A Revision of the Rotatorian Genus *Keratella* with Descriptions of Three New Species and Five New Varieties

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Article XII.—A REVISION OF THE ROTATORIAN GENUS *KERATELLA* WITH DESCRIPTIONS OF THREE NEW SPECIES AND FIVE NEW VARIETIES

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A REVISION OF THE ROTATORIAN GENUS *KERATELLA*

In this paper an attempt is made at a critical revaluation of the species of the genus *Keratella*. This genus was known as *Anuraea* until rather recently, when Harring, applying a strict interpretation of the international code of nomenclature, resurrected the older generic name of *Keratella*.

The first adequate description of members of this genus was given by Ehrenberg, who described species of the genus as early as 1832, although he published no figures until the appearance of his epic work, "Die Infusionsthierchen," in 1838. However, the first description of a species of this genus was made more than fifty years previous to the latter date, but the description of *Brachionus quadratus* by O. F. Müller (later to be made the monotype of *Keratella* Bory de St. Vincent) is very inaccurate, and it is only because this species has such a distinctive shape that we are able to place Müller's organism at all.

Species of *Keratella* are quite variable in certain characters to be discussed later, and, as in most cases where species are both common and variable, there has been a multiplication of synonyms. This is especially true of the type species, *Keratella quadrata*. However, there has been a more marked tendency to multiply varieties of the few common species than to rename them as separate species; this tendency would not be at all reprehensible if many of the characters used to separate varieties were less trivial.

Contrariwise, an opposite tendency has as often prevailed among rotifer workers, that of placing distinct species of *Keratella* as synonyms or varieties of the two common species, *Keratella quadrata* and *Keratella cochlearis*. The marked variability of these two species was early recognized, and it apparently led workers to believe the variation was greater than is really the case. Consequently a number of distinct species have been overlooked or suppressed.

It is the purpose of this paper to clarify the limits of species in *Keratella*, to give an adequate picture of the variability within each species and to give a more adequate basis for making varieties and forms within the species.

DISTRIBUTION

The genus *Keratella* is found throughout the world in fresh water habitats, and one species and several varieties occur in brackish or marine situations. *Keratella* can be stated, without qualification, to be the most common genus of rotifers in the world. It is a rare body of water that does not support at least one species of this genus. The hydrogen ion concentration of a habitat is not a limiting factor in the distribution of this genus, as it is in the distribution of the related genus, *Brachionus*. Neither is temperature a limiting factor in the distribution of the genus, for *Keratella* occurs from temporary pools in the Arctic to ponds in equatorial regions. Then, too, many species of *Keratella* are truly limnetic: they form part of the true plankton of lakes and often are numerically the most important rotifers in our large bodies of water. There are comparatively few truly limnetic species of rotifers, consequently this aspect of the distribution of species of *Keratella* cannot be too strongly stressed.

However, not all species of *Keratella* are world wide in distribution. In fact, *Kera*-

tella cochlearis is perhaps the only species of the genus that is truly cosmopolitan. *Keratella quadrata* is limited in its distribution by temperature and possibly also by hydrogen ion concentration (it is an alkaline water species); it is apparently confined to Arctic or temperate waters and to the winter plankton of waters having a relatively high summer temperature. The related species, *Keratella valga*, seems to be limited by temperature in an inverse manner: it flourishes in the tropics, but is less common in temperate regions. *Keratella serrulata* is rather widely distributed, but the distribution of this species is "spotty." It appears to be most common in sphagnum bogs and similar acid habitats, although it is a transcursion species; also it may be confined to the littoral. These four species are the most common species of *Keratella* as far as world wide distribution is concerned.

Several species of *Keratella* are apparently acidobionts. In this group are the rare *Keratella mixta* and the more common *Keratella taurocephala*. The latter is known only from temperate North America, and the former from U.S.S.R. and the United States. *Keratella paludosa* seems to be more common in acid waters. This species is rare in the United States but appears to be somewhat more common in northern Europe.

Keratella crassa is very common in the United States and is a transcursion species but is not known, as yet, to occur on other continents. *Keratella earlinae*, less common than *K. crassa*, is known only from northern United States and Canada, and almost entirely from alkaline habitats. *K. irregularis* is the Eurasian cousin of *K. earlinae*. It has not been found in the United States, although it did occur in a collection from Kodiak Island adjoining Alaska.

Keratella gracilenta is a common species in both Americas, but it is not known definitely to occur elsewhere; it is a transcursion species. *Keratella reducta* is known from South Africa only. Several of the above species, from present knowledge, seem to be endemic to certain regions or continents. *Keratella* does occur in marine or brackish habitats. *Keratella cruciformis* and its variety *eichwaldi* are confined to such localities, and both *K. cochlearis* and *K. quadrata* have a brackish water variety. However, species of *Keratella* found in marine situations are probably confined to a zone close to shore and are usually found in localities with a lesser saline content than the usual; they are an unimportant element in the marine plankton as a whole.

CHARACTERS IMPORTANT TAXONOMICALLY

The internal anatomy of species of *Keratella* is too uniform from species to species to be of value in drawing taxonomic distinctions; even were it diverse it would be difficult to observe due to the heavy lorica covering the body. The lorica, however, is very variable in size, shape and ornamentation and furnishes a sufficient basis for differentiating a number of species.

The characters of most importance in the differentiation of species are discussed under the following six categories, arranged, as nearly as possible, in the order of their importance.

1. The presence or absence of posterior spines, their number and position.

The majority of species of *Keratella* have a single posterior spine. The lorica terminates in a single, median posterior spine in the following species: *K. cochlearis, taurocephala, crassa, earlinae, irregularis* and *gracilenta*. In *K. mixta* and in *K. serrulata* var. *levanderi* the short but stout posterior spine arises somewhat to the right of the median, while in *K. paludosa* it has its origin somewhat to the left.

Several species of *Keratella* have two lateral posterior spines. Between *K. valga* and *K. quadrata* the point of origin of the paired posterior spine is used to differentiate one species from the other. In *K. quadrata* the subequal posterior spines are separated by the whole width of the body and are more or less strongly divergent, while in *K. valga* the posterior spines are closer together, the right is almost always longer than the left, and the spines are not strongly divergent. *K. serrulata* may have two subequal, widely separated, posterior spines.

The problem is further complicated by the fact that several species having posterior spines have cyclic or ecologic forms without posterior spines; this is known to be true of *K. cochlearis, paludosa, irregularis, quadrata, valga* and *serrulata*, and may be true of other species. The length and shape of posterior spines are exceptionally variable in *K. quadrata* and *K. valga*. The latter even has a common variant having only the right posterior spine developed. For a more detailed discussion of this phase of variation in *Keratella* refer to the descriptions of the individual species.

Two species of *Keratella* entirely lack posterior spines: *K. cruciformis* and *K. reducta*.

2. The pattern of dorsal sculpture on the lorica is of the greatest importance in differentiating species of *Keratella*. In fact, among the species of this genus there are but two pairs of species that cannot be separated from each other on the basis of this character alone: the sculptural patterns on *K. quadrata* and *K. valga* are quite similar, and *K. taurocephala* has a pattern similar to *K. cochlearis*. The foundation pattern of the dorsum varies relatively little in any species. In identifying species of *Keratella* care should be taken to decipher the sculptural pattern accurately, and in making figures of *Keratella* more than usual care should be exercised in accurately depicting the details of the pattern. (Various investigators have too hastily sketched in details of sculpture of *Keratella*, to which many inaccurate published figures bear mute testimony.) However, on some specimens of *Keratella* the pattern is at times so indistinct as to be distinguished with difficulty, if at all; consequently, this character must be used often in conjunction with others if a species is to be accurately identified. The patterns of dorsal sculpture in *Keratella* are discussed at some length in a separate section.

3. Proportions of the body, especially as regards size, shape, width and depth, are of considerable importance in differentiating species and varieties of *Keratella*. *Keratella crassa*, for example, is a large-bodied species in which both the width and depth are proportionately greater than in related species; *K. cochlearis* var. *faluta*, on the other hand, though quite wide and large-bodied, is much compressed dorso-ventrally; *K. gracilenta* is proportionately narrower than other species.

4. The number of anterior spines is of importance in differentiating *K. reducta*, which has but four anterior spines; all other species of *Keratella* have six spines on the anterior dorsal margin. However, due to the antero-intermediate spines not infrequently obscuring the antero-laterals or vice versa, various species from the dorsal or ventral view sometimes appear to have only four spines. If a specimen has six antero-spines it can readily be ascertained from a lateral view, which can usually be obtained by gently tapping the cover glass with a needle.

The relative size of anterior spines is of some importance in specific diagnosis. Antero-medians are usually the longest anterior spines. However, on *K. taurocephala* the antero-laterals are both longer and stouter than the medians. The antero-intermediates are usually shorter than either the laterals or medians. An exception is *K. cochlearis* var. *recurvispina* which has the intermediates both rather long and very markedly divergent.

5. The ornamentation of the ventral plate may be of aid in differentiating species of *Keratella*. The ventral plate usually has a basic pattern of minute, irregular, polygonal areolations and is often more or less pustulate; it is the latter character that may be of aid in specific differentiation. Some species are not at all pustulate, e.g., *K. crassa* and *K. paludosa*, other species have pustules confined to the upper third of the ventral plate, e.g., *K. earlinae*, *K. irregularis*, the usual forms of *K. cochlearis*, while in other species the pustules are scattered more or less over the entire ventral plate, e.g., *K. taurocephala*, *K. serrulata*, *K. cochlearis* var. *hispida*, *K. gracilenta*, etc. *K. mixta* not only has pustules extending most of the length of the plate but has a pronounced

ridge about a third of the way back on the plate.

6. The ornamentation of the dorsal plate (other than the foundation pattern of the dorsum) is an aid in distinguishing a few species of *Keratella*. Most species of *Keratella* have a basic pattern of minute areolations forming a fine, intricate network over the whole lorica (this should not be confused with the foundation pattern of the dorsum). Often at the corners of the irregular polygons making up the network are developed minute pustules. In *K. paludosa* the relatively large pustules are grouped in a number of oval areas that constitute the most notable feature of this species. On *K. earlinae* and *K. irregularis* the large, shouldered, irregularly scattered pustules are unlike the pustules found on other species of *Keratella*. The dorsal plate of *K. gracilenta* is often clothed with dense, nearly truncate pustules (spinelets), while the dorsal plate of *K. cochlearis* var. *hispida* is densely clothed with even longer, more pointed pustules (spinelets). It should be noted that most species of *Keratella* have forms with dorsal pustulation (*K. reducta* and *K. cruciformis* are probably exceptions) and also forms lacking dorsal pustulation. The development of pustulation is a character that presents gradational variability in most species of *Keratella*. In other words, a series of intergrades may be encountered between marked pustulation and no pustulation, occasionally even in the same habitat.

THE FOUNDATION PATTERN OF THE DORSUM

In addition to the fine areolate network that covers the lorica of species of *Keratella*, there is present on the dorsal plate a larger pattern which is usually quite evident. This marked sculptural pattern, which I will refer to throughout the body of the paper as the foundation pattern of the dorsum, divides the dorsal plate into a number of facets or plaques. The arrangement of the facets is relatively constant in any species and is a highly important taxonomic character.

There are two arrangements of the facets on the dorsum that occur in so many of the species that we are justified in calling them the basic patterns. The arrangement found in species having two posterior spines (along with their forms lacking posterior spines) consists of a number of median polygons, usually three, with several enclosed lateral polygons on either side. For convenience we will call this the "quadrata" pattern. Two species with a median posterior spine also belong in this category.

The other basic pattern has the facets mesially divided, with one or several pairs of polygons separated by the median line, and with several lateral polygons to the sides of these. All species known to have this pattern possess a single median posterior spine, although several of the species do have forms lacking posterior spines. For convenience we will call this arrangement the "cochlearis" pattern.

For the sake of clarity, a figure of *Keratella quadrata* is given in which the more important areas of the dorsal pattern are given names, and the corresponding plaques are shown for *Keratella valga*, *K. serrulata* and *K. gracilenta*.

No two species have exactly the same detailed arrangements of facets of the "quadrata" pattern. However, *Keratella valga* has essentially the same pattern as *Keratella quadrata*, differing mainly in minor details of the posterior portion of the pattern. *Keratella serrulata* has only two median enclosed facets, the anterior one being a hexagon, the posterior one a heptagon, and back from this extends a short median line. *Keratella gracilenta*, which has a single median posterior spine, has a pattern of three median polygons, the posterior one of which is open at its distal end; and the arrangement of the lateral facets on this species differs in various details from those on *Keratella quadrata*, the lateral frontal areas, especially, being much more extensive. *K. reducta*, the small South African species with four frontal spines and no posterior spines, has three enclosed median plaques but has a greater number of lateral and posterior plaques than is usual for species with the "quadrata" pattern. *Keratella paludosa* has a modified pattern about which there may be some question as to its being a variant of the "quadrata" pattern at all; the same is true of *Keratella mixta,* although this species appears to be related to *K. serrulata.*

There are a number of interesting modifications of the "cochlearis" pattern. To keep the discussion of this group brief yet lucid, the accompanying figure is included, showing the arrangement of facets on several of the species. It is necessary to give names to the facets to follow the modifications of the "cochlearis" pattern.

The basic "cochlearis" pattern is seen to consist of a single pair of enclosed carinal plaques (invariably hexagons), posterior to which are the postero-carinal areas (often enclosed to form the postero-carinal plaques). A median line separates the carinal plaques, and it may have a more or less abrupt jog to the right below the antero-carinal plaques.

The "cochlearis" pattern is complicated in related species by the addition of plaques. In *Keratella crassa* the antero-carinal polygons are divided into two pairs of plaques. The median line jogs to the left posterior to the first pair of antero-carinal plaques and jogs as abruptly to the right beyond the second pair (called medio-carinal plaques).

Another interesting modification of the "cochlearis" pattern is found in *K. irregularis.* In this species there is a medial pentagon, the accessory medial plaque, developed between the carinal plaques somewhat to the right of center, which interrupts the median line; also the postero-carinal plaque is divided into two pairs of polygons, the posterior pair being small and rectangular (called the accessory postero-carinal plaques). On *Keratella earlinae* the addition of plaques is carried even further, for, besides having an accessory medial plaque (which in this species is six-sided), there is developed between the antero-carinal plaques an accessory antero-

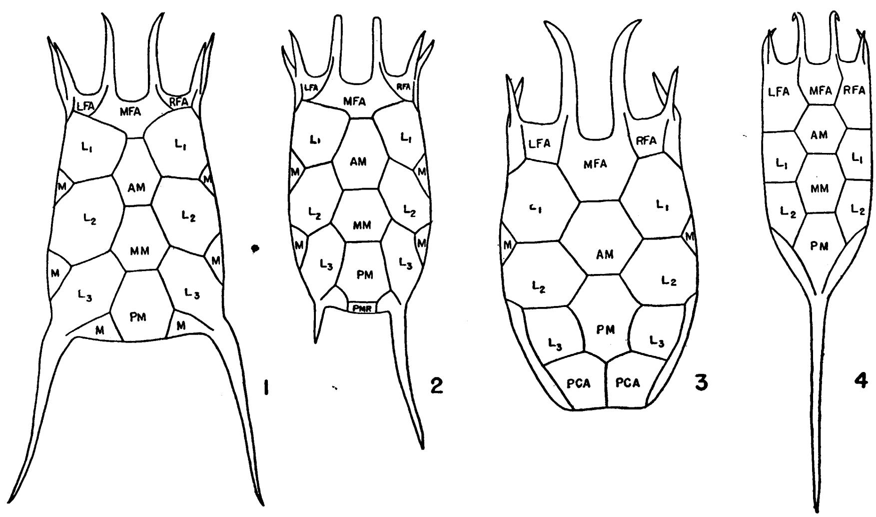


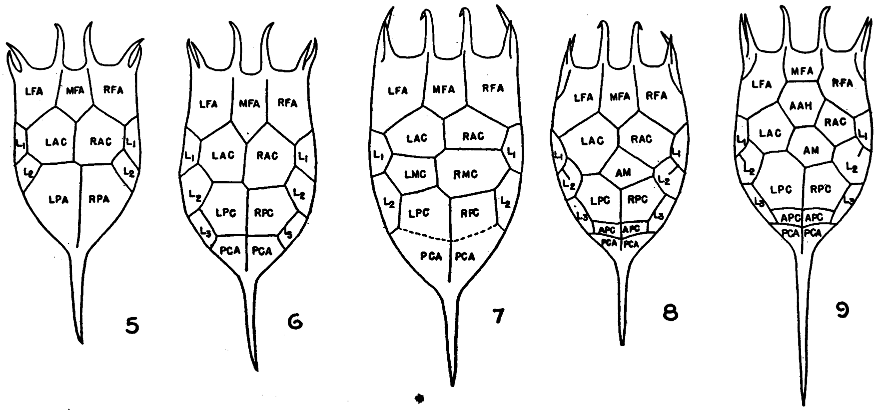
Fig. 1. *Keratella quadrata.*
Fig. 2. *Keratella valga.*
Fig. 3. *Keratella serrulata*
Fig. 4. *Keratella gracilenta*

ABBREVIATIONS

AM, antero-median plaque; L (numbered), lateral plaques; LFA, left frontal area; M, marginal plaques; MFA, median frontal area; MM, meso-median plaque; PCA, postero-carinal area; PM, postero-median plaque; PMR, postero-median remnant; RFA, right frontal area.

median hexagon; the postero-carinal plaques are also subdivided as in *K. irregularis*. Consequently in this species the median line is developed only posterior to the accessory medial hexagon.

Although *Keratella cruciformis*[*] has a median line running nearly the entire length of the dorsum, the rest of the pattern has little resemblance to the "cochlearis" arrangement of plaques.



Figs. 5, 6. *Keratella cochlearis.*
Fig. 7. *Keratella crassa.*
Fig. 8. *Keratella irregularis.*
Fig. 9. *Keratella earlinae.*

ABBREVIATIONS

AAH, accessory antero-median hexagon; AM, accessory medial plaque; APC, accessory postero-carinal plaque; L (numbered), lateral plaques; LAC, left antero-carinal plaque; LFA, left frontal area; LMC, left medio-carinal plaque; LPA, left postero-carinal area; LPC, left postero-carinal plaque; MFA, median frontal area; PCA, postero-carinal area; RAC, right antero-carinal plaque; RFA, right frontal area; RMC, right medio-carinal plaque; RPA, right postero-carinal area; RPC, right postero-carinal plaque.

THE PROBLEM OF CYCLOMORPHOSIS IN *KERATELLA*

Cyclomorphosis is not an uncommon phenomenon among plankton organisms, being well exemplified in both fresh water rotifers and Cladocera. Among rotifers cyclomorphosis is more obviously present in the family Brachionidae than in any other and perhaps has its fullest development in the genus *Keratella.*

Cyclomorphosis, or cyclic variation, is shown in a sequence of generations in the same strain of organisms which are marked by progressive modifications until the entire population is noticeably different in appearance, yet the whole cycle usually takes place by means of parthenogenetic reproduction in an unbroken line of unfertilized females. The cycle may end in the reduced forms by the intervention of a sexual phase, or the changes may again occur in reverse order and complete the cycle in that manner.

