;
(7) Shape and extension of the lateral and dorsal fields;
(8) Ornamentation.

Comparison of the criteria used in establishing species of *Tremataspis* gives the present author some qualms, since only one species recognized as valid in my 1938 paper had been based on material other than that of the Patten Collection at Dartmouth College. Patten had erected but very inadequately characterized two species, *T. milleri* and *T. mammillata* (1931), so that, in addition to naming and describing four new species, my paper was the first actual description of the two erected by Patten. Thus the problem facing me here is the discussion of the criteria I used at that time and the attempt to correlate this with the criteria recognized in the above list for the cephalaspids.

Unfortunately only one species has been recognized in the genus *Oeselaspis* and only one in the genus *Dartmuthia*. The same is true of the genera *Saaremaaspis* and *Rotsiküllaspis*. Two species of *Witaaspis* were recognized (Robertson, 1945). They were distinguished on the basis of ornamentation, including the form of the median dorsal crista.

The specific criteria used for the species of *Tremataspis* were as follows:

(1) Form and proportions of the shield;
(2) Form of the naso-hypophysial fossa and relation of the aperture to the fossa;
(3) Form of the median dorsal crista of the shield;
(4) Ornamentation of the shield;
(5) Microscopic appearance of the superficial layer of the shield, especially the distribution of the fine "pores."

There are certain fundamental differences in shield plan in the *Tremataspidae* from that in the *Cephalaspidae* which make some of the cephalaspid criteria unusable for tremataspids. The rostral margins of the shields are similar throughout in the tremataspids. Cornua, pectoral sinuses, and interzonal region are absent in tremataspids, correlated with the greater extent posteriorly of the shield. Dorsal and lateral fields are in general very uniform, although in *T. patteni* the form of the anterior lateral field differs from that found in any of the other species.

The criterion of specific distinction I used was difference in one or more of these characteristics. Conversely, identity of species was based on similarity in all the diagnostic features.

On the basis of shield proportions the seven species could be divided into two groups, one including *T. schmidti*, *T. rohoni*, *T. scalaris*, and *T. panderi*, the other including *T. milleri*, *T. mammillata*, and *T. patteni*, although the distinctly larger size of *T. milleri* might be used as a basis for placing it in a separate group.

On the basis of form of the naso-hypophysial fossa and aperture *T. schmidti*, *T. milleri*, *T. rohoni*, and *T. patteni* fall into one group, *T. mammillata* into another. This feature is not adequately preserved on the specimens of the other species.

The form of the crista appears to be different on each of the seven species, although the preservation of that region on the specimen of *T. scalaris* is not good.

On the basis of the ornamentation of the shield, chiefly the pattern of tubercle distribution, *T. milleri* resembles *T. schmidti*, although there are fairly definite differences. *T. patteni* and *T. mammillata* are similar in this, with the exception of the thinness of the *T. patteni* shield, which was one of the major reasons for Denison's decision (1947) that it might be a juvenile stage of the other species. *T. scalaris* and *T. panderi* resemble *T. mammillata* in tubercle distribution, but each has a peculiar, "ladder-like" marking on the dorsal shield surface which I used as the differentiating criterion.

The microscopic appearance of the shield surface, especially the distribution of the fine "pores," was a final character used. On this basis *T. schmidti*, *T. milleri*, and *T. rohoni* were definitely distinguishable as separate forms. *T. patteni*, *T. scalaris*, and *T. panderi* resembled *T. mammillata*.

In 1947 Denison stated that *T. patteni* was based on immature specimens of *T. mammillata*, and that *T. scalaris* and *T. panderi* were based on specimens of *T. mammillata* showing growth anomalies which accounted for the "ladder-like" ornamentation. His major criterion for conspecificity was the microscopic (histologic) structure of the bony shield, *i.e.* the last character I listed above.

