

## VARIATION IN THE GENUS KERATELLA

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### Abstract

The literature on variation in *Keratella* is reviewed. The old idea of a thorough endogenous control has to be rejected, but internal factors ought to play a certain role beside influences from current and previous environment. In certain cases there is probably a succession of genetically different clones during the course of the year (cf. King, 1972, 1977), but the seasonal variation in lake populations of, e.g., *K. cochlearis* ought to be mainly non-genetical. There is some evidence that temperature and food exert an influence on the morphology, via rate of growth, but probably other abiotic and biotic factors are at work as well. The existence of allometric relationships is clearly demonstrated for several species. The variation in spine length has been suspected by some authors to constitute just the function of size variation which is thus considered primary. Some of the variation found is obviously non-adaptive. An attempt is made at explaining the existence of discontinuous variation within a single lake. Implications on taxonomy and speciation are briefly discussed.

The topic of this paper represents a classical research object within limnology. Studies began about at the same time as those on seasonal variation in the genus *Daphnia*. However, the work made on *Keratella* has mainly concerned the specialists. The investigations on daphnids have been cited much more in text-books and popular publications, probably because such fascinating theories have been connected with them.

The pioneer work on variation in *Keratella* (and on rotifers in general) was done by Lauterborn (1898, 1900, 1904) on material from the Rhine and some neighbouring localities. In these studies he found a continuous morphological variation in *K. cochlearis* (Gosse) during the course of the year. A winter form, f. *macracantha*, with a relatively uniform appearance (a long posterior spine etc) was succeeded by three different series, each of them being more and more pronounced morphologically during the course of the summer. A reduction in spine length also occurred in each of the series. In addition there exists a complex of forms, deviating morphologically from the three series and not undergoing reduction in spine length, thus not representing a series. This complex was called f.

*robusta* and the three series *tecta*-series, *hispid*a-series and *irregularis*-series. *F. robusta* is said to be restricted to ponds with a heavy growth of macrophytes, whereas the forms of the three series only occur in waters with a more or less large area devoid of such vegetation. The latter were found in ponds as well as in lakes (e.g. L. Constance) and slowly flowing rivers. According to Gillard (1948, 1949) f. *robusta* can be regarded as an 'ecological race' and is designated with his nomenclature as '*K. cochlearis* OE *robusta*'.

Lauterborn presents a really comprehensive and convincing material of data. On the other hand he is very restrictive concerning interpretations of his results, quite contrary to some other earlier workers. Thus Krätzschar (1908, 1913) founded a theory of 'cyclomorphosis' based on his studies of the seasonal variation in the *K. quadrata* (Müll.) complex. His scheme of the life cycle (condensed in Krätzschar, 1908, Fig. 20) has been quoted in many text-books because of its perspicuity. The following pattern is described: From the resting eggs long-spined amictic females are hatched, which produce a sequence of other amictic individuals, in which the posterior spines get successively shorter for each generation. After a certain number of amictic generations, mictic females appear and, arisen from these, males and resting eggs, which after a resting period will form the starting-point of a new cycle. Krätzschar speaks of a 'successively decreasing vitality of the parthenogenetic females' and a 'degenerative process', which finally causes sexual propagation.

Krätzschar based his view on experimental work: He cultured his animals at different temperatures, light intensity, amount of food, concentration of chloride etc, which factors, however, did not apparently influence the morphology. Therefore, Krätzschar concludes that endogenous factors alone are decisive for the seasonal variation.

Hartmann (1918) adheres to Krätzschar's opinion, though he believes that external factors may modify the extent of the variation (which is to some extent also admitted by Krätzschar). Apparently Suzuki (1964,

pp. 28 and 32) shares these ideas as well. However, Ruttner-Kolisko (1949) presents convincing evidence that Krätzschmar partly based his view on misinterpretations. She worked with material from the same lake as the senior author, L. Lunzer Obersee, and found that two species of the *K. quadrata*-complex existed there (three species in later decades) with different spine length. Both these species (*K. quadrata* s. str. and *K. hiemalis* Carlin) were incorporated into Krätzschmar's scheme. The individuals of *K. quadrata* s. str. cultured by Ruttner-Kolisko produced reductional forms as in Krätzschmar's experiments, but she interpretes this result in another way. As Krätzschmar's ideas are thus rejected, Ruttner-Kolisko also proposes that the term 'cyclomorphosis' not be used any more, as it has been connected with an obligatory relation between morphological variation and sexual cycle.