In *Keratella* cyclomorphosis is most noticeable in the variation in length of the posterior spine (or spines) and is best exemplified in the two common species, *Keratella quadrata* and *Keratella cochlearis.* In the former species there are two posterior spines. The usual form of cyclomorphosis in this species consists of a cycle of reduction, the form with long posterior spines initiating the cycle, and the spines are progressively reduced in succeeding generations until a form with short posterior spines together with a form lacking posterior spines dominate in a habitat, at which time a sexual generation may terminate the cycle. In *Keratella cochlearis* we commonly find a form with a long posterior spine (this species has a single, median posterior spine) in the collections during the winter months; there is a gradual reduction in size until July or August at which time a form with a short posterior spine or the *tecta* form without posterior spines dominates. During the remainder of the year there is a gradual reversal until the form with a long posterior spine again dominates.

The changes in form cannot be ascribed simply to an inherent cycle, or to changes in the habitat in which the organisms occur, but must be due to a complicated interaction between the organisms and their environment. The types of cyclomorphosis just described for *Keratella* occur completely only in certain habitats and in certain seasons; the cycle is not exhibited at all in other habitats or may be but partially manifested. It may be helpful if concrete illustrations are given for one of these species.

Keratella cochlearis, being the more common species, will be chosen, and three habitats will serve to illustrate the problem. In the deep water plankton of Lake Michigan cyclomorphosis of *K. cochlearis* is practically non-existent, the form with a rather long postero-spine occurring throughout the year. In such large-sized, relatively cold lakes the species is apparently acyclic. In western Lake Erie, which is shallower as well as warmer in summer, the cyclomorphosis is more marked, there is a gradual reduction in size from March until the middle of August and a reverse trend thereafter. The *tecta* form was noted in Lake Erie in April and May only and seemed to have no direct connection with cyclomorphosis; during July and August when a short postero-spined form dominated there were no individuals of the *tecta* form observed. Furthermore, in Lake Erie the phenomenon is further complicated by the occurrence of some long postero-spined forms throughout the summer months, showing that cyclomorphosis does not occur in all individuals of a population. It is not clear when the sexual phase would enter into cyclomorphosis in such a situation. Wesenberg-Lund states that mictic females appear mainly in spring (may also appear in autumn) in *K. cochlearis.* If such is the case the sexual phase of the cycle does not coincide with the most reduced portion of the cycle in *K. cochlearis.* In a pond on Middle Bass Island only some fifty feet distant from Lake Erie and probably receiving water from the lake during rough weather, the cyclomorphosis was quite different from that in the lake. The water in the pond is warmer than in the lake but is also subject to greater fluctuations in temperature. The pond was studied during several summer seasons, and throughout this time the *tecta* form entirely dominated, with a short postero-spined form being rare. What forms occur in the pond during the colder months is not known; however, the *tecta* form probably persists throughout the year, while the postero-spined form becomes more abundant during the colder months.

It will be noted that the posterior spine is usually longest in cold months and shorter during the summer months in *Keratella cochlearis.* Much of the early work on cyclomorphosis was based on observations of *Daphnia* (especially *Daphnia cucullata*) and in this cladoceran the "winter" form was the reduced form and the "summer" form has a greatly developed head process or helmet. To explain cyclomorphosis Wesenberg-Lund (1900) offered his "buoyancy theory"; Ostwald (1902) in his "plankton theory" modified the Wesenberg-Lund theory. The flotation theory of these two workers held that helmets, spines and other processes offered resistance to sinking and thus were more needed in summer than in winter; the viscosity of the water was supposedly the important variable influencing velocity of sinking. Woltereck (1909, 1913, etc.) cast much doubt upon the flotation theory, especially by his study of locomotion in *Daphnia.* He correlated the variation in helmets of *Daphnia* with the food supply, helmets being longest in summer when the food supply was best. Obviously neither of the theories postulated to explain cyclomorphosis in *Daphnia* applies to *Keratella,* for there is a reduction in the posterior spine in summer months which is just opposite to what we would expect from the flotation theory and which does not accord with the Woltereck conception of the importance of the food supply in determining size of protuberances. Coker (1939), working with *Daphnia longispina,* has demonstrated the importance of temperature in the cyclomorphosis of that species. Cyclomorphosis in *Daphnia longispina* consists in the change from the "winter form" with round heads to a "summer form" with a pointed head. Coker, working with cultures under controlled conditions of temperature, found that at temperatures below 11° C. only round heads were obtained, at temperatures above 15° C. only pointed heads, while mixed broods of round and weakly pointed heads were obtained at intermediate temperatures. The demonstration of the importance of temperature in cyclomorphosis is in accord with what has been noted in *Keratella cochlearis,* although there has been no careful study made as to the influence of temperature under controlled conditions on the cyclomorphosis of *Keratella cochlearis.* Such a study is needed.

Much variation in *Keratella* is cyclic in nature; however, the extent of cyclomorphosis is by no means known for every species of *Keratella.* This complicates the problem of taxonomy in *Keratella.* Cyclic variation is known to influence chiefly the length and form of the posterior spine (or spines) in *Keratella.* For this reason the posterior spine is often a very poor character on which to base varieties in *Keratella,* yet it has been the most used character. Variation within a species which is of a cyclic nature should perhaps not be given taxonomic designations for the various phases of cyclomorphosis. However, there are certain advantages in having a tag for very reduced forms, such as the *tecta* form of *Keratella cochlearis,* and in giving names to certain other cyclic forms, such as f. *brevispina* of *Keratella quadrata.* Such a procedure will be followed in this paper, but cyclic form names will be kept to a minimum; such names have no value as taxonomic categories in a strict sense but are useful, nevertheless, to the limnologist and taxonomist.

An artificial key to the species of *Keratella* is proposed. In a genus where most of the species are quite variable in a number of characters, it is impractical to attempt to key out all the possible variants that might be encountered in nature. It is suggested that the key be used in conjunction with the figures of *Keratella.* It is advisable to have thoroughly in mind the facts presented in the foregoing section on "The Foundation Pattern of the Dorsum" before the use of the key is attempted. It will be noted that the more variable species are keyed out in several places. A key to the varieties of *Keratella quadrata* is given in the text discussion of that species.

Key to Species of *Keratella*

A.—One or two posterior spines developed.
- B.—A single posterior spine present.
  - C.—Posterior spine median or nearly so.
    - D.—Median line present in foundation pattern of dorsum.
      - E.—Median line unbroken by an accessory medial plaque.
        - F.—Antero-lateral spines shorter than medians, not bowed .... *K. cochlearis.*
        - FF.—Antero-lateral spines longer than medians, usually strongly bowed .... *K. taurocephala.*
      - EE.—Median line interrupted by an accessory medial plaque.
        - F.—Median line developed both anterior and posterior to a single accessory medial plaque .... *K. irregularis.*
        - FF.—Median line developed only posterior to two accessory medial plaques .... *K. earlinae.*
    - DD.—Median line not present.
      - E.—A central row of plaques present.
        - F.—Median plaques three in number, postero-spine exactly median .... *K. gracilenta.*

FF.—Median plaques four in number, postero-spine extends at an angle to left of center........................*K. paludosa.*

EE.—Central plaques not in a row but in an irregular group of six plaques (postero-spine somewhat to right of center)..............*K. mixta.*

CC.—Posterior spine more or less lateral.

D.—Posterior width of body greater than anterior width........*K. quadrata.*

DD.—Posterior width of body less than anterior width..............*K. valga.*

BB.—Two posterior spines present.

C.—Width between postero-spines less than anterior width.

D.—Postero-spines subequal, foundation pattern with two enclosed median plaques..*K. serrulata.*

DD.—Postero-spines unequal, right usually much longer, foundation pattern with three enclosed median plaques..........................*K. valga.*

CC.—Width between postero-spines greater than anterior width..........*K. quadrata.*

AA.—No posterior spines present.

B.—Anterior spines four...*K. reducta.*

BB.—Anterior spines six.

C.—Foundation pattern of dorsum characterized by a long median line.

D.—Typical carinal plaques not developed; a marine or brackish water species. ....*K. cruciformis.*

DD.—Typical carinal plaques developed; fresh water forms.

E.—Median line unbroken by an accessory medial plaque............. ....*K. cochlearis* f. *tecta.*

EE.—Median line interrupted by an accessory medial plaque........... ....*K. irregularis* f. *wartmanni.*

CC.—Foundation pattern of dorsum characterized by a series of median plaques.

D.—A short median line developed posterior to two enclosed median plaques... ....*K. serrulata* f. *curvicornis.*

DD.—Median plaques alone present.

E.—Antero-median plaque divided to form two plaques............... ....*K. quadrata* var. *curvicornis.*

EE.—Antero-median plaque not so divided.

F.—Postero-median plaque enclosed posteriorly, leaving a small unenclosed remnant.....................*K. valga* f. *brehmi.*

FF.—Postero-median plaque not enclosed posteriorly............ ....*K. quadrata* f. *araneosa.*

The writer has been fortunate in obtaining material of all recognized species of *Keratella*, save *Keratella javana* Hauer which is known from a single specimen. Due to the great variability of species of *Keratella*, a number of illustrations of each species are included to portray graphically some of the variability encountered within species. The locality is indicated for each illustration given, since some species of *Keratella* are more variable in some regions than in others. The reader is referred to the discussions under *Keratella cochlearis* and *Keratella valga* for marked instances of regional variability.

Specimens of all species discussed in this paper are in the collection of The American Museum of Natural History.

I am greatly indebted to Mr. Frank J. Myers for material and bibliographical aid on *Keratella*, to Mr. W. T. Edmondson for material from a number of regions, to Dr. G. E. Hutchinson for use of some collections from South Africa and India, to Dr. R. W. Miner of The American Museum of Natural History for the loan of the *Keratella* collection of the museum, to Dr. Carlin-Nilsson for European material, to G. H. Wailes for material from Lake Windermere, England, to Dr. Stillman Wright for use of collections made in Brazil and Argentina, to Morley Neal for Canadian material from British Columbia and Ontario, to Larry Whitford, R. K. Salisbury, Dr. Robert Pennak and Dr. Clarence Taft for American material. I am much indebted to my wife, Leota E. Ahlstrom, for help in preparing the manuscript for publication.

KERATELLA Bory de St. Vincent

Bory de St. Vincent, 1822, p. 470.

Brachionid rotifers with loricate body, separated into a dorsal and a ventral plate, which is more or less compressed dorsoventrally. Head retractile and illoricate.

Anterior dorsal margin with six (or four) spines; mental margin rigid, rounded, with a median sinus. Postero-spines often present, one or two in number, single postero-spine usually median. Foot not developed. Dorsal plate with a sculptural pattern, the foundation pattern of the dorsum, which is relatively constant for any species. Both plates of lorica usually covered with a fine areolate network (not to be confused with the foundation pattern of the dorsum); pustulation commonly present.

SYNONYMS.—*Anuraea* Ehrenberg; *Anourella* Bory de St. Vincent.

Keratella cochlearis (Gosse)

Plate XXXV, figures 1–14

Anuraea cochlearis GOSSE, 1851, p. 202; HUDSON AND GOSSE, 1886, p. 124, Pl. XXIX, fig. 7; LAUTERBORN, 1898, p. 598, fig. 2; WEBER, 1898, p. 709, Pl. XXV, fig. 8; LAUTERBORN, 1900, p. 421, Pl. X, figs. 2–4, text figs. 1, 2.

?*Anuraea longistyla* SCHMARDA, 1859, p. 62, Pl. XIV, fig. 132.

Anuraea longispina IMHOF, 1883, p. 470, fig. 1.

Anuraea intermedia IMHOF, 1885, p. 323.

Anuraea tuberosa IMHOF, 1885, p. 323.

Anuraea cochlearis var. *carinata* LEVANDER, 1892, p. 142.

Anuraea cochlearis var. *stipitata* WEBER, 1898, p. 712, Pl. XXV, fig. 9.

Anuraea cochlearis var. *macracantha* f. *micracantha* LAUTERBORN, 1900, p. 421, Pl. X, figs. 5, 6.

Anuraea cochlearis var. *macracantha* f. *tuberculata* LAUTERBORN, 1900, p. 421, Pl. X, figs. 7, 8.

Anuraea cochlearis var. *irregularis* f. *connectens* LAUTERBORN, 1900, p. 431, Pl. X, figs. 15, 16.

Anuraea cochlearis var. *leptacantha* LAUTERBORN, 1900, p. 428, Pl. X, fig. 24.

Anuraea cochlearis var. *revoluta* BREHM, 1910, p. 191.

Anuraea cochlearis var. *scutiformis* DELACHAUX, 1927, p. 47, Pl. I, fig. 1.

Lorica terminates in a stout median posterior spine which usually varies in length from as long as the body proper to one-third as long but which may be even more reduced or completely wanting. Lorica oval shaped in dorsal view, depth of the dorsal plate is a little more than half the width; the greatest width of the lorica is slightly behind the middle of the body, although the lorica tapers but slightly anteriorward; the lorica is about two-thirds as wide as long (width varies from 0.56–0.71 of length of body exclusive of spines). Anterior dorsal margin with six spines: medians longest, curve ventrally, intermediates usually slightly divergent, somewhat shorter than lateral spines which are convergent at their tips and which arise at a slight angle toward the ventral.

The lorica has the usual pattern of minute interlacing areolations on both plates. The ventral plate is usually pustulate on the upper third only, although this feature is somewhat variable (refer to discussion following). The dorsal plate is often somewhat pustulate, the small pustules being at the corners of areolations and scattered over the entire plate. The foundation pattern of the dorsum is characterized by a median line extending longitudinally from behind the median frontal area to the base of the posterior spine. Often there is but one pair of fully enclosed carinal plaques: the antero-carinal polygons (hexagons). Not infrequently, however, the postero-carinal polygons are fully formed; when this is the case there are two very small unenclosed carinal areas posterior to the two enclosed pairs of carinal plaques. There are two pairs of enclosed lateral polygons to the sides of the antero-carinal polygons; a third pair may be present to the sides of the postero-carinal plaques.

DISTRIBUTION.—Cosmopolitan in fresh water habitats. This is probably the most widely distributed and common rotifer in nature. It is also a truly planktonic species.

Lauterborn (1898 and 1900) conducted an outstanding investigation of the variation tendencies of *Keratella cochlearis.* This work is especially notable for the excellence of the illustrations, which are exact yet detailed. This is in marked contrast to most illustrations of *Keratella* which are notoriously inaccurate and incomplete. However, excellent as Lauterborn's work is, it was limited to an investigation of some middle European habitats. A study of variation tendencies of *Keratella cochlearis* in many parts of the world but especially in North American habitats has made a critical revaluation of Lauterborn's work necessary.

Lauterborn described five main lines of

Keratella cochlearis (Gosse)

Locality	Date	Total Length	Width	Length Body	W/L Ratio	Post. Spine	Ant. Spines
NORTH AMERICA							
Minerva Lake, Columbus, Ohio	VIII.22.34	119μ	49μ	77μ	0.64	27μ	17-10-25μ
Forestry Bog, Wisc.	VII.8.35	120μ	53μ	76μ	0.70	26μ	20-15-30μ
Pond, Bass Island region, Ohio	VII.5.32	122μ	52μ	77μ	0.67	25μ	20-13-30μ
Pond, Asheboro, N. C.	VI.17.36	126μ	55μ	78μ	0.70	26μ	19-13-30μ
Pocono Lake, Pa.	VI.17.39	132μ	51μ	75μ	0.68	32μ	21-17-30μ
Lake Xochimilco, Mexico	VIII.—32	133μ	52μ	80μ	0.65	29μ	21-19-33μ
Bear Lake, Vancouver Is., B. C.	VII.23.25	136μ	57μ	82μ	0.70	30μ	22-18-32μ
Lincoln Park Lake, Los Angeles, Calif.	III.20.32	138μ	51μ	80μ	0.64	32μ	20-15-31μ
Pistakee Lake, Fox Lake, Ill.	VI.5.32	143μ	59μ	80μ	0.74	41μ	19-17-30μ
Pond, Princeton, N. C.	VI.14.35	146μ	53μ	76μ	0.70	48μ	21-14-29μ
Public Reservoir, Lexington, Ky.	VIII.29.32	152μ	52μ	83μ	0.63	50μ	21-18-30μ
Lake Minnewanka, Banff, Alberta	VIII.3.36	155μ	59μ	93μ	0.63	42μ	22-15-32μ
Carlyle Lake, Kamloops region, B. C.	VII.1.38	158μ	63μ	92μ	0.68	50μ	21-18-31μ
Echo Park Lake, Los Angeles, Calif.	XI.25.31	160μ	68μ	96μ	0.71	42μ	21-17-31μ
Lake near Wildwood, Fla.	XII.28.34	165μ	55μ	90μ	0.61	55μ	20-14-30μ
Edward's Lake, Kamloops region, B. C.	VII.15.38	170μ	58μ	85μ	0.68	69μ	23-19-31μ
Rio Santiago near Lake Chapala, Mexico	III.30.32	174μ	59μ	90μ	0.66	60μ	25-20-33μ
Nicola Lake, B. C.	1931	175μ	71μ	100μ	0.71	48μ	21-17-30μ
Lake Mendota, Wisc.	VIII.7.15	180μ	57μ	88μ	0.65	67μ	19-18-31μ
Sandpits, Lillington, N. C.	V.13.35	180μ	55μ	98μ	0.56	57μ	22-17-32μ
Terwilliger's, Put-in-Bay, Ohio	VII.11.32	184μ	58μ	92μ	0.63	76μ	22-20-30μ
	VIII.12.32	124μ	49μ	76μ	0.64	28μ	18-15-30μ
Lake Michigan	VI.9.31	187μ	62μ	97μ	0.64	65μ	24-20-34μ
	VIII.26.31	160μ	55μ	86μ	0.64	47μ	21-16-30μ
Lake Washington, Seattle, Wash.	V.11.33	184μ	61μ	92μ	0.67	68μ	21-17-32μ
Silver Lake, Wisc.	VI.5.32	193μ	64μ	100μ	0.64	72μ	24-21-33μ
Lenape Lake, N. J.	IV.16.34	203μ	61μ	98μ	0.62	83μ	23-21-31μ
Wallace Lake, Isle Royale, Mich.	VIII.—30	208μ	53μ	87μ	0.61	100μ	21-19-29μ
Flathead Lake, Mont.	....	210μ	65μ	98μ	0.66	85μ	24-22-36μ
Murray Lake, B. C.	VIII.12.38	214μ	58μ	96μ	0.60	86μ	24-21-35μ
EUROPE							
Walton on Thames, England	....	140μ	55μ	84μ	0.65	40μ	20-14-30μ
Lake, Rusane, Prov. Latgale, Latvia	VII.13.23	140μ	62μ	91μ	0.68	33μ	20-16-28μ
Pond, Hyby, Sweden	V.5.35	167μ	65μ	94μ	0.69	57μ	18-14-30μ
Pond, Lovestad, Sweden	VII.15.34	168μ	66μ	96μ	0.69	54μ	22-19-36μ
Lake Windermere, England	VIII.15.38	178μ	61μ	96μ	0.64	60μ	24-17-30μ
OTHER LOCALITIES							
Bod Dal Lake, Kashmir Valley, India	V.1.32	143μ	57μ	85μ	0.67	32μ	17-13-28μ
Lagune, San Luis Prov., Argentina	XII.9.36	144μ	57μ	93μ	0.61	32μ	17-13-28μ
Potchefstroom Dam, S. Africa	X.1.27	157μ	60μ	85μ	0.71	53μ	20-19-32μ
Ororotse Tso, Indian Tibet	VII.11.32	170μ	66μ	96μ	0.69	54μ	25-14-26μ

variation in *Keratella cochlearis:* the *macracantha, hispida, irregularis, robusta* and *leptacantha.* On the whole his analysis is still valid when applied to European material of *K. cochlearis* but is inadequate when dealing with this species from other regions, particularly from North America. *Keratella cochlearis* does not present the same variation pattern in American waters that it does in middle European habitats. The *macracantha* series is really the variation series of the typical *cochlearis.* In the *hispida* and *irregularis* series of Lauterborn, some of the forms he postulated as connecting links with the typical *cochlearis* are open to question; I am treating *irregularis* as a separate species, for reasons given later. The large forms of *Keratella cochlearis* fall into at least three categories: *robusta*, *recurvispina* and *faluta*, of which the *robusta* series is quite variable and probably not homogeneous. The value of designating *leptacantha* as a distinct variety is open to question; it is probably a local variant of the typical *cochlearis* series. A discussion of the variation tendencies noted in *K. cochlearis* is necessary as a background before units smaller than species are discussed in the *cochlearis* complex.