I am willing to concede that Denison's contention might be correct, that *T. patteni* may be based on immature specimens, the shield characters which superficially seem to distinguish it from other species being due to immaturity. However, until additional specimens definitely establish the validity of his contention I believe it wiser to retain the species. There were only a few specimens of this type in the collection. Moreover on the basis of the other characters listed above there is doubt as to its identity with *T. mammillata*. It resembles this species in pore distribution, distribution of the dorsal tubercles, and shield proportions; differing from it in the form of the nasal fossa, in which it is more like *T. schmidti*, in the form of the dorsal crista, and in the emargination of the anterior lateral field. In a foot-note (1947, p. 358) Denison discounted these differences on the basis of the thinness and poor preservation of the shields.

The crucial point on this question is whether identity in histologic structure of the bony exoskeleton is a valid criterion of conspecificity. In his paper Denison states (p. 337): "It was found that the microstructure of the exoskeleton, viewed either superficially under xylol or in thin sections, offered clear characters which sufficed for a *specific identification* of even a small fragment of *T. mammillata*, *T. milleri*, *T. schmidti*, and *T. rohoni*. The other species described by Robertson were shown to belong to *T. mammillata*." It is on the basis of this microstructure of the bone and the extreme thinnness of the exoskeleton of the specimens referred to *T. patteni* that Denison regarded them as being simply juvenile specimens of *T. mammillata*.

Denison's hypothesis, that "the exoskeleton was formed only after the attainment of full growth" (p. 362) and that these specimens of *T. patteni* offer conclusive proof of the hypothesis, is attractive, since many of us who have worked with the ostracoderms have been puzzled over growth methods. It is important, however, to be more certain of this before the conclusion can be accepted.

My use of the microstructure of the shield as a taxonomic character (1938) perhaps needs explanation if I am to contend that Denison's union of species on its basis is not justified. I have never regarded histological characters as adequate basis for specific *identification.* Rather it was a character in which there were definite differences in pattern, and I used it as an additional criterion for *separation* of species. If histology of the bone were to be used as a basis for union of vertebrates at the specific level I suspect that we would very markedly reduce the number of species. Certainly I would regard it as a totally different grade of organization than the characters listed earlier for cephalaspids.

The case against the other species, *T. scalaris* and *T. panderi,* is somewhat different, although here again Denison has used the microstructure of the shield as the basis for uniting them with *T. mammillata.* When I first found the specimens which I later separated as *T. scalaris* and *T. panderi* I considered the question of anomalous characters. My reason for rejecting that explanation of the ladder-like markings was the symmetry of these markings. They may be related to the pores and polygonally-arranged canals ("sensory canals" of Denison), but that in itself does not indicate that the difference from the usual pattern is simply due to "growth deficiency in these specimens." It is not demonstrated that these peculiar markings might not have been permanent markings of a variant form rather than anomalous characters of *T. mammillata.* Had they shown less symmetry of pattern; had they been unilateral or irregularly-arranged markings on the shield, I would not regard them as taxonomically significant.

Denison's contentions regarding these three species may be correct, but it still appears to me to be wiser to retain the independence of distinguishable forms until we can be somewhat more certain that they represent either juvenile specimens or anomalous specimens of another species.

I wish here to express a doubt regarding the conclusion that the system of "mucous canals" in the skeleton of *Tremataspis* was a part of the "sensory canal system." Denison's careful work on the exoskeletal structure (1947) seemed to indicate that the grooves of the lateral line system followed lines of these canals and apparently had openings into them. That does not necessarily mean that they were parts of a functional whole. I puzzled a good bit over the pathway of innervation of the lateral line canals in *Tremataspis* and had come to the conclusion (1938, pp. 199-200) that the pathway through the exoskeleton must be by way of these pore canals, but I know of no morphological or physiological reason why the fine nerve branches might not make their way via these canals at the same time that the canals performed additional functions of their own, such as, perhaps, mucous secretion. I stated (p. 199) regarding the relation of the sensory canal grooves to the exoskeleton that there were "at least occasional apertures in the bottoms of grooves. These apertures prove, on dissection, to connect with the system of channels which pervades the bony shield in the same way as do the pores so abundant over the general surface." I then quoted from Stensiö (1927) that he had found on *Tremataspis* "branches from the vascular system opening into the mucous canals on the basal side, a state of things which shows that the mucous canals received vessels and nerves through the vascular canal system," and then commented: "Possibly this is the solution of the innervation difficulty. At least for the present no other appears available."