As early as 1911 Dieffenbach & Sachse obtained experimental results which contradicted Krätzschmar's theory, and more recently very clear evidence against endogenous control has been put forward by Rauh (1963) and Halbach (1970), based on studies of species of the related genus *Brachionus*. The original aim of Rauh's study was in fact to analyse the variation of *Keratella cochlearis*, but on account of the difficulty in cultivating this species, *Brachionus* was chosen instead. Regarding the evidence from field studies against an endogenous periodicity, reference is made to Ruttner-Kolisko, op. cit. and the extensive discussions by Buchner, Mulzer & Rauh (1957) and Buchner & Mulzer (1961).

The form hatching from the resting egg is a crucial point in this argumentation. However, it appears that a successful hatching has very rarely occurred. Dieffenbach & Sachse (op. cit.) mention such a result, in which the resulting forms were long-spined (thus in accordance with Krätzschmar's scheme). Likewise Sudzuki (op. cit., p. 28) says in connection with *K. cochlearis* that he has 'verified the fact that the specimens with the longest spine hatch out from the dormant eggs'.

Nipkow (1961, pp. 417-419) succeeded in hatching resting eggs of *K. quadrata* (as well as of several other rotifers). The individuals appearing from such eggs had evidently spines of intermediate length. When further cultivated they produced offspring of reductional forms, similar to those of Ruttner-Kolisko. The mictic females found in the lake (L. Zürich) had relatively long spines.

Other authors call attention to the difficulty of obtaining offspring from resting eggs in the laboratory, and, thus, they conform to an indirect argumentation. E.g., Amrén (1964b) mentions that many of the ponds and

puddles he investigated on Spitsbergen freeze to the bottom during winter and that the first appearing individuals in the spring therefore have to take their origin from resting eggs. This first generation is characterized by very short or non-existent posterior spines, quite contrary to the cases reported above. The offspring of these females are equipped with somewhat longer spines (verified in cultures) and they give to a generation with still longer spines, a sequence which could be followed through some generations.

As stated above, an overwhelming evidence against endogenous control has now been cumulated. However, this must not mean that such forces are never at work. Nobody now ought to question the nice results obtained by Nipkow (1952), showing that the first generation of *Polyarthra* is devoid of fins. Almost as good evidence is obtained by Amrén (1964a), regarding *K. quadrata*, in favour of internal factors determining the appearance of the generation hatching from the resting eggs, as well as of those following next. Possibly this is a widespread phenomenon within Rotatoria.

The seasonal variation analysed by Amrén had no apparent connection with either temperature or food. In most cases, however, a very obvious correlation to temperature exists, long appendages being found at low temperatures, short or none at high. For *K. cochlearis* especially, many univocal studies were made, showing this connection in a variety of lakes and ponds: Lauterborn, 1900 and 1904 (excl. f. *robusta*); Züscher, 1912; Ammann, 1913 and 1923; Schreyer, 1921; Schneider, 1922; Vialli, 1924; Robert, 1925; Wesenberg-Lund, 1930; Varga, 1941; Carlin, 1943; Entz & Sebestyén, 1946; Buchner, Mulzer & Rauh, 1957; Parise, 1960; Buchner & Mulzer, 1961 and Hillbricht-Ilkowska, 1972. Experimental evidence proving the influence of temperature has been put forward by Pourriot (1964) and Lindström & Pejler (1975). Regarding *K. quadrata* f. *frenzei*, a form typical of larger lakes, the same conditions seem to occur according to Carlin, 1943. Klement (1957) reports a similar cycle for a form within the '*quadrata*-series' living in a pond. For the eulimnoplanktic *Kellicottia longispina* (Kellicott), belonging to the same subfamily, the indication of a similar influence of temperature is very strong, to judge from Ammann, 1913; Schreyer, 1921; Vialli, 1924; Robert, 1925; Varga, 1941; Carlin, 1943 and Hakkari, 1969. Such is the case for the related genus *Notholca* as well, not only for the true plankters, but also for benthic and periphytic forms, e.g. those occurring in rockpools (see Björklund, 1972). This comprehensive material should be enough to