Keratella cochlearis is a very variable species in several respects. It has a cycle of reduction in which the posterior spine is gradually shortened until it may become completely wanting; of this more later. Independent of cyclomorphosis, this species has a number of interesting variants, several of which are so distinct as to constitute well defined varieties, while other deviants display lesser modification of the usual *cochlearis* type, many of which are too "unstable" to be dealt with taxonomically. Variability in *Keratella cochlearis* will be discussed under the three following categories: (1) variation in the foundation pattern of the dorsum, (2) variation in pustulation, particularly of the ventral plate, and (3) variation in size and proportions of the body.

The foundation pattern of the dorsum in *K. cochlearis* is characterized by a median ridge called the median line. The median line may be straight for its entire length or it may have a jog to the right immediately behind the antero-carinal plaques. The usual form of *cochlearis* encountered in the United States has a more or less abrupt jog to the right in the median line, while the usual form encountered in Europe has the median line about straight for its entire length. This is an interesting difference. The anterior pair of plaques to the side of the median line, the antero-carinal plaques, are always fully formed; there are two pairs of lateral plaques to the side of them. The foundation pattern is somewhat variable in the posterior portion of the dorsal plate, in that the postero-carinal plaques may or may not be enclosed. When they are not enclosed this portion of the dorsal plate on either side of the median line is referred to as the postero-carinal areas; when the postero-carinal plaques are enclosed there is also a third pair of lateral plaques formed. In a single collection one may encounter various degrees of formation of the postero-carinal plaques; consequently this character is too variable to be of taxonomic significance. Forms having a foundation pattern similar to that described above are considered as belonging to the *cochlearis* complex (exception, *K. taurocephala*, which is excluded on the basis of other characters). This eliminates *K. irregularis* from the *cochlearis* complex and justifiably so. Lauterborn gave a series of forms showing gradations between *cochlearis* and *irregularis*. However, this series is open to question, especially since f. *connectens* of the series is not an intermediate form but really corresponds to the common form of typical *cochlearis* in America where *irregularis* does not even occur.

A second feature to be considered is variation in pustulation. *Keratella cochlearis* has a number of variants with respect to pustulation. Moreover, the development of pustulation displays gradational variability, which complicates the problem. Not all specimens in a collection are pustulate to a similar extent, and when material from a number of localities is compared, it is realized that all the variants to be discussed probably grade gradually into a non-pustulate form.

Variants with respect to pustulation in the typical *K. cochlearis* series will be considered first. The common form encountered in the United States has the upper third of the ventral plate clothed with fairly large truncate pustules, while the dorsal plate has small pustules at the corners of the areolate network; not uncommonly, however, pustulation may be lacking on the dorsal plate. Less commonly there is encountered in North American habitats a small-sized form having pustules (spinelets) all along the ventral plate on most individuals. This form is commonly found in acid situations. However, in these habitats there are almost always some individuals having pustules for one-half to one-third of the ventral plate only;

consequently this variant does not appear to be constant enough to warrant making it a separate variety. The usual size of this form is from 119–140μ in total length. Occasionally there is found in American habitats a form which lacks pustulation on the ventral plate or else has a few small pustules at the anterior end, while the dorsal plate lacks pustulation. The form I have observed most commonly from European collections corresponds to the latter variant. The usual size of typical *cochlearis*, incidentally, is from about 100μ to 210μ, although both smaller and larger-sized specimens are occasionally found.

In addition to the above variants of typical *cochlearis* there are several large-sized varieties of *cochlearis* whose claim to varietal rank will not be discussed at this point as we are here interested in the variety of pustulation patterns they present. *Keratella cochlearis* var. *faluta* lacks pustulation on either plate, but the basic network of areolations is very prominent; variety *recurvispina* also lacks pustulation on the material I have studied. *Keratella cochlearis* var. *robusta*, on the other hand, is exceedingly variable with respect to pustulation, and has variants that parallel the types discussed under the typical *cochlearis*, with the notable exception that I have found no specimens of *robusta* with the upper third of the ventral plate markedly pustulate, which is the pustulation pattern of the common form of typical *cochlearis* in America. The three common pustulation patterns observed for variety *robusta* are: (1) large pustules all along the ventral plate, while small pustules may or may not be present on the dorsal plate; (2) a few small pustules at the upper end of the ventral plate, while the dorsal plate may or may not be pustulate, or (3) not pustulate on either plate. In variety *robusta*, individuals from a single collection often vary greatly in development of pustulation.

The most exuberant variety of *cochlearis* with respect to pustulation is variety *hispida*, in which both dorsal and ventral plates are densely covered with spinelets which are several micra long and usually bluntly pointed or even truncate. This variety is usually so hispid that the foundation pattern of the dorsum is obscured as is also the areolate network.

It is somewhat difficult to deal with size variation in *Keratella cochlearis*. In some habitats (especially ponds and shallow lakes) the size of *K. cochlearis* varies greatly at different times of the year. This is partially bound up with the problem of cyclomorphosis; in other bodies of water (especially large, deep lakes) there is little variation in size during the course of the year. On a given date of collection in most habitats the material of *K. cochlearis* is of much the same size. Because this is so, I believe the table giving measurements of *K. cochlearis* from a number of habitats is of value, especially as the dates of collection are indicated; the table shows the size range to be expected for *cochlearis*, the variation one finds in proportions of the body, etc.

In some collections there are two very distinct size forms of *cochlearis* present, which often differ in other characters besides size. Two examples will be given. (1) In Cobin Lake, Alberta (VII.20.39), the large-sized form (variety *robusta*) had a length of 218μ; width, 75μ; length body, 113μ; length posterior spine, 76μ; while the typical *cochlearis* measured but 132μ long; width, 59μ; length body, 86μ; length posterior spine, 29μ. Furthermore, the large-sized form had no jog in the median line, and the ventral plate had pustules (spinelets) along entire length, while the smaller typical *cochlearis* had a slight jog in the median line posterior to the antero-carinal plaques and had pustules on only the upper third of the ventral plate. (2) In a collection from Bear Lake, Vancouver Island, B. C. (VII.23.35), the large-sized form (var. *robusta*) measured in total length, 195μ; width, 68μ; length body, 100μ; posterior spine, 70μ; while the smaller-sized form measured in total length, 142μ; width, 57μ; length body, 82μ; posterior spine, 36μ. The large-sized form had the median line practically straight, had a few minute pustules on the upper part of the ventral plate and a few pustules on the dorsal; the small-sized form had a slight jog in the median line and had pointed spinelets all along the ventral plate and no pustulation on the dorsal. It is from instances such as the above two that the identity of *robusta* as a separate variety can be established beyond question.

The larger-sized forms of *K. cochlearis* are usually readily separable from the typical series of *cochlearis*, although both series commonly occur in the same habitats. The large-sized forms studied can be conveniently placed in four categories. The most exuberant size variety is var. *faluta*, which may be over 300μ in length and 100μ in width. This variety, encountered so far only in temperate North American localities, is proportionately more compressed dorso-ventrally than other forms of *cochlearis* and is also correspondingly wider, having a width–length ratio of 0.68–0.84; the intermediate and lateral anterior spines are usually rather divergent. The divergence of anterior spines is carried to an extreme development in var. *recurvispina*, in which the long intermediates may extend laterally at right angles to the head and also extend dorsally, while the laterals bend markedly toward the ventral. In the *robusta* series the anterior spines are similar to those occurring on typical *cochlearis*, while the lorica is quite deep, which is in marked contrast to the depth of the lorica of var. *faluta*. These varieties also differ in pustulation, as was indicated in a preceding paragraph. The fourth large-sized form of *cochlearis* is f. *macracantha*, which possesses the characteristics of typical *cochlearis*, save that it is larger in size and has a posterior spine of about equal length to the body proper.

In most habitats *Keratella cochlearis* exhibits a cycle of reduction. The longer postero-spined forms usually occur during the colder months, while short postero-spined forms occur during the summer months, at which time the *tecta* form (i.e., forms lacking posterior spine) may dominate. This cycle is most marked in ponds, rivers and small lakes. In larger lakes the cycle is usually incomplete or wanting. Thus in Lake Washington, near Seattle, there was little reduction in the length of the posterior spines during the warmer months of 1933; this is also true of material studied over several years from Lake Michigan. In these localities *K. cochlearis* is apparently acyclic. In Terwilliger's Pond, an embayment of Lake Erie, there is a reduction in length of the posterior spines during the warmer months, becoming shortest in late July and early August (1932); however, during the summer months there were occasional long-spined individuals persisting, and the *tecta* form did not occur. As a contrast, a true pond on an adjacent island during the same season had reduced forms of *cochlearis* only, and the *tecta* form outnumbered the short postero-spined form during July and August by about a hundred to one. This problem is discussed in some detail in an introductory section of the paper. Taxonomic names are not given in this paper to cyclic forms of *cochlearis*, nor are taxonomic names applied to differences due to the ecological habitats in which the species develops.

The following table gives the dimensional range of *Keratella cochlearis* and its more common varieties as observed by the writer:

	cochlearis cochlearis	form *tecta*	variety *hispida*	variety *robusta*	variety *faluta*
Total length	92–210μ	89–125μ	162–212μ	192–228μ	185–320μ
Width	45–68μ	48–62μ	58–67μ	66–76μ	76–106μ
Post. spine	3–100μ	0	44–82μ	66–85μ	46–128μ
Antero-lat. sp.	11–25μ	6–21μ	18–23μ	22–30μ	15–33μ
Antero-inter. sp.	9–22μ	6–18μ	14–19μ	14–21μ	11–25μ
Antero-med. sp.	22–36μ	18–31μ	29–34μ	31–38μ	23–45μ
Length body	67–100μ	73–100μ	92–102μ	103–115μ	100–144μ
Depth	30–37μ	....	(41μ)	44–53μ	25–44μ
Width/length ratio	0.56–0.71	0.59–0.72	0.62–0.71	0.60–0.72	0.68–0.84
Depth/width ratio	0.55–0.62	....	....	0.62–0.71	0.32–0.42

Keratella cochlearis f. **macracantha** (Lauterborn)

Plate XXXVI, figure 8

Anuraea cochlearis var. *macracantha* LAUTERBORN, 1898, p. 598, Fig. 1; LAUTERBORN, 1900, p. 421, Pl. X, fig. 1.

This is a large-sized form of *cochlearis* which is characterized by its larger size and by the heavy, long, posterior spine which is about as long as the body proper. In my experience this form is not common. On the material I have seen of this form as well as in the figures of Lauterborn the foundation pattern of the dorsum has the simplest *cochlearis* pattern. The antero-carinal plaques with their accompanying pair of lateral plaques are the only plaques formed.

DIMENSIONS.—From Penask Lake in British Columbia a specimen had the following dimensions: total length, 270μ; greatest width, 65μ; length body, 118μ; length posterior spine, 118μ; length anterior spines, 39-37-40μ. Lauterborn gives a total length of 261μ, a posterior spine of 100μ.

Keratella cochlearis f. **tecta** (Gosse)

Plate XXXV, figures 15, 16

Anuraea tecta GOSSE, 1851, p. 202; HUDSON AND GOSSE, 1886, p. 123, Pl. XXIX, fig. 10; WIERZEJSKI, 1893, p. 255, Pl. VI, fig. 78.

Anuraea cochlearis tecta LAUTERBORN, 1898, p. 599, Fig. 3; LAUTERBORN, 1900, p. 421, Pl. X, figs. 9–10.

Anuraea cochlearis tecta f. *major*, *punctata* LAUTERBORN, 1900, p. 429, Pl. X, figs. 26, 27.

Anuraea cochlearis leptacantha f. *ecaudata* LAUTERBORN, 1900, p. 428, Pl. X, fig. 24.

Form lacking the postero-spine. This is the most reduced form in the typical *cochlearis* series. The general shape of the body is ovoid. The anterior spines may be quite reduced in some habitats. When this is the case the laterals and intermediates are proportionately more reduced than the medians and are almost always rounded. The length of laterals and intermediates may vary quite considerably in the same collection, while the medians usually do not vary much in length in a given collection; the shape of intermediates and laterals in the same collection may vary from acutely pointed (when of normal length) to mere rounded papillae. Individuals have been observed on which the lateral spines have been entirely obsolete.

This form is also quite variable with regard to ornamentation. The network of minute interlacing areolations is usually evident. The ventral plate often is pustu-

Keratella cochlearis f. *tecta* (Gosse)

Locality	Date	Total Length	Width	Length Body	W/L Ratio	Anterior Spines
West Reservoir near Akron, Ohio	VIII.30.31	89μ	48μ	73μ	0.67	12-10-21μ
Pond, Lnare, Czechoslovakia	VI.6.35	90μ	52μ	74μ	0.70	6-6-18μ
Swan Creek, northwest Ohio	VIII.14.31	96μ	55μ	76μ	0.72	17-14-25μ
Pond, Port Clinton, Ohio	VIII.28.31	100μ	51μ	77μ	0.67	21-16-31μ
Lake Mattamuskeet, N. C.	V.22.37	103μ	53μ	80μ	0.66	19-14-30μ
Totteridge, England	VII.15.10	109μ	59μ	88μ	0.67	21-18-27μ
Duckpond, Lovestad, Sweden	VII.15.34	111μ	57μ	92μ	0.62	18-13-22μ
Western Lake Erie	IV.25.29	113μ	60μ	95μ	0.63	9-8-18μ
Canal, Riga, Latvia	VIII.24.24	115μ	61μ	97μ	0.63	18-14-27μ
Long Lake, B. C.	VI.14.38	118μ	65μ	100μ	0.65	17-13-30μ

Keratella cochlearis var. *hispida* (Lauterborn)

Locality	Date	Total Length	Width	Length Body	W/L Ratio	Post. Spine	Anterior Spines
Prov. Kurzeme, Latvia	VIII.8.31	162μ	62μ	95μ	0.65	44μ	21-15-29μ
Lake Windermere, England	VIII.15.38	167μ	58μ	93μ	0.62	50μ	18-14-29μ
Lenape Lake, N. J.	IV.16.34	170μ	65μ	92μ	0.71	54μ	23-16-31μ
Karluk Lake, Kodiak Island, Alaska	VIII.21.26	170μ	63μ	101μ	0.63	43μ	22-18-34μ
Cheshire, England	VIII.2.14	170μ	67μ	99μ	0.67	47μ	20-19-31μ
		212μ	...	102μ	..	82μ	......

late on the upper third in American habitats but lacks pustulation in most European localities. The dorsal plate may have minute pustules but usually lacks pustulation.

The foundation pattern of the dorsum is similar to that of typical *cochlearis*. The median line may have a jog to the right behind the antero-carinal plaques. The postero-carinal plaques are almost always completely formed, and at times there is a suggestion of a partition in the postero-carinal plaques.

This form is most common in shallow lakes, ponds and rivers. Usually it is accompanied by the *micracantha* form of *cochlearis*, but occasionally it is the only form present in a habitat. At times one can line up a complete series of intermediates between the *micracantha* form and the *tecta* form. Such intermediates have been given the name *tuberculata* by Lauterborn and have rounded postero-spines gradually becoming obsolete; however, I see no value in having a form name for such intermediate specimens. Form *tecta* may persist in a habitat throughout the year.

In larger lakes f. *tecta* is rarely found. In Lake Erie (1929, 1932) it was found in collections of April and May (rare), accompanied by forms with a rather long postero-spine but did not occur during the summer months when postero-spines on *cochlearis* were much more reduced. Such seasonal distribution is hard to interpret, as the *tecta* form occurred when numbers of individuals of *cochlearis* present were few and had no apparent relationship to cyclomorphosis.

Keratella cochlearis var. **hispida** (Lauterborn)

Plate XXXV, figures 17, 18

Anuraea cochlearis var. *hispida* LAUTERBORN, 1898, p. 600, Fig. 4; LAUTERBORN, 1900, pp. 430–431, Pl. x, figs. 13, 14.

Anuraea cochlearis var. *hispida* f. *pustulata* LAUTERBORN, 1900, p. 430, Pl. x, figs. 11, 12.

K. cochlearis var. *hispida* f. *microcantha* SLONIMSKI, 1932, p. 453, Figs. 1, 2.

Lorica terminates in a moderately thin median posterior spine, usually about half as long as the body proper (may be nearly as long); posterior spine apparently never entirely wanting. Shape of the lorica much as in *K. cochlearis*, although the lorica often has the appearance of being somewhat wider than in typical *cochlearis*. The anterior spines are of about the same proportions as in typical *cochlearis* except that they are definitely less stout, intermediates are slightly divergent, while the lateral spines are incurved.

The variety is characterized by having the lorica densely hispid. The small spinelets covering the lorica on both plates are bluntly pointed or even truncate and completely obscure the usual pattern of minute areolations. The foundation pattern on the dorsum is likewise obscured but is similar to that of *K. cochlearis*. The median line is not interrupted but is nearly straight for the entire length. Both the anterior spines and the posterior spine are smooth or but slightly stippled, the hispid ornamentation of the lorica not extending onto the spines.