My major reason for doubting the sensory character of this intricate network is perhaps teleological. Denison states (1947, pp. 350-52): "It thus appears that the Silurian *Tremataspis* had its body entirely covered, even on the scale-covered tail, with a network of canals whose function was to receive vibratory stimuli. Such a generalized system of surface receptors may have been the primitive arrangement in *Osteostraci*, and indeed in vertebrates. We can see in *Tremataspis* the beginnings of specialization of parts of the canal system into what is known as the lateral line system of later fishes. This involves the assumption of a linear arrangement of the canals in certain regions, the acquisition of a more open connection with the exterior, and presumably the enlargement and specialization of the nerve branches which supply the definitive lateral line canals."

To me it does not make sense. I realize that the teleological argument is frowned upon by biologists, but I cannot resist in this case asking why a semi-benthonic, weak-swimming creature like *Tremataspis* should have been so extravagantly blessed with receptors. The canals in question may have served to secrete mucus or may have been used for some other function, but the fact that they indicate possible pathways for the nerve fibres whose endings innervated the sensory canals of the lateralis system does not seem to me to justify the assumption that they themselves constituted "sensory canals."

In summary, it would appear possible in the *Osteostraci*, in so far as those groups are concerned which contain more than single species, to use specific criteria of what seem to be comparable "grades of organization," although the detailed characters on which specific distinctness is based in one genus cannot be carried over to all other genera within the order, and sometimes cannot be used for different genera within the same family. This was to be expected on the basis of what we know of taxonomic work in general and what we believe to be the nature of the evolutionary processes by which species arise.

The class *Ostracodermi* differs sufficiently from other vertebrates that it seems justifiable to place it in a super-class, *Agnatha* (Robertson, 1942, pp. 147-149), characterized by lack of true vertebrate jaws and by gill pouches of the cyclostome type, characters which have led to the union of the modern cyclostomes with the fossil ostracoderms.

The class has been subdivided into two sub-classes, *Pteraspidomorphi* and *Cephalaspidomorphi*, on the basis of type of exoskeletal pattern and apparent differences in the relation of the individual branchial apertures to one another, the order *Osteostraci* constituting the best-known group of the cephalaspidomorphs, differentiated from the other order or orders, dependent on the detailed classification adopted, by the type of shield structure.

Familial characters of this order (Robertson, 1945, p. 186) include form and extent of the shield, presence or absence of cornua and the associated pectoral sinuses, number of lateral fields, extent of dorsal field, and size and number of oralobranchial plates.

Sub-families have been recognized only in the *Cephalaspidae* and are based on characters to some extent intermediate between those used for family differentiation and those characterizing genera, namely, the extent of the cornua and pectoral sinuses, size of the dorsal and lateral fields, and, in

Stensiö's differentiations (1927), differences in distribution of nerves to the lateral fields.

Generic distinctions are of importance chiefly in the cephalaspids, since the other families, with the exception of the *Dartmuthiidae*, are as yet based on single genera. *Rotsiküllaspis* (Robertson, 1938, pp. 490-493; 1945, p. 190) has been placed in the *Dartmuthiidae*, the generic differences being conformation of the posterior margin of the shield, type of ornamentation, extent of the lateral fields, and form and arrangement of the oralo-branchial plates. Romer (1945, p, 572) concurs in this placement of *Rotsiküllaspis*, but also lists *Didymaspis* in this family, as mentioned earlier in this paper. I am inclined, however, toward disposition of this genus (1945, p. 789) as a separate family. The possession of rudimentary pectoral sinuses, the peculiar form of the lateral fields, and the general resemblance in form to *Oeselaspis* are the major reasons for this decision.

The series of distinctions listed for genera within the *Dartmuthiidae* does not differ materially in what I have termed "grade of organization" from those used for cephalaspid genera, namely, general form of the cornua and pectoral sinuses, extent of the dorsal and lateral fields, extent of the shield, and relation of the dorsal shield to the ventral armor.

Specific criteria have been discussed earlier in this paper.

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