refute the general applicability of the well-known buoyancy theory suggested by Wesenberg-Lund and Ostwald, which is based upon quite reverse conditions existing in certain cladocerans. In spite of this, the mentioned theory is often reported in text-books still to-day as the probable explanation for the seasonal variation of all plankters!

However, there are exceptions from the trend discussed above. The pond-living f. *robusta* of *K. cochlearis* has already been mentioned as an example. Gallagher (1955 and 1957) reports a reverse course of variation for a form of *K. cochlearis* found in an artificial pond. Likewise, the pond-living forms of *K. quadrata* do not follow the regular pattern described, their variation being rather erratic: in some cases non-existent, in some cases correlated to temperature in one way or the other (see especially Ruttner-Kolisko, 1948 and Buchner & Mulzer, 1961). Even in true lakes *K. quadrata* sometimes does not show any pronounced seasonal variation (Ruttner-Kolisko, 1949; Parise, 1969). An interesting deviation from the close correlation with temperature is constituted by the 'spring peak' discussed by Carlin (op. cit.): Though the temperature is constant or somewhat increasing, the spines get obviously longer during April and May in *Keratella cochlearis*, *K. quadrata* and *Kellicottia longispina*. Carlin ascribes this peak to the improved food conditions during these months. A similar peak develops in *Notholca caudata*, which is cold stenothermal and disappears in summer, thus not being capable of demonstrating any variation related to temperature.

*Keratella hiemalis*, which is a cold-water form, normally does not show any seasonal variation (Ruttner-Kolisko, 1949), but Hutchinson (1967, pp. 891-892) attempts to trace a tendency, basing his argument upon the limited material of Pejler (1957). In arctic lakes no obvious seasonal variation seems to have been reported, but in smaller water bodies the pattern discussed by Amrén (cf. above) may occur, whereby temperature is apparently not involved.

Going to the other extreme, seasonal variation has in some cases been shown to exist in tropical waters. The species studied are *Keratella tropica* (Apstein), *Brachionus calyciflorus* Pallas and *B. caudatus* Barrois & Daday (see Green, 1960 and 1977; Nayar, 1965 and Arora, 1966). In these cases temperature cannot be considered responsible for the morphological changes.

As temperature is evidently not the only factor lying behind seasonal variation, other agents have to be sought for. As much more experimental evidence is obtained concerning some species of *Brachionus*, some hints could

be expected from the studies of this genus. Thereby it is interesting to find agreeing conclusions in Rauh (1963) and Halbach (1970) on the basis of their very elaborate investigations. Both authors talk of temperature and food as important factors, which influence developmental rate: At low temperatures and low concentration of food particles the development is slow, whereby the length of the spines increases.

Beside temperature and food Halbach (op. cit.) analyses another factor, the so-called 'Asplanchna-substance', now a central topic within rotifer research and summarized in several other papers (see, e.g., Gilbert, 1966 and Halbach, 1971a). The *Asplanchna*-substance acts even more strongly upon the morphology of *Brachionus* than temperature and food.