DISTRIBUTION.—Apparently moderately common in Europe; I have also seen good material from Karluk Lake, Kodiak Island, Alaska. However, this variety is apparently uncommon in the United States for I have seen material from only one locality that could be referred to this variety, and it was less hispid than the European form.

This variety often narrows somewhat more anteriorward than does typical *cochlearis* and narrows abruptly to the posterior spine, which is less stout at the base than in the species proper.

It is probable that var. *hispida* grades into the species, but I have seen no material definitely showing the transition. Several localities in which this variety was observed also had *K. irregularis* present, and in several localities typical *K. cochlearis* was also present. This agrees with the observations of Lauterborn. Lauterborn observed the seasonal distribution of this variety to extend from June to October; during the present investigation the variety was observed in samples collected from April to August.

Keratella cochlearis var. *robusta* (Lauterborn)

Locality	Date	Total Length	Width	Length Body	W/L Ratio	Post. Spine	Ant. Spines
Bear Lake, Vancouver Is., B. C.	VII.23.35	196μ	68μ	103μ	0.66	70μ	26-18-31μ
Prospect Lake, Vancouver Is., B. C.	VII.27.36	200μ	66μ	104μ	0.62	68μ	24-16-33μ
Nicola Lake, B. C.	1931	200μ	76μ	105μ	0.72	66μ	24-21-33μ
Pond, Lnare, Czechoslovakia	VI.30.35	206μ	71μ	106μ	0.67	66μ	25-17-38μ
Lake Michigan	VIII.26.31	215μ	71μ	109μ	0.65	85μ	30-19-33μ
Cobin Lake, Jasper Nat. Park, Alberta	VII.20.39	218μ	75μ	113μ	0.67	76μ	27-18-33μ
Lake Windermere, England	VIII.17.38	227μ	72μ	111μ	0.66	82μ	25-18-36μ
Lake Erie, off Kelley's Is.	IV.12.29	228μ	69μ	115μ	0.60	88μ	27-18-33μ

Keratella cochlearis var. *recurvispina* (Jägerskiöld)

Locality	Date	Total Length	Width	Length Body	Ant. Points	Post. Spine	Ant. Spines
Beaver Lake, B. C.	VII.—34	222μ	83μ	115μ	142μ	70μ	40-41-40μ
Baltic Sea	V.10.11	247μ	82μ	121μ	101μ	101μ	40-48-42μ
Baltic Sea (Jägerskiöld)	....	256μ	...	..	..	110μ	......

Keratella cochlearis var. **robusta** (Lauterborn)

Plate xxxvi, figures 1–6

Anuraea cochlearis var. *robusta* Lauterborn, 1900, p. 435, Pl. x, figs. 21–23.

Lorica terminates in a long and moderately stout, median posterior spine which may extend markedly toward the ventral. The lorica is larger, wider and deeper than in typical *cochlearis* but is rather similar in general appearance; the anterior spines are longer than is usual for typical *cochlearis* but are similar in shape and divergence. The median line may be either straight for its entire length or have a slight jog to the right behind the antero-carinal plaques; the postero-carinal plaques are usually completely enclosed. The pustulation of the lorica is exceedingly variable in different localities. It is quite possible that there are several distinct forms with respect to pustulation. Types of pustulation encountered were (1) the lorica may lack pustulation on either plate, (2) there may be a few small pustules at the anterior end of the ventral plate, while the dorsal plate may or may not be pustulate, (3) pustulate all along ventral, while dorsal may or may not be pustulate.

Distribution.—Found principally in large lakes but may occur even in ponds. This variety is not common in the material studied, occurrences being from British Columbia, Alberta, Lake Michigan, Lake Erie, Lake Windermere (England) and Czechoslovakia. There are various European records.

The posterior spine is apparently always long in variety *robusta*, being from 0.6 to 0.8 as long as the body. This variety is nearly always accompanied by the typical species.

Keratella cochlearis var. **faluta,** new variety

Plate xxxvi, figures 9–15

Lorica terminates in a moderately long, stout, median posterior spine, wide at the base and tapering gradually to a blunt point. The lorica is comparatively large for *Keratella* with a median posterior spine, much wider than is usual, and very markedly compressed dorsoventrally. The maximum width is about three-fourths the length of the lorica and occurs about two-thirds of the way back from the anterior end. The lorica narrows quite a bit anteriorward to the base of the divergent lateral spines. The dorsal plate is markedly compressed dorsoventrally, so that the depth is only about four-tenths of the width.

Anterior dorsal margin with six stout spines: medians longest, do not curve much ventrally; laterals usually a little longer than intermediates, both laterals and intermediates are quite divergent, lateral spines also extend ventrally at about a thirty degree angle, laterals and intermediates may be rather short; medians occasionally are narrower than other spines.

An outstanding feature of the variety is the

Keratella cochlearis var. *faluta*, new variety

Locality	Date	Total Length	Width	Length Body	W/L Ratio	Post. Spine	Ant. Spines
Horseshoe Lake, Jasper Nat. Park, Alberta	VIII.23.39	185μ	96μ	115μ	0.84	46μ	15-11-23μ
Forestry Bog, Wisc.	VII.5.35	195μ	81μ	108μ	0.75	51μ	19-15-30μ
Isa Lake, Yellowstone Park, Wyoming	IX.14.32	208μ	90μ	116μ	0.77	56μ	21-20-30μ
Herbert Lake, B. C.	IX.3.36	217μ	76μ	105μ	0.72	80μ	21-22-32μ
Iris Lake, Jasper Nat. Park, Alberta	VII.28.39	219μ	105μ	130μ	0.81	66μ	21-18-33μ
Veda Lake, Mt. Hood Nat. Forest, Oregon	VIII.30.35	228μ	93μ	115μ	0.81	88μ	23-16-27μ
Lake near Lake Houghton, Mich.	....	233μ	86μ	117μ	0.73	65μ	25-18-37μ
Beaver Lake, Okanagan, B. C.	IX.—34	245μ	106μ	127μ	0.83	77μ	32-30-41μ
Roadside Pool near Gaylord, Mich.	....	284μ	106μ	144μ	0.74	107μ	33-21-45μ
Cobin Lake, Jasper Nat. Park, Alberta	VII.20.39	287μ	100μ	136μ	0.73	117μ	23-23-34μ
Pinantan Lake, B. C.	1936	320μ	98μ	144μ	0.68	128μ	28-25-45μ

prominence of the areolate network covering the dorsal plate of the lorica, which often has the appearance of being pulled away from the body, especially at the base of the posterior spine. The size of the meshes in the network is often comparatively large. Neither the dorsal nor the ventral plate is at all pustulate. The foundation pattern of the dorsum is similar to that on *Keratella cochlearis*. The median line may have a very slight jog posterior to the antero-carinal plaques but is straight for its entire length in some localities. There are two pairs of lateral plaques to the side of the antero-carinal plaques. The postero-carinal areas are seldom enclosed posteriorly. The foundation pattern is at times only faintly discernible; on such specimens the median line often stands out when the rest of the pattern cannot be defined.

This form may be a separate species, rather than a variety of *Keratella cochlearis*.

The type is Cat. No. 1194, in The American Museum of Natural History.

DISTRIBUTION.—Known from northern United States and Canada. I have studied material from Michigan, Wisconsin, Wyoming, Oregon, Alberta and British Columbia.

The areolate network on this species gives it the appearance of being encased in "chain-armor." It can readily be distinguished from *Keratella cochlearis* by its larger size, much greater width and by being more compressed dorso-ventrally. The lorica is never pustulate on either plate, and the posterior spine is hardly at all at an angle ventrally.

The length of the postero-spine is rather variable, ranging from 0.4 to 0.9 as long as the body proper, but has always been present on all material studied. The shape of the body is also somewhat variable. This can best be seen by comparing the figures of this form; in material from Beaver Lake, B. C., the body becomes quite tumid at its greatest width.

The name given to this variety was suggested by Mr. Frank J. Myers.

Keratella cochlearis var. **recurvispina** (Jägerskiöld)

Plate XXXVI, figure 7

Anuraea cochlearis recurvispina JÄGERSKIÖLD, 1894, p. 19, Fig. 2.

Anuraea tecta recurvispina ZERNOV, 1901, p. 30, Pl. IV, fig. 8.

Lorica terminates in a long, stout, posterior spine. Lorica larger than for typical *Keratella cochlearis*. The most noticeable feature of this variety is the anterior margin. The intermediates are long and stout and extend markedly to dorsal and at the same time are very divergent laterally, bending at nearly right angles to the head on some specimens; the medians may be less stout than the intermediates, bend markedly to the ventral; the laterals extend at a very pronounced angle toward the ventral; all three pairs of spines are of much the same length. The areolate network on the lorica is very evident, but the lorica is not pustulate. The foundation pattern of the dorsum is similar to the typical *cochlearis*. There is practically no jog in the median line posterior to the antero-carinal plaques, and the postero-carinal plaques are not fully formed.

DISTRIBUTION.—Known from brackish water habitats. Originally described from the Baltic Sea. There is a slide of this variety in the U. S. National Museum, Washington, from the Baltic Sea, 1913, and in the collection of the Academy of Natural Sciences of Philadelphia, from the Baltic, 1911. I have seen specimens of this variety from brackish Beaver Lake, British Columbia, collected in July, 1934 (a slide of this material is on deposit in the American Museum, Cat. No. 241).

One specimen on the slide from the Baltic in the Philadelphia Academy collection has the anterior spines similar to those on typical *cochlearis*, the spines being 27-22-32μ in length. This suggests that this variety may grade into typical *cochlearis*. However, the size of the body is much larger than is usual for typical *cochlearis*.

Keratella taurocephala Myers, new combination

Plate XXXVII, figures 9–14

Keratella cochlearis var. *taurocephala* MYERS, 1938, p. 14, Figs. 35, 36.

Keratella cochlearis var. *punctata* MYERS, 1938, p. 14.

Lorica terminates in a stout, moderately long, median postero-spine which bends slightly to the right near tip; in lateral view the postero-spine is seen to bend gracefully ventralward, recurving slightly in the distal third. Depth of dorsal plate is usually about half the width; lorica oval-shaped in dorsal view. The most distinctive feature of this species is the antero-lateral spines, which are stout, widely divergent with incurved tips, and longer than the antero-medians; antero-medians are less stout than laterals, usually only about three-fourths as long (may be nearly as long) and curve ventrally; antero-intermediates are parallel or slightly divergent, taper to acute points and are seldom half as long as other frontal spines. The ventral plate is clothed with small truncate pustules (spinelets) for the entire length. The dorsal plate is often lightly pustulate. The foundation pattern of the dorsum is of the same pattern as *K. cochlearis;* the antero-carinal plaques are the only fully formed carinal plaques; the median line usually has an abrupt jog behind the antero-carinal plaques. The foundation pattern is scarcely evident on specimens from some localities.

DISTRIBUTION.—Known from eastern United States and Canada: Maine, New Hampshire, New Jersey, Pennsylvania, North Carolina, Florida, Wisconsin, Michigan and Ontario. This species is apparently an acidobiont.

Keratella taurocephala Myers

Locality	Date	Total Length	Width	Width at Antero-lat.	Length Body	Post. Spine	Ant. Spines
Lauzon Lake, Ontario	IX.14.34	182μ	63μ	77μ	104μ	64μ	36-15-36μ
Cathernis Lake, N. C.	VIII.12.37	200μ	67μ	84μ	105μ	82μ	40-18-38μ
Pond, Fayetville, N. C.	V.13.35	209μ	71μ	82μ	105μ	77μ	41-18-36μ
Brown's Mills, N. J.	IX.5.37	216μ	69μ	100μ	104μ	78μ	47-16-33μ
Keystone Lake near Odessa, Fla.	XII.26.34	216μ	68μ	102μ	101μ	82μ	51-14-40μ
Lake near Apopka, Fla.	XII.29.32	220μ	69μ	95μ	105μ	82μ	51-19-40μ
Fearins Pond, N. H.	VII.18.38	229μ	71μ	107μ	103μ	92μ	53-18-38μ
Pool near Egg Harbor, N. J.	VII.24.31	230μ	70μ	118μ	110μ	82μ	42-15-38μ
Tamaque Lake, Lutherland, Pa.	VIII.22.37	240μ	69μ	136μ	112μ	93μ	45-15-35μ
Margaret Lake, Wisc.	VIII.19.28	247μ	68μ	112μ	108μ	103μ	46-12-36μ
Red Hill Pond, N. H.	VIII.17.38	252μ	71μ	114μ	106μ	110μ	57-16-38μ
Black Lake, Ontario	VIII.24.34	256μ	76μ	92μ	109μ	118μ	50-14-36μ
Forestry Bog, Wisc.	VII.5.35	198μ	69μ	105μ	105μ	60μ	33-16-31μ
	VIII.20.35	270μ	78μ	140μ	116μ	112μ	55-13-40μ

This species is characterized by the stout, bowed, antero-lateral spines which are both longer and stouter than the antero-medians, being nearly twice as thick as the medians on some specimens. There are minute spinelets on the antero-lateral and antero-median spines; the antero-intermediates and the postero-spine are smooth, however.

There is quite a bit of variation in the divergence of the antero-lateral spines; however, they are always rather strongly bowed, consequently the species can be distinguished readily in any material. This species is somewhat larger than *K. cochlearis*. The posterior spine has always been well developed on all material investigated, hence there is no evidence that the postero-spine ever becomes reduced or wanting in this species. Material of this species usually has the dorsal plate lightly pustulate; however, there would seem to be little value in designating the pustulate form as a separate variety, as Myers has done.

Interesting material of this species was obtained from Dr. Robert Pennak from "Forestry Bog" near the Limnological Laboratory of the Wisconsin Geological and Natural History Survey in northeastern Wisconsin. This is a small, shallow, sphagnum-bog lake, with an observed pH range of 4.4 to 5.2. Two collections are singled out for contrast. On July 5, 1935, the material of *K. taurocephala* was rather characteristic for the species, having a depth of about half the width, having the ventral plate clothed with truncate pustules for the entire length; the antero-laterals were but moderately bowed, however; total length was slightly less than 200μ, which is smaller than most material of *taurocephala*. On August 20, 1935, specimens were very large (largest size observed for the species dimensions are given in the size chart for the species) but were quite compressed dorso-ventrally and entirely lacked pustulation on the ventral plate. The antero-lateral spines were exceptionally stout and very divergent. It is worthy of note that this large-sized form occurred at the very time of the year when we would expect to find the most reduced form.

Accompanying *K. taurocephala* in Forestry Bog was *K. cochlearis* var. *faluta*. The latter variety, it will be recalled, is noteworthy for its very compressed lorica, and it entirely lacks ventral pustulation. It is an interesting coincidence that these are the two features that make the large-sized *taurocephala* specimens so unusual. Could we possibly have here a case of hybridization?

Keratella irregularis (Lauterborn), new combination

Plate XXXVII, figures 1–3

Anuraea cochlearis var. *irregularis* Lauterborn, 1898, p. 601, Figs. 5, 6; Lauterborn, 1900, pp. 431–435, text figs. 3, 4, Pl. x, fig. 19.

Lorica terminates in a moderately long, median, posterior spine, usually a third to half as long as the body proper, may be wanting. The width of the body is usually about seven-tenths of the length; the lorica is moderately compressed dorso-ventrally.

Anterior dorsal margin with six spines, essentially similar in shape to anterior spines of *K. cochlearis;* laterals are usually somewhat convergent.

The ventral plate has large pustules on the upper third, and somewhat smaller pustules may extend to halfway down the plate. On the dorsal plate there are large-shouldered pustules irregularly distributed. The foundation pattern of the dorsum is characterized by the presence of a medial pentagon, the accessory medial plaque, developed somewhat right of center between the carinal plaques, and by the subdivision of the postero-carinal plaque to form two pairs, the posterior pair being small and rectangular (called the accessory postero-carinal rectangles).

Distribution.—Known principally from European habitats, where it appears to be not uncommon. I have examined material from Latvia and England and a collection from Karluk Lake, Kodiak Island. This species apparently does not occur in the United States; however, in the United States there is a related species, *K. earlinae*, which is not known to occur in Europe.

According to Lauterborn (1898) and Wesenberg-Lund (1930) this species has been observed to occur from May to October, being essentially an aestival form.

Keratella irregularis var. angulifera (Lauterborn)

Plate XXXVII, figure 4

Anuraea cochlearis irregularis f. *angulifera* LAUTERBORN, 1900, p. 431, Pl. x, figs. 17, 18.

In this variety the accessory medial pentagon is not entirely developed. Lauterborn in two separate papers (1898 and 1900) gives a schematic representation of the formation of the accessory medial pentagon (he terms it the X plate). I have partially verified these observations in material from Lake Windermere, England. On some specimens from this habitat the medial pentagon was not completely formed, and the dorsal pustulation was weak and unshouldered. However, I am not convinced that this variety ever completely grades into typical *cochlearis;* in fact, I rather doubt that it ever does. This point can be definitely settled only by studies of *K. irregularis* in culture, and this is an experiment that should be undertaken soon by an investigator with access to living material of this species. It may be that this species has not become completely stabilized. In the other collections studied containing this species only typical *irregularis* was present; in the Latvian material it was accompanied by typical *cochlearis* and typical *hispida.* Variety *angulifera* is similar in size to the typical variety of the species.

Keratella irregularis f. wartmanni (Asper and Heuscher)

Anuraea stipitata var. *wartmanni* ASPER AND HEUSCHER, 1889, p. 257, Pl. III, fig. 5.

Anuraea cochlearis irregularis f. *ecaudata* LAUTERBORN, 1900, p. 431, Pl. x, fig. 20.

This is the reduced form in the *irregularis* series, lacking the postero-spine. No material of this form occurred in my collections.

Keratella earlinae, new species

Plate XXXVII, figures 5–7

Lorica terminates in a long and moderately stout median posterior spine which, in lateral view, is seen to extend somewhat ventrally, being slightly recurved in its distal half. The lorica as seen from above is campanulate-shaped; the dorsal plate is usually about six-tenths as deep as wide and slightly more than two-thirds as wide as long. Anterior dorsal margin with six spines: anterior medians longest, curve ventrally; antero-laterals and intermediates slightly divergent, with laterals usually recurved at tips, laterals longer than intermediates.

The ventral plate is conspicuously pustulate on the upper third. The dorsal plate has large, shouldered pustules irregularly distributed. The foundation pattern on the dorsum is distinctive. Although somewhat similar to that of *K. irregularis*, there is an extra hexagon, the accessory antero-median polygon, present anterior to the accessory medial polygon, the latter being an irregular hexagon (whereas it is an irregular pentagon in *K. irregularis*). The left antero-carinal plaque is an irregular hexagon while the right antero-carinal plaque is an irregular pentagon. There may be one or two pairs of accessory postero-carinal plaques, which are quadrangular. The sculptural pattern can best be understood by referring to figures of this species.

The type is Cat. No. 1195, in The American Museum of Natural History.

