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Is dorsoventral flattening of the body an adaptation to torrential life?

By ANKER NIELSEN (Hilleröd).

Summary.

The term torrential is here restricted to animals living on the naked, smooth stones in swift-flowing water, whereas animals living in the vegetation have been excluded.

In 1907 STEINMANN put forward the theory that the most striking morphologic feature of torrential animals is a dorsoventral flattening of the body, a shape which was said to offer two advantages: In the first place a smaller surface of attack to the current. Secondly, since the ventral side of the animal is flat and the dorsal side slightly vaulted, the action of the current will, according to the law of the parallelogram of forces, be partly transformed into a downward directed pressure, which should help the animal to maintain its hold into the substratum. STEINMANN's theory was very well received. It is quoted in almost every text-book of freshwater biology, so it must be said to be generally accepted. The aim of my lecture was to critisize this theory.

Through examples from various systematic groups (Ephemeroptera, Trichoptera, Hydrachnellae, Gasteropoda) I tried to show that dorsoventral flattening by no means is commoner in the torrential representatives than in their lenitic relatives. In fact, the opposite seems to be the case, so that dorsoventral flattening must be said to be rather a rare feature in torrential animals. And then of course it is a bit hazardous to state that it is an adaptation to torrential life.

Moreover, this shape of body would seem to be an inadequate method to withstand the action of the current. It must namely be borne in mind that the current is not laminar, but turbulent: At the same time as the water particles move forward, they also perform a rolling movement, with the result that the stream-lines will be irregularly wavy, as is easily seen on the surface of swift-flowing water. Hence, just as often as the current exerts a downward directed pres-

sure upon animals on the bottom, it will exert an upward directed suction. And such a suction will of course have the strongest effect upon a flat body. It is also a well known fact that flattened mineral particles are moved more easily by the current than rounded ones. A dorsoventral flattening of the body will thus be disadvantageous to the animals, at least if they are not provided with devices by means of which they, from a physical point of view, can make themselves a part of the substratum. Such devices have also been described under the name marginal contact. As to the marginal contact, however, the same is true as said about the dorsoventral flattening: it is by no means restricted to torrential animals. On the contrary, it may seem that the finest developed marginal contacts are found in lenitic forms.

STEINMANN's theory perhaps cannot be entirely abandoned. Nor can it, however, be considered as a proved fact, until it has been further corroborated by observations in nature and, if possible, also by experiments in the laboratory. In my opinion such a trial is most likely to give a negative result. The comparatively few cases of dorsoventral flattening actually found in torrential animals probably are an adaptation not to withstand the current directly, but to avoid it by seeking shelter in narrow crevices.

A more detailed treatise on the problem will be found in a paper to be published in the journal Oikos.

Discussion.

A. THIENEMANN weist u. a. auf die Bedeutung des BEIHER'schen Ausnutzungsprinzips für das Verständnis der Torrentikolfauna hin. Er erinnert außerdem daran, daß im typischen Gebirgsbach die Hydracarinen nicht zur Steinfauna, sondern zur sog. Moosfauna gehören.

NIELSEN: I have very little experience in the group Hydrachnellae; I quoted VIETS. Maybe it is not a good example, but this does not apply to the other groups I have mentioned. My own experiences have chiefly been obtained in Danish streams, and this of course is a weak point. We have rather fast streams in Jutland — up to more than 1½ m/sec. — but montaineous streams they are not. Last summer, however, I had the opportunity to make some few observations in the Alps (Karwendel and Ötzthaler-Gebiet) and they did not cause me to change my opinion. I do not find that either *Epeorus* nymphs or Blepharocerid larvae are very flat, though in the former the sucking disc may give the abdomen a flat appearance. — It has been said that the animals are not flat because they live in torrents, but

they have been able to immigrate into the torrents because they were flat. Personally, I even think that flattening of the body will make it difficult for an animal to migrate into the torrential habitat.

H. B. N. HYNES: In connection with the question of stream animals it may be of interest to point out that in Trinidad, where the mountain streams are liable to very large and sudden spates, I noticed that many of the invertebrates, particularly Ephemeroptera, were much smaller than they are in Europe. I noticed also that the flat larvae of Blepharoceridae and *Psephenus* were on, not under the stones.

NIELSEN: In the animal groups with which I am most familiar, the torrential representatives are not particularly small. Some of them are even rather big.

E. M. HUBAULT: La question de l'adaptation des organismes torrenticoles au courant est extrêmement complexe. A part les moyens presque parfaits de fixation des larves de Blépharocéridés ou de certaines Phryganes, les autres adaptations sont peu nettes. La taille et la forme n'en sont pas : les larves de *Perla* et d'*Epeorus* sont parmi les plus grandes qui vivent dans les eaux douces et beaucoup d'Invertébrés torrenticoles ne sont pas plats. De nombreuses formes (larves d'Éphémères, de Perlides, Planaires ... etc...) qui le jour s'abritent sous les pierres, là où il n'y pas de courant, sortent le soir à la surface de ces pierres, là où le courant est le plus violent. Une reconnaissance faite la nuit avec une forte lampe électrique dans un torrent de montagne aux eaux claires, le démontre sans peine. Ce rythme nycthéméral est la conséquence d'un phototropisme négatif auquel s'ajoute un rhéotropisme positif, car on peut remarquer que tous ces organismes ont la partie antérieure du corps face au courant.

H. DAMAS: J'ai eu l'occasion de répéter dans un ruisseau d'Ardennes les constatations de M. HUBAULT sur la phototaxie négative des animaux torrenticoles. *Epeorus* se tient durant la journée sous les pierres et durant le nuit sur les pierres. Mais dans les endroits très sombres du ruisseau, sous le convert des arbres, on peut trouver, durant la journée, des *Epeorus* sur la face supérieure des pierres. La lumière a donc une action certaine sur le comfortement de cet animal.

NIELSEN: I have not made observations on the behaviour of the animals in night. I know that e. g. *Heptagenia sulphurea* has a strong negative phototaxis. The result of it, however, is that the nymph is forced into crevices, where it is protected against the current.

K. STRÖM called attention to the fact that marine animals on surf rocks are not at all particularly flat.

Dr. MACAN found himself heartily in agreement with nearly all that Dr. ANKER NIELSEN had said, but felt that not enough mention had been made of the family Ecdyonuridae (Ephem.). In Britain it contained three genera, *Ecdyonurus*, *Heptagenia* and *Rithrogena*, and all were typical inhabitants of torrential streams and rivers. It was difficult to resist the conclusion that their flattened bodies did not represent an adaptation to life on the surface of stones and therefore secondarily to life in torrential conditions.

NIELSEN: As to *Rhithrogena* I will say the same as about *Epeorus*. I do not know *Heptagenia lateralis*, but I think that it like *H. sulphurea* and *Ecdyonurus* lives beneath the stones.