Now it remains to be considered if the mentioned results from the *Brachionus* experiments can be applied upon seasonal variation in *Keratella* as well. The influence of temperature has already been discussed. Also, it was reported above that Carlin regarded food to be active concerning the 'spring peak' of some species. However, the effect was here quite reverse to that expected from Rauh's and Halbach's investigations. On the other hand, the studies on local variation in *K. cochlearis* made by Pejler (1962) are quite consistent with the mentioned research on *Brachionus*. In fact, Pejler suggested the same idea as Rauh and Halbach regarding the influence of food and temperature, referring to Edmondson (1960), who had found that birth-rate is positively correlated with temperature, as well as with quantity of phytoplankton. (These ideas are still more developed in Edmondson, 1965). Pejler found in Swedish lakes during the summer, at roughly equal temperatures, a very strong correlation between trophic degree and spine length of *K. cochlearis*: In oligotrophic lakes only more or less long-spined individuals occurred all through the summer, while forms with short spines or without spines dominated in the eutrophic. *F. tecta*, devoid of spines, was even shown to be one of the best indicators of eutrophy. Quite similar results from Polish lakes were obtained by Hillbricht-Ilkowska (1972).

The third factor stated to be active by Rauh and Halbach, the *Asplanchna*-substance, has not been considered regarding *Keratella*. However, it is probably of less importance to the true lake plankters, on account of the dilution effect.

On the other hand, recent ecological investigations (also in rotifers) have shown that the abiotic interrelations have been too often overestimated and the biotic ones

neglected. Many possibilities exist concerning biotic effects. Thus, Halbach (1970, pp. 311-312) refers to several earlier papers concerning a direct or indirect effect of food quality. The role of competition is discussed by Snell (1977), that of selective predation by Halbach & Jacobs (1971), Nilsson & Pejler (1973) and Green (1977).

However, abiotic factors other than temperature may also be conceived as agents. Edmondson (1948), for example, points at a possible effect of calcium, Green (1960) at the connections with floods in tropical lakes. The influence of turbulence on cladocerans has been discussed very much, and it is interesting to find that some authors connect rotifer variation with morphometric conditions of the lake. Thus, Green (1977) says that 'dwarfing' occurs in lakes with a low ratio of drainage area to surface area. Ruttner-Kolisko (1972, p. 143) maintains that *hispida* forms of *K. cochlearis* mainly occur in strongly turbulent shallow and small water bodies. Finally, Berzinš (1958) and Hillbricht-Ilkowska (1972) describe a vertical stratification concerning the morphology of *Kellicottia longispina* and *Keratella cochlearis*, respectively. In both cases, more short-spined forms are found, on an average, in the superficial layers than farther down.

The two last examples show that ecocline variation can be of local as well as temporal character. Another local ecocline was reported by Wermel (1930), who showed that the morphology of *Keratella serrulata* (Ehrbg) changed successively within a boggy pool parallel to a gradient of pH. Similarly, Pejler (1957, 1958) found that the length of the posterior spines of *K. hiemalis* decreased concomitantly with the annual heat budget of the water body (i.e. on the whole with rising height above sea-level).

Concerning the adaptive value, it is quite easy to understand the meaning of the predator *Asplanchna* eliciting longer spines in its prey *Brachionus*. As Halbach (1970, 1971b) has pointed out, this arrangement is of advantage to both predator and prey. It is much more difficult to understand which benefit could be connected with a variation induced by temperature or food. Several authors have speculated regarding this matter. Hartmann (1918), for example, mainly considers the mechanism of locomotion, while Carlin (1943) believes that the appendages have the function of 'catching' the turbulent currents and utilizing them for floating.

It has been noted by some authors that the variation in spine length may be just a function of a varying size of the body, the last being the primary phenomenon (see Green 1960; Pejler, 1962; Hutchinson, 1967, p. 877; Ruttner-Kolisko, 1972, pp. 115 and 126). In fact it is possible to

discern this way of thinking in as early a work as Lauterborn (1904, p. 612). Now several studies (on different species) have been made showing allometric relations between spines and size of the body: Margalef, 1947; Green, 1960; Magis 1962; Pejler, 1962; Fergg, 1963; Amrén, 1964a; Hutchinson, 1967; Halbach, 1970; Björklund, 1972; Guiset, 1977; Nauwerck, 1978. Regarding the paper by Halbach on *Brachionus calyciflorus*, it ought to be noted that the growth of separate individuals was also followed.