DISTRIBUTION.—Known only from North America. Material has been stũdied from Connecticut, New Jersey, Illinois, Wisconsin, Michigan, Lake Erie, Lake Michigan, Alberta and British Columbia. This species was observed in material collected from April to late September.

K. earlinae is most readily identified by the distinctive sculpture of the dorsum, also by its large size, by the long posterior spine and by the large, unevenly distributed, shouldered pustules on the dorsal plate. The dorsal sculpture is usually conspicuous, and pustulation is usually prominent. Occasionally there are collections in which the dorsal plate is hardly at all pustulate (as Lake Mendota, April 29, 1939) or collections in which even the pustules on the upper third of the ventral plate are very reduced while the dorsal is not pustulate (as was especially noticeable in material from Terwilliger's Pond, Put-in-Bay, Ohio, 1932).

A distinctive feature of this species is the length of the posterior spine which is seldom less than two-thirds as long as the body proper, is usually about nine-tenths as long as the body and may even be longer than

Keratella earlinae, new species

Locality	Date	Total Length	Width	Length Body	W/L Ratio	Post. Spine	Ant. Spines
Lenape Lake, N. J.	....	152μ	68μ	92μ	0.74	37μ	23-20-34μ
Linsley Pond, N. Branford, Conn.	V.31.38	200μ	70μ	100μ	0.70	76μ	27-18-38μ
Murray Lake, B. C.	VIII.12.38	207μ	71μ	101μ	0.70	72μ	26-22-36μ
Lake Elizabeth, Twin Lakes, Wisc.	VI.5.32	220μ	72μ	102μ	0.70	94μ	26-20-40μ
Lake Mendota, Wisc.	IV.29.39	222μ	74μ	114μ	0.65	90μ	28-19-36μ
Fox Lake, Fox Lake, Ill.	VI.5.32	222μ	72μ	106μ	0.68	90μ	29-20-42μ
Petit Lake near Antioch, Ill.	VI.5.32	227μ	76μ	103μ	0.73	98μ	30-21-42μ
South Trout Lake, Wisc.	VII.11.39	248μ	70μ	111μ	0.63	106μ	28-20-39μ
Talbot Lake, Jasper Nat. Park, Alberta	IX.26.39	251μ	77μ	114μ	0.68	112μ	27-21-35μ
Terwilliger's, Put-in-Bay, Ohio	VI.23.32	192μ	64μ	97μ	0.66	72μ	26-20-40μ
	VI.9.32	218μ	73μ	110μ	0.66	78μ	32-20-43μ
	V.13.32	235μ	72μ	108μ	0.67	105μ	30-20-39μ
Lake Michigan	VI.25.31	211μ	72μ	108μ	0.67	73μ	27-18-35μ
	VI.9.31	244μ	75μ	108μ	0.69	102μ	30-22-40μ

Keratella earlinae var. *nesiotica*, new variety

Locality	Date	Total Length	Width	Length Body	W/L Ratio	Post. Spine	Ant. Spines
Bear Lake, Vancouver Island, B. C.	VII.23.35	206μ	72μ	110μ	0.65	73μ	26-19-37μ

Keratella irregularis (Lauterborn)

Locality	Date	Total Length	Width	Length Body	W/L Ratio	Post. Spine	Ant. Spines
Prov. Kurzeme, Latvia	VIII.8.30	152μ	66μ	90μ	0.73	37μ	22-14-36μ
Lake Windermere, England	VIII.17.38	164μ	67μ	93μ	0.72	44μ	21-17-35μ
	V.—38	190μ	68μ	99μ	0.69	64μ	24-18-35μ
Karluk, Alaska	VIII.21.26	162μ	70μ	94μ	0.74	47μ	22-15-36μ
		212μ	73μ	103μ	0.71	77μ	25-19-38μ

the body. On only one specimen was the posterior spine notably shortened (Lenape Lake, New Jersey). There is no evidence that the posterior spine is ever entirely wanting, as it is on some specimens of the related species, *K. irregularis*. *K. earlinae* is usually larger than *K. irregularis*, both in size of body and in the length of the posterior spine.

It is with deep pleasure that I dedicate this species to my wife, deriving the name from her middle name.

Keratella earlinae var. **nesiotica**, new variety

Plate xxxvii, figure 8

This variety does not have the medial polygon developed, and the accessory antero-median polygon is not always completely enclosed anteriorly, although its line of demarcation is usually indicated. The pustulation is similar to that of *K. earlinae*, there being conspicuous pustules on the upper third of the ventral, and irregularly distributed, shouldered pustules on the dorsal plate. There is one pair of accessory carinal plaques developed. This variety probably bears the same relationship to *K. earlinae* that variety *angulifera* bears to *K. irregularis*. However, no typical *K. earlinae* were observed in the collection from Bear Lake in which this variety was rather common, and in the more than twenty-five collections from various parts of the country containing *K. earlinae*, the species always had both the medial polygon and the accessory antero-median polygon completely developed. I do not know whether hybrids exist in *Keratella*, but the characters possessed by this variety strongly suggest that it might be a hybrid between *K. earlinae* and *K. cochlearis*.

The type is Cat. No. 1196, in The American Museum of Natural History.

Distribution.—Known only from Bear Lake, Vancouver Island, B. C.

Keratella crassa, new species

Plate XXXVIII, figures 1–3

Lorica terminates in a very stout and moderately long median postero-spine, usually between one-half to two-thirds as long as the body proper; in lateral view the postero-spine is seen to extend slightly ventralward but is quite straight. Depth of dorsal plate is about two-thirds of the width; the greatest width of the body is about three-fourths of the length (without spines). Anterior dorsal margin with six rather stout spines: antero-medians longest, curve ventrally, antero-laterals usually somewhat convergent, especially near tips, extend somewhat ventrally, longer than antero-intermediates, which are parallel or slightly divergent. The ventral plate has a pattern of rather coarse areolations but is not at all pustulate. The dorsal plate has the usual pattern of minute areolations and is often somewhat pustulate, the small pustules being at the corners of the minute, irregular, polygonal network. Foundation pattern on the dorsum is quite distinct and characteristic. The facets are mesially divided, there are two pairs of carinal plaques in the region in which *Keratella cochlearis* has but the single pair of antero-carinal plaques; the median line has a jog to the left between the more posterior of these pairs of polygons (called medio-carinal plaques), beyond which it jogs again to the right. The postero-carinal areas are usually enclosed to form the postero-carinal plaques. The broad details of the pattern are quite constant from habitat to habitat. The pattern can best be understood by referring to figures of this species. The pattern is often quite prominent but occasionally is difficult to decipher.

The type is Cat. No. 1197, in The American Museum of Natural History.

DISTRIBUTION.—Known only from North America, where it is both widely distributed and common. Material has been studied from New Hampshire, Connecticut, Pennsylvania, North Carolina, Florida, Ohio, Illinois, Wisconsin, Lake Erie, Lake Superior, Washington, Ontario and British Columbia. It may occur in a habitat throughout the entire year. This is a transcursion species, being found in both acid and alkaline waters.

Material of this species was studied in which the posterior spine was quite reduced, the short spine being rounded at its tip. However, the posterior spine is usually well developed, and no material has been found in which the posterior spine was altogether wanting. In most habitats in which this species was observed the posterior spine was between 0.50 to 0.64 as long as the body proper; in a few localities it was somewhat shorter. However, the proportion between length of body and the length of the posterior spine is more nearly constant than in any other species of *Keratella*.

Keratella crassa, new species

Locality	Date	Total Length	Width	Length Body	W/L Ratio	Post. Spine	Ant. Spines
Oliver's Pond, Raleigh, N. C.	V.27.35	140μ	73μ	98μ	0.74	19μ	19-13-34μ
	V.13.36	168μ	78μ	106μ	0.74	38μ	21-17-37μ
Lake at Winter Park, Fla.	XII.28.32	174μ	85μ	108μ	0.79	54μ	27-18-38μ
Red Hill Pond, N. H.	VIII.17.38	178μ	77μ	109μ	0.71	46μ	25-16-35μ
Ditch near Orlando, Fla.	XII.28.32	197μ	85μ	113μ	0.75	73μ	31-18-42μ
Lake Summit, N. C.	VI.12.37	204μ	85μ	114μ	0.74	62μ	28-20-40μ
Terwilliger's, Put-in-Bay, Ohio	VII.24.32	208μ	88μ	121μ	0.73	65μ	29-20-40μ
Silver Lake, Wisc.	VI.25.28	212μ	92μ	118μ	0.78	68μ	40-19-43μ
Sandpit, Lillington, N. C.	V.13.35	213μ	84μ	118μ	0.71	61μ	30-19-42μ
Lake Washington, Seattle, Wash.	I.28.33	216μ	84μ	117μ	0.72	68μ	30-20-38μ
Lake Mendota, Wisc.	IV.29.39	217μ	91μ	131μ	0.69	66μ	32-21-41μ
Cedar Swamp Lake, Conn.	I.24.41	220μ	86μ	123μ	0.70	64μ	29-20-42μ
Thetis Lake, Vancouver Is., B. C.	VII.29.36	223μ	87μ	123μ	0.71	74μ	34-21-43μ
Pocono Lake, Pa.	VI.3.39	225μ	84μ	126μ	0.67	76μ	32-22-42μ
Lake Nipissing, Ontario	IX.15.34	225μ	85μ	120μ	0.71	77μ	34-21-40μ
Paddock Lake near Salem, Wisc.	VI.5.32	230μ	97μ	122μ	0.80	74μ	34-22-40μ
Bluff Lake near Antioch, Ill.	VI.5.32	236μ	90μ	134μ	0.68	80μ	33-20-42μ
Lake Zurich, Ill.	VI.5.32	240μ	91μ	130μ	0.70	82μ	35-22-49μ
Florence Lake, B. C.	VII.—34	244μ	87μ	130μ	0.67	82μ	33-20-44μ

The resting egg is covered with truncate spinelets, 3–6μ long, on half of its surface, but spinelets are absent from the portion of the egg adjacent to the ventral plate where the egg is carried. The egg is oval-shaped, somewhat compressed, and truncate or even concave along the wide end.

K. crassa is both large and heavy. Although *K. cochlearis* var. *faluta* may have a somewhat larger-sized body, it is a very compressed species, while *K. crassa* has the greatest depth of any species of *Keratella*. *K. crassa* may be readily distinguished both by its size and bulk, and by the distinctive pattern on the dorsal plate.

Keratella javana Hauer, new combination

Keratella cochlearis var. *javana* HAUER, 1937, p. 382, Fig. 29.

Lorica terminates in a stout and moderately long median posterior spine. Body tapers but slightly anteriorward from point of greatest width. Depth of lorica not indicated by Hauer. Anterior dorsal margin with six spines: antero-medians longest, curve ventrally, intermediates and laterals are slightly divergent. Lorica apparently not pustulate.

The distinguishing feature of this species is the foundation pattern of the dorsum which is so very modified from the *cochlearis* pattern as to leave some question as to its relationship to the *cochlearis* group. There are nine plaques developed in the main portion of the foundation pattern. The antero-median area is very small. Apparently the two longitudinally divided accessory antero-median plaques have enclosed the main portion of what is the antero-median area in *cochlearis*. Posterior to the accessory antero-median plaques there are present three medial plaques, one of which may correspond to the accessory medial polygon of *K. irregularis*. To the side of these three medial plaques are two pairs of plaques which undoubtedly correspond to the carinal plaques in *cochlearis*. If this interpretation of the plaques is correct, this species has modified the *cochlearis* pattern by developing five accessory plaques: three between the carinal plaques and two by enclosing the main portion of the antero-median area. The median line is practically obliterated in this species by the extra plaques. Hauer shows three pairs of lateral plaques as well as two small postero-median areas separated by what may be a vestige of the median line.

DISTRIBUTION.—Known from a single specimen, collected on June 3, 1929, in Telaga Pengilan in middle Java.

DIMENSIONS.—The measurements given by Hauer are but two: total length, 168μ; length posterior spine, 67μ. However, in the figure the posterior spine appears to be considerably shorter than the length indicated by Hauer.

This is the only species discussed in this paper of which the writer has not personally examined material. However, the figure given by Hauer is of so unusual a foundation pattern of the dorsum that there is no doubt that he was dealing with an undescribed species of *Keratella*.

Keratella gracilenta, new species

Plate XXXIX, figures 1–5

Keratella stipitata Harring non Ehrenberg, HARRING, 1914, p. 531; UENO, 1939, p. 111, Fig. 4.

?*Anuraea longistyla* SCHMARDA, 1859, p. 62, Pl. XIV, fig. 132.

Lorica terminates in a long and moderately thin median posterior spine. The lorica is rather narrow in proportion to its length, more so than in other species of *Keratella;* lorica moderately compressed dorso-ventrally. Anterior dorsal margin with six spines: antero-medians longest, curve ventrally, laterals somewhat divergent, recurved at tips and longer than the slightly divergent intermediates. In lateral view the postero-spine is seen to extend somewhat ventralward, being more or less recurved in its distal third. The anterior margin of the ventral plate has a shallow, U-shaped, median notch; the ventral plate is usually clothed with truncate pustules (spinelets) for the entire length; the dorsal plate is also thickly clothed with similar truncate pustules. The foundation pattern of the dorsum is unusual for species with a median postero-spine, being a variant of the *quadrata* pattern. Posterior to the median frontal area are three median plaques, the most posterior of which is open at its distal end; there are two enclosed lateral plaques on either side.

The type is Cat. No. 1198, in The American Museum of Natural History.

DISTRIBUTION.—Known from both North and South America. I have seen

Keratella gracilenta, new species

Locality	Date	Total Length	Width	Length Body	W/L Ratio	Post. Spine	Ant. Spines
Pond, Shelby, N. C.	VI.11.37	152μ	52μ	85μ	0.61	53μ	25-17-32μ
Isa Lake, Yellowstone Park, Wyo.	IX.14.32	153μ	50μ	85μ	0.59	49μ	24-18-32μ
Pond, Raleigh, N. C.	VI.14.35	166μ	52μ	90μ	0.58	50μ	24-18-31μ
Lake Xochimilco, Mexico	VIII.—32	170μ	48μ	90μ	0.53	61μ	22-15-31μ
Pocono Lake, Pa.	VII.4.39	173μ	50μ	94μ	0.53	49μ	24-18-31μ
Evans Lake, Michigan	IX.20.31	182μ	53μ	100μ	0.53	67μ	23-16-35μ
Lagoon, Catawba, Ohio	VIII.11.31	189μ	49μ	97μ	0.51	66μ	27-16-38μ
Public Reservoir, Lexington, Ky.	VIII.29.32	194μ	52μ	93μ	0.56	82μ	25-20-35μ
Graham Lake, Maine	VIII.—30	196μ	47μ	92μ	0.51	80μ	24-17-35μ
Pool at Punta Lara, Argentina	I.—37	205μ	58μ	98μ	0.59	77μ	29-18-43μ
Keystone Lake near Odessa, Fla.	XII.26.34	212μ	48μ	103μ	0.47	80μ	24-15-28μ
Lake Warren, Pa.	X.15.39	220μ	57μ	105μ	0.54	88μ	28-19-39μ
Pond near Jasper, Fla.	XII.29.34	228μ	49μ	101μ	0.49	104μ	23-15-30μ
Kenilworth, Washington, D. C.	VII.7.12	242μ	54μ	100μ	0.54	110μ	30-20-38μ
Sandpits, Lillington, N.C.	V.13.35	260μ	47μ	108μ	0.44	120μ	25-19-38μ
Tank, Dufaur, Argentina	I.14.37	276μ	62μ	115μ	0.54	132μ	30-22-46μ

material from Maine, New Jersey, Washington, D. C., North Carolina, Florida, Pennsylvania, Ohio, Indiana, Kentucky, Michigan, Wyoming, Mexico, Panama and Argentina.

In some states this species is very common. Such is the case in North Carolina and Florida. On the whole, however, this species is much less common in the United States than *Keratella cochlearis*. It apparently flourishes in somewhat warmer regions than *K. cochlearis*.

Ehrenberg described a species having a median postero-spine and a *quadrata*-like foundation pattern as *Anuraea stipitata*. However, there is considerable doubt as to just what Ehrenberg was really describing. Harring (1914, p. 531) contended that until "confronted with the 'corpus delicti' from the neighborhood of Berlin" he considered Lauterborn "correct in his opinion that Ehrenberg drew the *quadrata* (*aculeata*) tesselation in the *cochlearis* outline. This is not inexplicable, as Ehrenberg does not record *K. cochlearis* at all. Now, it is well known through the work of later investigators that this species (*K. cochlearis*) is to be found nearly everywhere in Germany, and the supposition is not unreasonable that Ehrenberg, finding a *Keratella* (*Anuraea*) with a median spine and a dorsal tesselation of some sort, concluded without any careful examination that it was the, to him, familiar *quadrata* pattern. In favor of this assumption is the fact that in a later paper Ehrenberg (1843, p. 391, pl. 4, I, fig. 40) figures under the name *stipitata* what is evidently a typical *cochlearis*."

The fact seems to be that Ehrenberg apparently lumped all material of *Keratella* with a median postero-spine under the name "*stipitata*," that he apparently paid little attention to the foundation pattern of the dorsum. From Ehrenberg's description of *stipitata* it is evident that he was dealing with a species that was common, for he lists three localities (near Berlin, Danzig and Ingolstadt) and states that this is the form figured by Eichhorn and recorded by Müller, Schrank and Oken. In other works, Ehrenberg intended to describe the common European *Keratella* with a median postero-spine, i.e., *K. cochlearis;* no form with the tesselation illustrated by Ehrenberg is known for Europe, which fact lends weight to the supposition that he drew in the wrong tesselation pattern. Such are the doubts concerning the authenticity of Ehrenberg's *Anuraea stipitata*.

Investigators have identified a curious assemblage of specimens of *Keratella* as belonging to *K. stipitata*. They have been more concerned with the length and shape of the posterior spine than with the foundation pattern of the dorsum. Wierzejski (1893, p. 255, Pl. VI, fig. 77) figures as *K. stipitata* a specimen without pattern that is remarkably similar in shape to the figure in Ehrenberg (1843, p. 391, Pl. IV-I, fig. 40) and undoubtedly is also *K. cochlearis*. Daday (1894, p. 375, Pl. XII, fig. 2d) gives little more than a copy of Ehrenberg's original illustration of *K. stipitata*. Skorikow (1896, p. 150, Pl. VIII, fig. 33) figures a *cochlearis* under the name of *stipitata*. Weber (1898, p. 712, Pl. XXV, fig. 9) makes *stipitata* a variety of *cochlearis* having a short postero-spine, and various investigators have followed his lead in identifying the short postero-spined form of *cochlearis* as variety *stipitata*. Thus Kofoid (1908, p. 152) refers all short-spined forms of *cochlearis* occurring in the Illinois River to variety *stipitata*.

That Ehrenberg did not describe the present species may be shown from the following facts: (1) the dorsal pattern is different—there are three median facets posterior to the median frontal area, not two as Ehrenberg shows for *stipitata;* (2) the shape is different—*K. gracilenta* is narrow in proportion to its length, having the smallest width/length ratio of any species of *Keratella* (0.44–0.61, median 0.55), while Ehrenberg figures a relatively wide *Keratella;* (3) the size is different—Ehrenberg indicates a total length for *stipitata* that is below the minimum size observed for *gracilenta* (however, the size and shape of *stipitata* as figured by Ehrenberg are similar to *cochlearis*); (4) the distribution is different—*gracilenta*, as far as known, is an American species that does not occur in Europe.

K. gracilenta is rather variable with respect to pustulation. When pustulation is well developed, both plates are densely covered with truncate spinelets; not uncommonly, however, specimens are encountered without dorsal pustulation in some localities; the ventral plate may have pustulation on the upper third more marked than over the remainder of the plate, and in a couple of localities pustulation was confined to the upper half of the ventral plate.

The description of *Anuraea longistyla* Schmarda may have been based on material of this species, but as both the description and figures of Schmarda are inadequate, the point cannot be settled. Schmarda obtained his material from a fresh water habitat near Kingston in Jamaica, a region where we would expect to encounter *K. gracilenta*.

Keratella paludosa (Lucks)

Plate XXXIX, figure 6

Anuraea paludosa LUCKS, 1912, p. 152, text fig. 55.

Anuraea aculeata var. *cochlearis* VOIGT, 1902A, p. 679; 1904, p. 86, Pl. III, fig. 31a–b; LEVANDER, 1908, p. 34, text figs. a–c.

Keratella paludosa HARRING, 1913, p. 57; CARLIN-NILSSON, 1934, p. 5.

Lorica ends in a short, stout, posterior spine, about a fourth as long as the body, directed to the left of the median at a slight angle, rarely wanting. The greatest width is slightly behind the middle of the body, the lorica narrows relatively little anteriorward; the width/length ratio is smaller than for most species of *Keratella;* the body is moderately compressed dorsoventrally.

Anterior spines six: medians longest, at times tend to converge slightly toward their tips, also bend a little to the ventral, sinus between medians is relatively wide; intermediates are slightly divergent, while the somewhat longer laterals are convergent at their tips.

Ventral plate not at all pustulate. The characteristic feature of the dorsal plate is, however, its pustulation. The foundation pattern of the dorsum is unusual. There are six median areas, four of which are completely enclosed, and there are four to five pairs of lateral areas. The feature that immediately attracts attention in this species is the "islands" of pustules on the dorsal plate, each of the various "areas" of the dorsal pattern being heavily pustulate.

DISTRIBUTION.—Known from Europe, United States and Mexico. In the United States it has been found thus far in states along the Atlantic seaboard but usually as isolated individuals. Carlin-Nilsson (1934) who gives a number of records of this species from Sweden, reports it from moors and sphagnum.

DIMENSIONS.—A specimen from Lake Hartridge, Polk County, Florida, had the following dimensions: total length, 168μ; width, 61μ; length body, 111μ; length posterior spine, 25μ; length anterior spines, 21-19-39μ. Voigt gave a total length of 152μ and a width of 53μ (from Plon); Lucks records a total length of 170μ and a width of 53μ (from west Prussia).

This species is not likely to be confused with other *Keratella*, because of the distinctive character of the dorsal plate and the asymmetrically placed postero-spine.

Keratella paludosa f. **obtusa** Hauer

Keratella paludosa f. *obtusa* HAUER, 1935, p. 80, Fig. 15.

The posterior margin of this form is rounded and lacks the postero-spine. A few examples of this form were found by Hauer, 1935, in the Black Forest region of Germany. He gives the total length as 138μ and the width as 55μ. Hauer refers to this species as "ein typischer moorbewohner."

Keratella mixta (Oparina-Charitonova), new combination

Plate XXXVIII, figures 4–6; Plate XXXIX, figure 7

Anuraea cochlearis var. *mixta* OPARINA-CHARITONOVA, 1924, p. 431, Figs. 3, 4.

Lorica terminates in a stout but short posterior spine which is not exactly median but arises a little to the right of center. In lateral view the posterior spine is observed usually to bend a little dorsally. The body is moderately compressed dorso-ventrally, is fairly large and does not narrow much anteriorly.

Anterior dorsal margin with six spines: medians are longest and are quite wide for most of their length, bend ventralward near tips, intermediates and laterals are about parallel, laterals slightly longer than intermediates.

The ventral plate is pustulate for most of its length. There is a prominent ridge about a third of the way back on the ventral plate. Pustules on the ventral plate are largest near the ridge and diminish in size both anteriorly and posteriorly. The pustules anterior to the ridge form more or less of a pattern.

The dorsal plate is also pustulate, the pustules being largest in the center of the dorsum and diminishing in size in all directions (especially noticeable posteriorward). Pustules do not extend down the posterior spine, but small pustules (spinules?) are usually found on the dorsal side of the anterior spines.

The foundation pattern of the dorsum is unusual. There is a central group of six polygons of irregular shapes, four of which are more or less paired. These are surrounded by four pairs of lateral polygons, in addition to the median and lateral frontal areas and the two postero-median areas. The foundation pattern may be a variant of the *quadrata* pattern but is so modified that the exact relationship of the plaques is obscured.

DISTRIBUTION.—This species is known principally from eastern United States, is apparently an acidobiont and appears to be uncommon. I have seen material from Pennsylvania, New Jersey and North Carolina. Also known from U.S.S.R.

Keratella mixta may be readily distinguished by the asymmetrically placed posterior spine arising to the right of center, by the unusual and characteristic foundation pattern of the dorsum and by the character of the ventral plate. It is not likely to be confused with any other species of *Keratella*. The posterior spine has always been developed on all material of this species so far seen.

Keratella mixta is probably most closely related to *Keratella serrulata*. The foundation pattern of the dorsum, although quite different from that of *K. serrulata*, has some features in common; the similarity of the posterior portion, especially, is suggestive. Also the anterior spines are rather similar, especially the anteromedians. Both species are markedly pustulate over both dorsal and ventral plates. The relationship of these two species is even more clearly shown through *K. serrulata* var. *levanderi*, which has a single pos-

Keratella mixta (Oparina-Charitonova)

Locality	Date	Total Length	Width	Length Body	Post. Spine	Ant. Spines
Beach pool, Morehead City, N. C.	I.1.37	181μ	83μ	117μ	30μ	27-19-45μ
Pocono Lake, Monroe Co., Pa.	VI.18.38	228μ	94μ	141μ	50μ	32-25-57μ
Lenape Lake, N. J.	IV.18.34	246μ	96μ	148μ	49μ	31-24-52μ

Keratella serrulata (incl. f. *curvicornis*)

Locality	Date	Total Length	Width	Length Body	Post. Spine	Ant. Spines
Pocono Lake, Pa.	VI.16.39	187μ	100μ	140μ	0	42-28-70μ
Lake near Apopka, Fla.	XII.29.32	200μ	101μ	148μ	0	40-29-68μ
Pond, Fayetville, N. C.	V.13.35	203μ	101μ	153μ	0	38-29-68μ
Pond, Bowen Island, Vancouver, B. C.	V.—35	218μ	104μ	156μ	0	44-27-71μ
		228μ	108μ	162μ	10μ	39-30-70μ
Creek near Government Camp, Oregon	VIII.30.35	231μ	105μ	153μ	29μ	43-30-68μ
Lake, Parvin State Park, N. J.	V.21.37	240μ	101μ	140μ	43μ	42-30-62μ

terior spine arising to the right of center, as in *K. mixta*.

The foundation pattern of the dorsum on *K. mixta* is typical of neither the *quadrata* nor *cochlearis* type and may be an intermediate type transitional between the two.

Keratella serrulata (Ehrenberg)

Plate XXXVIII, figures 7, 8

Anuraea serrulata EHRENBERG, 1838, p. 508, Pl. LXII, fig. 13; HUDSON AND GOSSE, 1886, p. 124, Pl. XXIX, fig. 8; LIE-PETTERSEN, 1910, p. 75, Pl. II, fig. 19.

Anuraea falculata EHRENBERG, 1838, p. 505, Pl. LXII, fig. 4.

Keratella serrulata var. *ehrenbergi* EDMONDSON, 1936, p. 216, Pl. XXVII, fig. 2.

Lorica commonly lacks posterior spines; when present they are widely separated, stout, subequal and rather short. The lorica is moderately compressed dorsoventrally. The greatest width is a little behind center of the body; the lorica narrows but slightly anteriorward and narrows but little more posteriorward. The posterior margin is often truncate.

Anterior dorsal margin with six spines: medians longest, bend pronouncedly ventralward in the distal half, quite wide for most of length; intermediates are slightly divergent and a little shorter than the somewhat convergent laterals. All anterior spines have small spinules along their dorsal and lateral borders. The ventral plate is completely covered with small spinelets; along most of the plate the spinelets are truncate, but they become pointed in the anterior portion. Small spinelets are often along the anterior margin, including the broadly V-shaped central sinus; these spinelets may be 5μ long and quite stout. There is some suggestion of a pattern in the arrangement of the spinelets in the anterior portion of the ventral plate. The dorsal plate is markedly pustulate. The pattern of minute interlacing areolations, present on most species of *Keratella*, cannot be discerned on this species but may be present. The foundation pattern of the dorsum is usually quite distinct. There are two enclosed central polygons posterior to the anterior median area. The more anterior of these is always a hexagon with sides of about equal length, while the posterior median plaque is a heptagon. Posterior to the heptagonal plaque is a short median line. There are three pairs of enclosed lateral plaques, and there are two fairly large postero-carinal areas in the posterior portion of the dorsal plate separated by the short median line.

There can be little doubt that *A. falculata* and *A. serrulata* of Ehrenberg are synonyms. I received a slide from Mr. Frank Myers of a soft-bodied form from Pocono Lake, Monroe County, Pennsylvania (collected IX.20.38) which had the lorica soft and collapsible, making the animal appear almost illoricate. However, on careful study dorsal sculpture could be discerned of the *serrulata* pattern. Pustulation was not marked; posterior spines were wanting. The material was very similar to that figured by Ehrenberg for *A. falculata*. Ehrenberg realized this similarity for he says at the end of the brief Latin description of *falculata:* "Diese Form ist der *A. serrulata* sehr ähnlich von der es auch Äbanderungen ohne hintere Stacheln giebt, hat aber keine facettirte Schaale." Although *A. falculata* has page priority, I think it unwise to replace the well known specific name of *serrulata*.

MALE.—The male of this species was observed by F. R. Dixon-Nuttall, who sent figures of it to some workers in rotifers. It was to be fig. 6 in a plate, but I have found no record of its ever being published. The male resembles that of *Keratella quadrata* quite closely in general shape of body and in the shape of the reproductive organs.

DISTRIBUTION.—A widely distributed species, rather common in some regions, almost absent from others. I have studied material from Florida, North Carolina, New Jersey, Pennsylvania, Oregon and British Columbia. Edmondson (1936) reports it as more common in New England than *K. quadrata*. There are records for most parts of Europe. Apparently most common in acid waters, commonly found in sphagnum bogs.

This species is found in quite different situations from *K. quadrata*. When the form with relatively long posterior spines is present in a habitat it is usually accompanied by individuals with short posterior spines, and often there is present a complete series of intermediates between the most exuberant development of the posterior spines, which are seldom more than a fourth as long as the body, and the form without postero-spines. In this species no instance has been noted in which one posterior spine alone has been developed, as is often the case in both *K. quadrata* and *K. valga*. The postero-spines may be somewhat unequal, and either the right or the left spine may be the longer; this can be illustrated from an Oregon habitat where on one specimen the left spine measured 23μ, the right 34μ, while on another specimen the reverse was true, the left measured 34μ, the right 23μ.

Keratella serrulata f. **curvicornis** Rylov

Plate XXXVIII, figure 9

Keratella serrulata var. *curvicornis* RYLOV, 1926, p. 26, Fig. 14.

Keratella serrulata var. *aspina* EDMONDSON, 1936, p. 216, Pl. XXVII, fig. 1.

The form lacking posterior spines. This is the common form encountered in nature. The posterior margin of this form is truncate or even somewhat concave toward the middle of the posterior border but rounded laterally.

It is unfortunate that the more common form cannot be considered the typical form of the species. However, Ehrenberg indicated that he considered the form with short posterior spines as the typical form.

Keratella serrulata var. **levanderi** (Lie-Pettersen)

Anuraea serrulata var. *levanderi* LIE-PETTERSEN, 1910, p. 75, Pl. II, figs. 20, 21.

This variety is characterized by the posterior portion of the lorica terminating in a single short posterior prolongation (spine?) arising at an angle to the right of median. The foundation pattern of the dorsum is exactly as in the typical form of the species, and the lorica is also pustulate.

Described from Norway by Lie-Pettersen who gives a good figure of both this form and the typical species. As the figures are quite accurate with respect to the foundation pattern of the dorsum, I assume that they are equally accurate in the details of the posterior portion of this variety. I have not seen material of this variety.

This variety resembles in the general shape of the body *Keratella mixta*, which also has a posterior spine arising to the right of the median.

Keratella quadrata (Müller)

Plate XL, figures 1–7

Brachionus quadratus MÜLLER, 1786, p. 354, Pl. XLIX, figs. 12, 13.

Keratella quadrata BORY DE ST. VINCENT, 1822, p. 470.

Anuraea aculeata EHRENBERG, 1832, p. 145; EHRENBERG, 1838, p. 508, Pl. LXII, fig. 14; HUDSON AND GOSSE, 1886, p. 123, Pl. XXIX, fig. 4; KRÄTZSCHMAR, 1908, pp. 623–675, 20 figs. (Fig. 20 illustrates cyclomorphosis); KLAUSENER, 1908, p. 399, Figs. 1, 2; HARTMANN, 1918, pp. 220–252, Figs. 16–64; WESENBERG-LUND, 1930, pp. 125–131, Pl. VII, figs. 1–47.

Anuraea frenzeli ECKSTEIN, 1895, p. 265, Fig. 7.

Anuraea aculeata divergens VOIGT, 1902B, p. 82, Figs. a, b.

Anuraea aculeata longispina THIEBAUD, 1911, p. 9.

Anuraea aculeata variabilis KRÄTZSCHMAR, 1913, p. 49.

Anuraea aculeata vulgata MOROZOV, 1915, p. 126.

Anuraea aculeata curvispina STEINECKE, 1924, p. 44.

Keratella quadrata f. *divergens, frenzeli, quadrata, valgoides*, EDMONDSON AND HUTCHINSON, 1934, pp. 166–169, Fig. 3, A–F.

Lorica terminates in two widely separated subequal posterior spines, usually divergent or bowed, varying in length from about as long as the body proper to very short or entirely wanting. The lorica is much compressed dorso-ventrally. The maximum width is about two-thirds of the way back along the body from the anterior margin. The lorica narrows very slightly posteriorward, so that the width of the lorica at the point of origin of the posterior spine (posterior breadth) is but slightly less than the maximum breadth. The lorica narrows to a greater extent anteriorward, so that the width at the base of the anterior spines is less than the posterior breadth. Anterior dorsal margin with six spines: medians longest and stoutest, curved ventralward; laterals usually somewhat longer than intermediates, intermediates are slightly divergent, laterals are slightly divergent or, as often, somewhat convergent. The lateral and intermediate spines are commonly rather wide in the basal two-thirds of the length and taper abruptly in the distal third. The lorica has a pattern of minute interlacing areolations. The dorsal plate is usually pustulate, the small pustules being at the corners of the areolations; the ventral plate usually lacks pustules. However, in some localities the lorica has a glassy appearance and is not pustulate on either plate. The foundation pattern of the dorsum is characterized by a series of median plaques. Behind the anterior median area are three median facets, the anterior two of which are enclosed hexagons, and the posterior plaque is usually not closed posteriorly. To the sides of the median plaques are three pairs of lateral polygons and three pairs of smaller-sized, triangular-shaped marginal plaques.

DISTRIBUTION.—Widely distributed in fresh water habitats in arctic and temperate regions but often absent from the aestival plankton. Probably absent from truly tropical waters. This is a limnetic species, forming part of the deep water plankton of lakes, but occurs as well in a great variety of situations.

The distribution of *K. quadrata* appears to be somewhat erratic. Harring, 1921, reports that this species is widely distributed in the Arctic. Wesenberg-Lund, 1930, reports that in Denmark it is found in almost every pond, and the species appears to be common throughout northern Europe. In collections from the United States I have found the species to be only moderately common. This may partly be due to the circumstance that a minority of my collections are from the colder months. This species was not observed at all in numerous collections from Florida and North Carolina, which covered all seasons of the year, and Mr. Frank Myers states that he has never encountered the species in the thoroughly studied habitats in Atlantic County, New Jersey. However, the species is common around Los Angeles, California, and I have material from near Mexico City, Mexico, so that the limiting factor in its distribution along the Atlantic coast states cannot be temperature.

MALE.—The male of *Keratella quadrata* was first described by Plate, 1886, p. 64. Marks and Wesche, 1903, described the male of *Anuraea brevispina*, p. 509, fig. 2. An excellent figure and discussion of the male are given in Krätzschmar, 1908, p. 629, Pl. XIV, figs. 1–3, and in Wesenberg-Lund, 1923, p. 245, Pl. XIII, figs. 1, 2. The body is broad, conical and widest in the middle. The lorica is feebly developed, without facets or thorns of any kind; there is a quadrangular ventral plate, and the dorsal plate has a mesial division. The alimen-

Keratella quadrata (*typica* and f. *testudo*)

Locality	Date	Total Length	Width	Length Body	Post. Spine	Ant. Spines
Phashakuri, Kashmir Valley, India	V.7.32	224μ	85μ	129μ	64μ	28-25-39μ
Lagoon, Monterey, Calif.	VII.7.39	225μ	89μ	134μ	56μ	24-19-35μ
Rio Santiago near Lake Chapala, Mexico	III.30.32	264μ	90μ	140μ	94μ	29-28-44μ
Totteridge, England	V.1.09	273μ	102μ	157μ	77μ	30-22-42μ
Lake Windermere, England	VIII.15.38	280μ	105μ	150μ	98μ	38-29-46μ
Open water, western Lake Erie	IV.23.29	284μ	98μ	147μ	82μ	39-35-58μ
Sundar Khun, Kashmir Valley, India	V.2.32	284μ	97μ	132μ	118μ	30-25-40μ
Deep waters, Lake Michigan	XI.2.31	290μ	110μ	146μ	102μ	44-43-60μ
Channel Lake, near Antioch, Ill.	VI.5.32	292μ	120μ	147μ	123μ	42-35-64μ
Lower Beaver Lake, Yellowstone Nat. Park, Wyoming	IX.1.32	319μ	101μ	151μ	117μ	34-26-54μ
Karluk Lake, Alaska	VIII.21.26	320μ	110μ	143μ	120μ	47-38-63μ
Clark Lake, Saskatchewan	VII.6.35	338μ	128μ	162μ	132μ	46-45-60μ
Lake Mendota, Wisc.	IV.29.39	356μ	114μ	168μ	132μ	45-42-60μ
Pool, Los Angeles, Calif. (f. *testudo*)	III.—36	360μ	109μ	150μ	148μ	38-40-60μ
Pool, Los Angeles, Calif.	III.—36	172μ	86μ	123μ	27μ	22-16-28μ
Westlake, Los Angeles, Calif.	II.22.36	385μ	110μ	160μ	182μ	45-40-56μ
Westlake, Los Angeles, Calif. (f. *testudo*)	II.22.36	182μ	83μ	125μ	31μ	30-27-36μ

tary canal is apparently lacking. The brain is very large, with a red eye spot; there are two lateral antennae in the posterior portion of the body, and there may be an anterior dorsal antenna. The testis is large, globular, with two sorts of spermatozoa; the penis is well developed, protruded and has a row of cilia at its distal end. Total length, 70–100μ; length of penis, 20μ.