This leaves the background of size variation to be discussed, a great topic treated in diverse general expositions (see, e.g., Margalef 1955). Here, only the relationship between metabolism and body size should be briefly touched upon. A short survey of this problem is given by Odum (1971, pp. 77-79). He does not discuss the applications on planktic organisms, which, however, is done by Brooks & Dodson (1965) and Brooks (1968). The well-known 'size-efficiency hypothesis', put forward by these authors, implies that larger zooplankters have a better metabolic economy than smaller ones, which stands in agreement with Winberg's law. According to Nilsson & Pejler (1973, pp. 69-71) a large body must, therefore, be an advantage in an environment poor in food, i.e. in oligotrophic lakes, and it is also shown that larger species and larger infraspecific forms are found in such lakes. However, what is here true in comparison of different lakes has also to be true for seasonal comparisons. It then appears as a striking fact that the conditions during winter are generally more oligotrophic than those of the summer. Thus, the winter forms should be larger, which is also the normal case. This may be conceived to form at least part of the explanation of the varying body size.

Of course the spines may be partly regarded as an adaptation for escaping predation (cf. above concerning *Asplanchna-Brachionus*), but a correlation between spine length and predation pressure has not been demonstrated for any *Keratella* or *Kellicottia* species (see also Nilsson & Pejler, loc. cit.)

However, surely not all variation is adaptive. Some examples where this is apparently not the case were mentioned by Pejler (1957, p. 41). Pure deformities are sometimes reported: Milković, 1934; Klement, 1955, 1957, 1959; Thomasson, 1957. Such forms are predominantly found in smaller waters and it seems probable that genetic drift is at work in these cases. It may also be mentioned here that students of brachionids in ponds and pools often talk of an erratic variation (see, e.g., Buchner & Mulzer, 1961), which should be compared with the

relatively uniform conditions in real lakes.

As 'microgeographical isolation' ought to be one reason for the local form variation, the question may be raised whether new species could originate in this way. However, the possibilities of dispersal are probably in general strong enough to counteract isolation, and no evidence of such a microgeographical speciation seems to have been demonstrated. On the other hand, speciation based on 'macrogeographical isolation' surely occurs, and Pejler (1977, pp. 275-276) mentions some examples of probably recent evolution of new species or subspecies.

For some species a discontinuous variation within single waters has been found. Regarding *Keratella cochlearis*, this phenomenon has been demonstrated by Carlin (1943, pp. 56-58); Pejler (1957, pp. 6-13 and 40-41, 1962); Parise (1960, pp. 31-34, 1961, p. 123); Fergg (1963); Hutchinson (1967, pp. 879-880) and Nauwerck (1978, p. 277). Fig. 4 in Hakkari (1969) seems to show an indication of a similar variation in *Kellicottia longispina*. Several explanations are conceivable—camouflaged sibling species, polymorphism connected with apomixis etc. (see Pejler, 1957). One fact to be stressed is that the lakes containing two or three separate forms of *K. cochlearis* are deep enough to be stratified during the summer, and possibly the long-spined forms have developed in the hypolimnion (also if they later on can be encountered in the epilimnion as well). This hypothesis suggested by Pejler (1962, p. 12) is supported by Hillbricht-Ilkowska (1972), who found the spine-less form (f. *tecta*) chiefly in the epilimnion of a Polish lake. Three separate forms of *K. cochlearis* were encountered only in two of the investigated Swedish lakes. Both these lakes form parts of lake chains (and, in addition, are stratified). It appears possible that one of the forms has developed in an adjacent water and then been brought to the investigated lake. This view is supported by comparisons of samples collected in different years (see further Pejler, 1962, pp. 12-13).