Keratella quadrata was the first described member of the genus. O. F. Müller, the early microscopist, described this species as *Brachionus quadratus* in 1786. At that early date practically all species of rotifers were placed in the genus *Brachionus*. The microscope at the time of Müller was a rather primitive instrument and was not amenable to exact observation of minute organisms. Consequently the description by Müller is quite inaccurate. He notes only two anterior spines and does not describe any dorsal sculpture. He pictures a quadrangular-shaped organism with two widely separated, parallel, posterior spines. It is the general shape of the organism he figures that suggests that he was dealing with the species now associated with his name. In 1822, that taxonomic bibliophile Bory de St. Vincent made a monotypic genus for this species, calling it *Keratella*. Bory de St. Vincent undoubtedly never studied *Keratella quadrata* at first hand. The microscope was greatly improved between the time of O. F. Müller and Ehrenberg, and the descriptions of the latter investigator reflect this improvement in their much greater accuracy. The first adequate description of this species was given by Ehrenberg, who called the organism *Anuraea aculeata*. However, Ehrenberg expressly states that he considered his species to be identical with *Brachionus quadratus*, albeit he did discard Müller's name. We shall follow Ehrenberg in considering the two species to be synonyms, although we do this somewhat reluctantly, for Müller's description is highly inadequate.

The most noticeable variability in *K. quadrata* is in the posterior spines. Occasionally the postero-spines are longer than the body, usually they are about four-fifths to one-half as long as the body, but they may be much shorter or even wanting. A part of the variation in length of the postero-spines is due to cyclomorphosis. There is a cycle of reduction in this species that is often observable in nature and which has been demonstrated in culture; of this more later. Postero-spines are usually subequal. When the postero-spines are long, there is seldom much difference in their length. However, on the form with short postero-spines there is more variability in the proportions of the left to the right postero-spines. The left spine may be markedly shorter than the right spine, or it may even be wanting. For this reason the short postero-spined forms might be confused with the *valga* series. However, in the *quadrata* series the width between the postero-spines is greater than the anterior width. The postero-spines are also quite variable in shape and divergence, especially when the spines are rather long. Usually postero-spines are somewhat divergent and may be quite divergent; less commonly they are subparallel and rarely somewhat convergent; also postero-spines are rarely straight, are usually somewhat sinuate and are not uncommonly so sinuate as to be quite bowed.

The length and divergence of postero-spines have been the chief characters on which varieties, forms and even separate species have been created in the *quadrata* complex. Due to the excessive variability in length, shape and divergence of the postero-spines these characters appear to me to be very poor criteria on which to base forms or varieties in *quadrata*.

Cyclomorphosis is more marked in *Keratella quadrata* than in other species of this genus and perhaps more marked than in any other species of rotifer. Of course, the usual sex of *Keratella* encountered in nature is female, and the usual method of reproduction is parthenogenetic. Only at certain seasons or under certain environmental conditions are males produced which fertilize eggs from certain females that have undergone a meiotic reduction division, the fertilized egg becoming a hard-shelled resting egg. In *Keratella quadrata* the first generation from resting (sexual) eggs are usually forms having long postero-spines. The parthenogenetic eggs produced by these individuals often hatch into forms with shorter postero-spines, initiating a cycle of reduction. As was pointed out earlier, a cycle of reduction does not necessarily occur in a habitat. The cycle of reduction, when it does occur in a habitat, continues through several parthenogenetic generations until a short postero-spined form dominates and continues further until forms lacking postero-spines are common. The reduced females have been found under experimental conditions (Kratzschmar, 1908, made the first thorough investigation) to end the cycle by producing males and sexual females with the resulting formation of resting eggs. The oval-shaped resting eggs have a wrinkled appearance and are readily distinguished from the smooth, more bluntly pointed, parthenogenetic eggs. It should be emphasized that the cycle of reduction takes place in an unbroken line of parthenogenetic females. The above outlined method of cyclomorphosis is the usual sequence but not the only cycle observed in *Keratella quadrata*. The first generation from sexual eggs may consist of individuals without posterior spines. Instead of a cycle of reduction there is a cycle of accretion, for in succeeding generations small postero-spines appear, and gradually a form dominates with two short subequal posterior spines. I suspect that this latter type of cyclomorphosis takes place in some of the varieties of *quadrata*, described later, and not in the typical *quadrata*.

The amount of cyclic variation is quite variable in different localities. From my observations it occurs most completely in small lakes and ponds. Thus, in small, shallow Westlake along Wilshire Boulevard in Los Angeles, California, the cycle was strikingly exhibited. In contrast, in many collections of deep water plankton from Lake Michigan (in 1931 the collections covered a period from May to early November) the species occurred only as the form with long postero-spines, thus displaying no cyclomorphosis at all. Cyclomorphosis is probably controlled by the ecological conditions in a habitat and is more likely to occur in an environment in which the physical and chemical conditions are quite variable.

Wesenberg-Lund, 1930, has noted a similar condition in lakes and ponds studied in Denmark. He reports that *Keratella quadrata* has a conspicuous summer minimum, is common during the winter, even under the ice, and may have large maxima in spring and autumn. In the winter plankton the form with long posterior spines is the only form encountered. During the spring maximum (May) a variety of forms is found, including brevispined forms and forms lacking posterior spines. It is at this season that mictic females appear. The spring maximum is followed by a summer minimum; the occasional individuals encountered during this season often have longer postero-spines than during the spring maximum. During the fall maximum, when it occurs, there is seldom evidence of mictic females being present. Dicycly in this species has never been established.

Wesenberg-Lund notes that the sexual period has not been observed in the pelagic region of larger lakes, and suggests that in such situations the species may be acyclic; also *K. quadrata* from larger lakes has a hyaline lorica and long, often well developed postero-spines. Wesenberg-Lund suggests that seasonal variations are not only dependent upon variation in external conditions but also depend upon an internal cycle, especially the distance of the generation from a sexual period. However, it is hard to understand how one reconciles the internal cycle with what is observed in the pelagic region of larger lakes, for forms found in that situation must often be many generations removed from a sexual phase, yet they continue to show no evidence of reduction in size.

As to the ornamentation of *Keratella quadrata*, the fine, areolate network is usually obscured by the pustulation of the dorsal plate, which is almost always present; the upper portion of the ventral plate may be pustulate but commonly is not. There is no constant correlation between pustulation and other characters, such as length of spines. However, pustulation is likely to be more marked on large forms than on reduced forms.

I have previously indicated that I did not consider variation in postero-spines as a reliable basis on which to build up a series of varieties and forms in *quadrata*. From present evidence better criteria for separating most varieties and forms in *Keratella quadrata* may be found in the foundation pattern of the dorsum, when this character is used in conjunction with other features, including the postero-spines. The usual foundation pattern on *quadrata*, and the only one observed on long postero-spined forms, has a series of three median plaques beyond the antero-median area, the posterior one of which is not enclosed posteriorly; there are three pairs of lateral plaques and three pairs of marginal triangular-shaped plaques. There is a whole series of forms having this pattern that are very variable with regard to postero-spines. Nearly all long postero-spined forms have this pattern, and there are brevispined forms and forms without postero-spines that have this pattern.

Four well marked series of variants having a modified foundation pattern have been observed. Three series are different because of additional plaques, and the fourth has a modified posterior portion. The four series are considered varieties. The modifications of the foundation pattern are discussed under the descriptions of the varieties later in the paper, the four varieties being vars. *edmondsoni*, *pyriformis*, *brevispina* and *curvicornis*.

In the typical *quadrata* series the form with long postero-spines is considered the typical *quadrata*. It is desirable to recognize, in addition to the typical form, two other cyclic forms in this series: forms *testudo* and *araneosa*.

A key to varieties and forms of *Keratella quadrata* is given as an aid in identifying the units smaller than species.

KEY TO VARIETIES AND FORMS OF *Keratella quadrata*

A.—Foundation pattern of dorsum consists primarily of three median facets, three pairs of lateral polygons and three pairs of triangular-shaped marginal plaques.
B.—Posterior spines present.
C.—Posterior spines long, usually half as long as body or more.
D.—Antero-intermediate and lateral spines partially fused.......... *K. quadrata* var. *adnata.*
DD.—Antero-intermediate and lateral spines free.
E.—Antero-spines unusually divergent; marine or brackish form.......... *K. quadrata* var. *platei.*
EE.—Antero-spines slightly divergent, if at all; fresh water form.......... *K. quadrata quadrata.*
CC.—Posterior spines short, usually less than one-fourth as long as body.......... *K. quadrata* f. *testudo.*
BB.—Posterior spines wanting.......... *K. quadrata* f. *araneosa.*
AA.—Foundation pattern modified in various ways from above outlined pattern.
B.—Postero-median plaque pentagonal and terminating in a short median line.......... *K. quadrata* var. *edmondsoni.*
BB.—Postero-median plaque hexagonal and not terminating in a short median line.
C.—Antero-median plaque subdivided to form two plaques.......... *K. quadrata* var. *curvicornis.*
CC.—Antero-median plaque not subdivided.
D.—Postero-lateral plaques subdivided, three pairs of marginal plaques present.......... *K. quadrata* var. *brevispina.*
DD.—Postero-lateral plaques not subdivided, nine to eleven marginal plaques present.......... *K. quadrata* var. *pyriformis.*

Keratella quadrata f. testudo (Ehrenberg)

Plate XLI, figures 1–3

Anuraea testudo EHRENBERG, 1832, p. 145; EHRENBERG, 1838, p. 507, Pl. LXII, fig. 12.
Keratella quadrata f. *brevispina*, *testudo*, *irregularis*, EDMONDSON AND HUTCHINSON, 1934, p. 168.

Foundation pattern as in typical *quadrata*. Postero-spines are short, seldom as long as a fourth the length of the lorica; the left postero-spine may be shorter than the right spine or wanting altogether. The frontal spines are shorter than in typical *quadrata*, and the antero-medians are much less curved forward. This form grades into the form lacking postero-spines (f. *araneosa*).

Investigators have been very careless in indicating details of the foundation pattern on *Keratella quadrata;* consequently, it is usually impossible to determine exactly what reduced form most investigators were dealing with. The figure given by Ehrenberg, 1838, seems to have a pattern indicated that is essentially similar to that of typical *quadrata*. Krätzschmar, 1908, Hartmann, 1918, and Wesenberg-Lund, 1930, investigators who have given the best accounts of variability and cyclomorphosis in *K. quadrata*, have been negligent in indicating details of the foundation pattern; in fact, Wesenberg-Lund omits the pattern entirely from his figures. Krätzschmar, 1908, whose work is the most thorough, indicates on all forms figured the same foundation pattern, that of typical *quadrata;* the same is true of the figures given in Hartmann, 1918. However, the detailed accuracy of Hartmann's foundation pattern is open to question as he has exactly the same pattern indicated for *K. valga*, which undoubtedly is inaccurate for the latter species. In several Los Angeles habitats in which I have obtained a complete series of cyclic forms, the reduced forms, including the form lacking postero-spines, had the same pattern as in the typical *quadrata*. I am emphasizing the fact of the similarity of the foundation pattern on all forms, reduced as well as long-spined, in the cyclomorphosis of *quadrata*, for it shows definitely that the reduced varieties to be considered later are not forms in the reduction cycle of the typical *quadrata*.

In nature the change from typical *quadrata* to f. *testudo* is often abrupt. There are few forms found that are intermediate between the typical form and f. *testudo.* The length of spines in the typical form varies in different localities from one-half as long to as long as the body, and this variation in length is definitely gradational. The change from the typical form to f. *testudo* is, on the other hand, not of a gradational nature in most habitats. In some habitats, however, the transition is more strikingly abrupt than in others. In one Los Angeles pond the typical form had spines as long as the body and gave rise in a generation to f. *testudo* with posterior spines only a sixth as long.

The proportions of the right to left postero-spine is often more variable in f. *testudo* than in the typical form. Occasionally in typical *quadrata* the right postero-spine is quite a bit longer than the left but usually if the right spine is any longer the disproportion is slight. In f. *testudo*, on the other hand, it is not uncommon to find the left spine greatly reduced or wanting when the right spine is not so reduced. This has led many investigators to classify the monospined individuals of f. *testudo* as *valga* and thus declare that *valga* was but a reduced form of *quadrata*. Both Wesenberg-Lund and Krätzschmar were led into this error. Such monospined individuals of f. *testudo*, although they resemble monospined forms of *K. valga* superficially, differ in a number of ways, the most noticeable of which is the width at the posterior spine.

Keratella quadrata f. **araneosa,** new form

Plate XXXIX, figure 12

?*Anuraea quadridentata* EHRENBERG, 1838, p. 504, Pl. LXII, fig. 2.
?*Anuraea squamula* EHRENBERG, 1832, p. 144; EHRENBERG, 1838, p. 504, Pl. LXII, fig. 3.

Form lacks postero-spines. The foundation pattern of the dorsum is like that of the typical *quadrata*. There are only three median plaques posterior to the antero-median area. This form should not be confusd with *K. quadrata* var. *curvicornis*, which has four median plaques posterior to the antero-median area.

The form lacking postero-spines in *quadrata* has been called *curvicornis* by investigators regardless of the foundation pattern of the dorsum. However, there appear to be several distinct varieties in *quadrata* that lack postero-spines. The non-postero-spined form in the cyclic series of the typical *quadrata* in the habitats in which I have been able to establish a connection between the forms is the above. This is also the form figured by Krätzschmar, 1908 (fig. 11), and Hartmann, 1918 (figs. 66, 68), but called by them *curvicornis*. It is also the form figured by Weber, 1898 (Pl. XXV, figs. 1–3). From all evidence at hand the form lacking postero-spines in the typical series of cyclomorphosis of *K. quadrata* has the same foundation pattern as in the typical *quadrata*.

It seems curious that I could find no name in literature to apply to a form as common as the above. *A. quadridentata* of Ehrenberg has the pattern of the typical *quadrata*, but Ehrenberg definitely shows only four antero-spines in lateral view; I doubt the accuracy of his observations as to the number of anterior spines but must place his species in the doubtful category. *A. squamula* of Müller is a synonym of *Notholca striata*, and it is not clear that the forms figured by Ehrenberg are really specimens of *Keratella*, for no dorsal sculpture is shown.

Dimensions from a pond in Los Angeles, California: total length, 146μ; greatest width, 78μ; length body, 122μ; anterior spines, 18-14-27μ.

Keratella quadrata var. **platei** (Jägerskiöld)

Plate XL, figure 8

?*Anuraea octoceros* EHRENBERG, 1834, p. 199.
Anuraea aculeata var. *platei* JÄGERSKIÖLD, 1894, p. 17, Fig. 1; LIE-PETTERSEN, 1910, p. 73, Pl. II, fig. 18.

This variety is characterized by an unusual divergence of the spines, both anterior and posterior. The antero-median spines extend very much toward the dorsal and often diverge strongly to the lateral as well (median spines in the typical *quadrata* bend over the head ventrally); the antero-intermediate and lateral spines are usually strongly divergent (laterals are not necessarily divergent). The postero-spines are long and very divergent, so much so that on some specimens they extend out from the body at nearly right angles; they may also extend dorsally.

The lorica is glassy appearing and stippled. The foundation pattern of the dorsum is indistinct but present and is similar to the typical *quadrata*. The foundation pattern as figured by Jägerskiöld is very inaccurate. He figures a number of facets that do not exist; the figure of Lie-Pettersen is fairly accurate.

DISTRIBUTION.—A brackish water form known from the Baltic Sea. I have seen a slide of material from the Baltic Sea which is Cat. No. 240 of the American Museum rotifer collection (collected July 24, 1913).

DIMENSIONS.—Total length, 245μ; width, 80μ; width at anterior points, 120μ; length body, 135μ; length posterior spines, 91μ; anterior spines, 40-36-60μ.

This may be the form described by Ehrenberg as *Anuraea octoceros*, for Ehrenberg obtained his material from the Baltic at Kiel.

Keratella quadrata var. **adnata**, new variety

Plate XL, figures 9, 10

This variety is characterized by the partial fusion of the antero-intermediate and lateral spines; these spines are united for more than half of their length and the free portion of the laterals is shorter than the free portion of the intermediates; median spines long and straight.

The lorica is large, posterior spines are long and divergent, especially near tips, and the body is much compressed dorso-ventrally. The foundation pattern of the dorsum is the typical *quadrata* pattern.

The type is Cat. No. 1199, in The American Museum of Natural History.

DISTRIBUTION.—Known only from Christine Lake, Jasper National Park, Alberta. Collection made on July 28, 1939.

DIMENSIONS.—Total length, 330μ; greatest width, 116μ; width at anterior points, 96μ; length body, 156μ; length posterior spines, 108μ; length antero-intermediates, 32μ (including fused basal portion); length free portion antero-laterals, 9μ; length antero-intermediates, 72μ.

This is an interesting mutant found in a single locality, where all specimens in the collection had the peculiarly fused anterior spines.

Keratella quadrata var. **brevispina** (Gosse)

Plate XLI, figures 5–8

Anuraea brevispina GOSSE, 1851, p. 202.

Anuraea aculeata brevispina, HUDSON AND GOSSE, 1886, p. 123, Pl. XXIX, fig. 5; CALLERIO, 1920, p. 205, Fig. 4.

Postero-spines short, right spine may be present when the left is wanting. Postero-spines are subparallel or slightly divergent.

Lorica in dorsal view is usually barrel-shaped. Often there is not much difference between the width at the base of the antero-spines and at the base of the postero-spines, although the latter is slightly greater. Antero-medians bend but slightly over the head.

The ventral plate may be pustulate on upper half or may lack pustulation. The dorsal plate is completely covered by fairly large, bluntly pointed pustules, which even may be slightly shouldered; pustulation is usually heavy on this variety and is more conspicuous than on the typical species. The foundation pattern of the dorsum differs from f. *testudo* in that there is an extra pair of plaques present to the side of the postero-median plaque, formed by a subdivision of the postero-lateral plaques. The two posterior pairs of marginal plaques are not triangular, as in f. *testudo*, but are quadrangular.