It is obvious that the knowledge or ignorance of variation has influenced taxonomy to a very great extent. At the time of the typological species concept a multitude of species was described within the variable form complexes now treated. However, during the first years after the appearance of the pioneer works on variation, a reverse tendency is often traced. Thus, the genus *Polyarthra* is treated as a single species by, e.g., Lauterborn (1904) and Hartmann (1918). Wesenberg-Lund (1900) takes offence at the 'non-scientific species making' and recognizes, e.g., only two species of *Synchaeta*, all the other being considered seasonal variants. Von Daday (1897, p. 132) even sus-

pects that *K. cochlearis* and *K. quadrata* ('*Anuraea aculeata*') should belong to the same species, basing his hypothesis upon studies in Lake Balaton. However, by biometric methods it has been possible to distinguish infraspecific variation from interspecific and to establish, on a firmer basis, new species within varying form complexes (e.g. by Carlin, 1943). Surely much more can be done within this field, especially if more modern methods are applied.

Different opinions have been expressed as well regarding the genetical background of the variation. The earlier writers were influenced by ideas of their time. Krätzschar's reasoning, apparently inspired by August Weismann, has already been mentioned. Purely Lamarckistic elements are incorporated into the explanations given by Hartmann, who writes, e.g., in 1918, p. 288, that some characters may be 'in certain cases acquired hereditarily due to external influence' (translated from German).

Using as a base the current scientific thinking, however, it is appropriate to ask to what extent the variation is genetically founded. This problem has been approached, e.g., by culturing forms from different ponds under equal conditions (see Buchner, Mulzer & Rauh, 1957; Buchner & Mulzer, 1961; Rauh, 1963 and Halbach, 1970). Thereby it was shown that the different clones derived in this way reacted similarly, though not identically, to the environmental factors to which they were exposed. Buchner & Mulzer (op. cit.) discuss three cooperating factor complexes: internal factors (evidently hereditary to their character), current environment and previous environment (with a subsequent effect).

Strictly genetical analysis has been performed by King (1972, 1977), who considers seasonal variation to be 'largely, but not entirely, non-genetic in origin'. Samples containing *Euchlanis dilatata* Ehrbg, or species of *Asplanchna* were collected at biweekly or weekly intervals and clones reared from them. These clones were found to differ in diverse physiological characters, and a genetic change through time was thus demonstrated (in two different rotifer families). King discusses two alternative hypotheses, those of 'incomplete' and 'complete genetic discontinuity', respectively. Most evidence is in favour of the model of complete discontinuity, which presupposes a low gene flow and a high competition between genotypes adapted to different environmental conditions. This model is also supported by the results of Snell (1977), who presents evidence of a succession of genetically distinct populations, each one developing from resting eggs at different times of the year. Though no corresponding

investigations have been made regarding brachionids it seems quite probable that a similar pattern can exist there as well. However, concerning the lake-dwelling populations of *Keratella* and *Kellicottia*, there are some circumstances contradicting this idea. Though very intense investigations were performed over 6 years by Carlin (1943, pp. 103-104 and 143) a sexual period was never recorded for the common species *Keratella cochlearis* and *Kellicottia longispina* and only once for *Keratella quadrata*. Similar results were obtained by Ruttner-Kolisko (1949, pp. 443 and 460) and Pejler (1957, p. 43<sup>1</sup>). If no resting eggs are formed, and consequently not hatched, the mentioned model of King & Snell cannot be applied. Out of the three models discussed by King (1972) then only one remains, viz. that of a purely physiological adaptation. In other words, the seasonal variation in lake populations of, e.g., *Keratella cochlearis* ought to be regarded as a mainly non-genetic phenomenon. On the other hand, genetic factors are probably largely responsible for the different pattern of variation shown in different lakes, which stands in agreement with the argumentation held by Buchner and his co-workers, as well as by Snell (1977).

The material and understanding of rotifer variation has indisputably increased since the days of Lauterborn and Krätzschmar. In spite of this, a simple universal solution has never seemed more remote than today. Probably, such a general solution does not exist. The problem may be compared with that of mictic-female production (see the review by Gilbert 1977), different conditions occurring in different species. Nature certainly does not always provide simple solutions for inquirers of truth. This should not, of course, discourage us from trying to clarify things as far as is possible.

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An unfortunate printing error was discovered on this page: Formations of resting eggs were observed in *K. longispina* in Lapland only in tarns, not in lakes (not the reverse, which was written).

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