DISTRIBUTION.—This variety is probably widely distributed. I have seen material from Alberta, British Columbia, Wisconsin and India. There are unquestionable records from England, Italy and Sweden. Many of the forms figured in literature as var. *brevispina* are referable to f. *testudo*. This is true of the figs. 10, 11 (Pl. XXV) of Weber, 1893.

Keratella quadrata var. **brevispina** f. **gossei**, new form

The form lacking posterior spines. Foundation pattern as in var. *brevispina* which grades into this form. A name is given to this form in keeping with the practice throughout this paper of giving a name to the most reduced forms in all series.

I have seen material only from Mystic Lake, Banff, Alberta. Dimensions in this locality were as follows: total length, 155μ;

Keratella quadrata var. *brevispina* (Gosse)

Locality	Date	Total Length	Width	Length Body	Post. Spine	Ant. Spines
Mystic Lake, Banff, Alberta	VIII.25.37	171μ	81μ	121μ	32μ	24-19-30μ
Ororotse Tso, Indian Tibet	VII.11.32	177μ	82μ	112μ	36μ	24-21-32μ
Lake Mendota, Wisc.	IV.29.39	182μ	80μ	122μ	30μ	26-23-32μ
Bear Lake, Vancouver Is., B. C.	VII.23.35	182μ	85μ	107μ	40μ	25-21-33μ
Lake Louise, Alberta	VIII.4.36	183μ	81μ	120μ	35μ	25-22-34μ

Keratella quadrata var. *pyriformis*, new variety

Locality	Date	Total Length	Width	Length Body	Post. Spine	Ant. Spines
Sta-rtsak-puk Tso, Indian Tibet	IX.5.32	136μ	95μ	118μ	0	16-10-25μ
Ororotse Tso, Indian Tibet	VII.11.32	183μ	91μ	126μ	43μ	25-16-34μ

width, 79μ; length body, 123μ; anterior spines, 23-18-32μ. Collected VIII.25.37.

Keratella quadrata var. **curvicornis** (Ehrenberg)

Plate XXXIX, figure 13

Anuraea curvicornis EHRENBERG, 1834, p. 197; EHRENBERG, 1838, p. 505, Pl. LXII, fig. 5; HUDSON AND GOSSE, 1886, p. 122, Pl. XXIX, fig. 9; WIERZEJSKI, 1893, p. 255, Pl. VI, fig. 79; DADAY, 1894, p. 371, Pl. XII, fig. 3c; LUCKS, 1912, p. 150, Fig. 54a, b.

Anuraea aculeata var. *ticinensis* CALLERIO, 1920, p. 206, Fig. 5.

Postero-spines wanting, lorica oval-shaped, rounded posteriorly. Antero-median spines somewhat bent over the head. Lorica areolate, dorsal may be pustulate, ventral not pustulate on material studied. Pattern differs from f. *araneosa* in that there are four median facets posterior to the antero-median area, the anterior facet of which is a square; the three posterior median facets are hexagonal. The extra plaque arises from a division of the antero-median plaque.

DISTRIBUTION.—Rather widely distributed in Europe. I have not seen material of this variety from America, although it may occur.

DIMENSIONS.—From Totteridge, England: total length, 140μ; width, 73μ; length body, 108μ; anterior spines, 25-20-38μ. Collected V.30.09. Lucks indicates a total length of 120μ and a width of 68μ.

This variety may never develop posterior spines at any time. At least there are no figures in literature of forms with posterior spines having the four median facets, especially the anterior square facet, characteristic of this variety, and I have not been able to find such spined forms in my samples. This variety should be studied in culture to determine whether it is a stable variety, as there is a slight possibility that it may be a cyclic variant of the typical *quadrata*.

Keratella quadrata var. **edmondsoni**, new variety

Plate XLI, figure 4

Lorica ends in two widely divergent, subequal, rather long postero-spines. The ventral plate is lightly pustulate for over half of its length; dorsal plate pustulate, pustules diminish in number in posterior portion.

The unusual feature of the foundation pattern of the dorsum in this variety is that the postero-median plaque is pentagonal and terminates in a short median line. This is an unusual variation for *quadrata* and is rather similar to the posterior portion of the foundation pattern of *Keratella serrulata;* however, in the latter species there are but two median plaques, and the posterior one is heptagonal.

The type is Cat. No. 1200, in The American Museum of Natural History.

DISTRIBUTION.—Known only from Lake Ootacamand, Madras, India. Collected on November 8, 1932.

DIMENSIONS.—Total length, 226μ; greatest width, 82μ; length body, 125μ; length postero-spines, 79–84μ; length antero-spines, 26-23-43μ.

I take pleasure in naming this variety for Mr. Thomas Edmondson.

Keratella quadrata var. **pyriformis**, new variety

Plate XLI, figures 9–12

Lorica may lack posterior spines; when present they are short, widely separated and subparallel; right spine only may be developed. Lorica pyriform and moderately compressed dorso-ventrally. The lorica is widest behind the middle and gradually narrows anteriorward, so that the width at the anterior end is less than two-thirds of the greatest width; the width at the posterior spines is greater than the anterior width. Anterior margin with six short but stout spines, only four of which are usually visible in dorsal view, medians longest, bend somewhat over the head and are also often slightly convergent; laterals are directed at an angle toward the ventral.

Ventral plate is areolate but not pustulate; there is a median ridge extending a third of the way back from the shallow median sinus on the anterior margin. Dorsal plate both areolate and pustulate.

The foundation pattern of the dorsum is more complex than in the typical *quadrata*. There are three median plaques, of which the postero-median plaque may be abbreviated, and there are three pairs of lateral polygons. This portion of the pattern is rather similar to *K. quadrata*. However, there are nine enclosed, contiguous marginal plaques; in lateral view these are seen to be more or less rectangular, well developed and fairly large plaques.

The type is Cat. No. 1201, in The American Museum of Natural History.

DISTRIBUTION.—Known from a small, shallow, fresh water lake Sta-rtsak-puk Tso, Rupshu, Indian Tibet, collected on Sept. 5, 1932, and from Ororotse Tso, just south of the Chang-Chenmo River, Indian Tibet, collected July 11, 1932.

Keratella quadrata var. **pyriformis** f. **hutchinsoni,** new form

Form lacking postero-spines.

In Sta-rtsak-puk Tso this was the more common form. This form is named for the collector. The material from this habitat had all the varietal characters accentuated. The lorica narrowed very much anteriorward, so that the anterior width was only six-tenths of the greatest width, thus accentuating the pyriform shape; the postero-median plaque was quite abbreviated and the marginal plaque very well developed, while the anterior spines were quite short. Posterior spine when present on individuals in this collection was very short. The form lacking postero-spines was not observed in the collection from Ororotse Tso.

Keratella valga (Ehrenberg)

Plate XLII, figures 1–21

Anuraea valga EHRENBERG, 1834, p. 198; EHRENBERG, 1838, p. 508, Pl. LXII, fig. 15; DADAY, 1894, p. 371, Pl. XII, figs. 2, 2a; SKORIKOW, 1896, p. 151, Pl. VIII, figs. 29–32; HARTMANN, 1918, pp. 258–285, Figs. 72–82.

Anuraea aculeata var. *valga* WEBER, 1898, p. 703, Pl. XXV, fig. 7; KRÄTZSCHMAR, 1908, p. 629, Fig. 10.

Lorica terminates in two unequal posterior spines, right spine longer than left, usually markedly so, left spine at times absent even when right spine is quite long; both spines may be wanting. The lorica is quite compressed dorso-ventrally. The maximum width is about two-thirds of the way back along the body. The lorica narrows more markedly to the base of the posterior spines than it does anteriorward, so that the width at the base of the posterior spines is perceptibly less than the width at the base of the anterior spines (the reverse is true of *K. quadrata*). Anterior dorsal margin with six spines: medians longest and stoutest, curved ventralward; laterals usually a little longer than intermediates; the latter are slightly divergent, while the laterals may be either slightly divergent or somewhat convergent. The lorica has a pattern of minute interlacing areolations. The dorsal plate is often lightly pustulate, and the ventral plate is pustulate on the upper half (pustulation may be wanting, see later discussion). The foundation pattern on the dorsum is quite similar to that on *Keratella quadrata*, except for details of the posterior portion. All three median plaques posterior to the antero-median area are completely enclosed, leaving a postero-median remnant. There are three pairs of enclosed lateral plaques, two pairs of latero-marginal, triangular-shaped plaques and a pair of smaller-sized postero-marginal, triangular-shaped plaques. This pattern appears to be quite constant, the only variation noted being the addition of a small pair of triangular-shaped, marginal plaques immediately adjacent to the postero-marginal plaques.

DISTRIBUTION.—World wide in distribution but most common in the warmer regions. De Beauchamp (1932) reports it as the most frequent and most abundant rotifer in the plankton of tropical Africa. It is equally common in South Africa, according to Hutchinson *et al.* (1932). It is common in Java and Sumatra, according

Keratella valga f. *tropica* and *brehmi*

Locality	Date	Total Length	Width	Length Body	W/L Ratio	Post. Spines*	Ant. Spines
NORTH AMERICA							
Near Myakka City, Fla.	VIII.17.32	130μ	62μ	101μ	0.61	0, 0μ	17-18-42μ
Canal near Lake Mattamuskeet, N. C.	V.22.37	135μ	62μ	108μ	0.57	0, 0μ	17-17-40μ
Pond, Monterey, Calif.	VII.7.39	145μ	75μ	130μ	0.58	0, 0μ	18-15-34μ
		158μ	76μ	129μ	0.59	9, 15μ	23-15-33μ
Reservoir, Oklahoma City, Okla.	....	252μ	76μ	131μ	0.58	34, 98μ	27-21-33μ
Bear River Refuge, Utah (f. *tropica-monospina*)	X.10.36	162μ	77μ	137μ	0.56	0, 0μ	28-19-33μ
		286μ	78μ	140μ	0.56	0, 121μ	32-25-36μ
Flathead Lake, Mont.	....	295μ	82μ	148μ	0.55	34, 115μ	34-28-38μ
SOUTH AFRICA							
Potchefstroom Dam	III.25.28	214μ	73μ	98μ	0.74	32, 84μ	28-19-44μ
	X.1.27	262μ	80μ	114μ	0.70	65, 117μ	33-23-46μ
Hartebeestpoort Dam	IV.29.28	246μ	77μ	110μ	0.70	55, 100μ	32-26-45μ
Frischgewaagd Dam, Transvaal	II.27.28	250μ	85μ	116μ	0.73	55, 104μ	30-23-45μ
Leeuwkraal Dam	III.17.28	257μ	80μ	115μ	0.70	58, 110μ	28-22-42μ
Brakpan, Transvaal	IV.15.28	274μ	80μ	123μ	0.65	36, 119μ	32-28-44μ
MALAYSIA							
Colombo Lake, Ceylon	V.4.05	200μ	60μ	102μ	0.59	12, 72μ	29-24-33μ
		237μ	62μ	104μ	0.60	35, 102μ	31-22-34μ
Lake Ootacamund, Madras, India	XI.8.32	242μ	72μ	114μ	0.63	37, 98μ	25-20-40μ
Sohawa, Punjab, India	III.3.32	260μ	73μ	128μ	0.57	24, 108μ	31-29-35μ
Wular Lake, Kashmir Valley, India (f. *tropica-monospina*)	IV.—32	273μ	71μ	128μ	0.55	0, 110μ	35-29-35μ
SOUTH AMERICA							
Açude Maria de Paes, Parahyba, Brazil	VI.22.34	119μ	53μ	91μ	0.58	0, 0μ	18-15-32μ
Açude Lima Campos, Ceara, Brazil	XII.19.34	136μ	58μ	110μ	0.53	0, 0μ	21-18-38μ
Encadenadas Oeste, San Luis Prov., Arg.	XII.9.36	197μ	72μ	125μ	0.58	29, 50μ	21-17-32μ
Pool at Punta Lara, Arg.	I.—37	211μ	69μ	110μ	0.63	60, 73μ	25-19-40μ
Lagunas Bombero, San Luis Prov., Arg.	XII.3.36	252μ	76μ	142μ	0.54	60, 91μ	21-18-36μ
Lagunas Plateado, San Luis Prov., Arg. (f. *tropica-monospina*)	XII.5.36	255μ	76μ	125μ	0.61	0, 103μ	25-20-33μ

* Left spine listed first.

to Hauer (1937–1938); and in Ceylon (Apstein, 1905); it is not uncommon in India (Edmondson and Hutchinson, 1934); Ueno (1938A, 1938B) reports that in eastern Asia this species seems to occur only in the southwestern parts of Japan proper, Formosa and southeastern China, as well as in the southern plains of Manchoukuo where it is widely distributed. It is common in south Russia (Fadeev, 1927). I found it common in collections from San Luis Province, Argentina. In the United States its occurrence is sporadic, and it cannot be listed as a common species; the same seems to be true of Europe.

Edmondson and Hutchinson (1934) clearly differentiated between *K. quadrata* and *K. valga*, giving a lengthy discussion of both species and their forms. For *Keratella valga* eight forms were listed, which differ from each other chiefly in the length, proportions and presence of posterior spines, and in the prominence of ornamentation on the lorica. Let us first consider the variation in the posterior spines on *K. valga*. In any locality the variation in

Table Showing Variations in the Length of Posterior Spines of *Keratella valga* in Several Widely Separated Localities (Data from a Single Date of Collection in Each Case)

Locality	Spec. 1	Spec. 2	Spec. 3	Spec. 4	Spec. 5	Spec. 6
Colombo Lake, Ceylon, May 4, 1905 (type locality, f. *tropica*)	35, 102*	32, 85	12, 72	0, 48	....	....
Frischgewaagd Dam, Bethal District, Transvaal, South Africa, Feb. 27, 1928	70, 96	55, 104	51, 98	48, 101	47, 102	....
Hartebeestpoort Dam, South Africa, Apr. 29, 1928	64, 104	58, 94	55, 100	53, 96	48, 83	47, 105
Brakpan, Transvaal, South Africa, Apr. 15, 1928	25, 91	32, 103	34, 98	36, 119	42, 101	46, 105
Lagunas Encadenadas Oeste, San Luis Prov., Arg., Dec. 9, 1936	30, 45	12, 57	11, 18	0, 59	0, 28	0, 3
Lagunas Plateado, San Luis Prov., Arg., Dec. 5, 1936	53, 77	54, 64	28, 64	7, 43	0, 103	0, 22
Bear River Refuge, Utah, Oct. 10, 1936	0, 121	0, 97	0, 64	3, 31	0, 18	0, 0
Oklahoma City reservoir, Oklahoma	34, 98	20, 63	4, 95	0, 94	0, 31	0, 17

* Length of left spine given first, then of right spine. Size indicated is in micra.

length and in the relative proportion between the right and left posterior spine is rather great; however, the variation occurring in some regions is much less than in other localities. The accompanying table showing the variation in the length of the posterior spines in several localities brings out this point; in each locality the material represents but a single date of collection. In the three South African localities both posterior spines were developed on all specimens, and the proportionate variation is not excessive, especially when compared with the other localities listed. Thus, in Frischgewaagd Dam the ratio between the left and right posterior spine varies from 0.73 to 0.46, in Hartebeestpoort Dam from 0.62 to 0.45; however, in the Brakpan the right spine is proportionately longer, the ratio varying from 0.44 to 0.28. These three samples are representative of all the South African material I have seen. From the Colombo Lake, Ceylon, the material being from the collections of Apstein from which he described var. *tropica*, the variation is more marked; here the proportion between the two spines varies from 0.34 to 0, the left spine being absent from some specimens; if this material is classified according to the diagnoses of Edmondson and Hutchinson we would have forms *tropica*, *asymmetrica* and *monstrosa* represented, and this in the type collections of f. *tropica*.

In samples from Argentina we find a much greater variability in the posterior spines. In Encadenadas Oeste, for example, there is an excessive amount of variation in the proportion (0.67–0) and degree of development of the posterior spines, and if the variants were given names according to the Edmondson and Hutchinson scheme we would have (1) a form approaching f. *longicornis*, (2) f. *tropica*, (3) f. *asymmetrica*, (4) f. *monstrosa*, (5) f. *valga*, (6) f. *reducta* and (7) a form approaching *brehmi*. In the other three American localities cited we have from four to five of the Edmondson and Hutchinson forms present in each instance. Such excessive variability certainly casts doubt upon the value of forms based primarily upon the length and proportions of the posterior spines in *K. valga*.

As to ornamentation, *Keratella valga* has a pattern of minute interlacing areolations on both plates; this may be more or less prominent but is always present. The foundation pattern of the dorsum may be more or less distinct (it is usually distinct), but occasionally it cannot be discerned with certainty. However, this is true of all species of *Keratella* and is of no taxonomic import. The chief variation in the ornamentation worth noting is the presence or absence of pustules at the corners of the areolate network. In the material examined from South Africa, India and Ceylon the dorsal plate was almost always lightly pustulate, and the ventral plate was pustulate on the upper half. However, in postero-spined material from Argentina and the United States the dorsal plate was not pustulate, and the ventral plate lacked the pustulation on the upper half. This would tend to show that pustulation of the lorica on *K. valga* was endemic to certain parts of the world, were it not for a notable exception. In material from Florida and North Carolina the form without posterior spines has been the only form encountered and on specimens from these two states the dorsal plate was pustulate, as well as the upper half of the ventral plate. Why the form without posterior spines is the only one encountered in Florida and North Carolina, and why it differs in ornamentation from the other American material offers an unsolved problem. In several localities in northeast Brazil (Parahyba and Ceara) the form lacking posterior spines was alone encountered; the dorsal plate on specimens from these localities was not pustulate nor was the ventral plate. Ornamentation of the lorica, especially pustulation, offers an interesting problem in *K. valga;* however, I doubt if there would be any value in making "forms" on the basis of this character.

An interesting point brought out by the regional grouping of size dimensions of this species is that the South African specimens have a more plump (wider) body than in other localities. This is brought out quite unmistakably by the width/length ratios (the proportion the width of the body is to the length of the body). The range in W/L ratios as found for geographic regions (based on many more observations than are included in the size dimension chart):

United States:	W/L ratio: 0.55–0.61
South America:	W/L ratio: 0.53–0.63
India and Ceylon:	W/L ratio: 0.55–0.66
South Africa:	W/L ratio: 0.65–0.80

The eight "forms" recognized by Edmondson and Hutchinson for this species are arbitrarily delimited forms. They take the position that it is useful to have a *form* stop at some definite plate by definition, such as "both posterior spines well developed, typically about half as long as the lorica" or "right spine well developed, typically about half as long as the lorica, left spine rudimentary" or "right spine well developed, typically about half as long as the lorica, left spine absent"; then one has a sort of map into which the *forms* fit, not necessarily in a straight row but more as cities (individuals) are separated from each other by arbitrary state lines. I do not entirely concur in this evaluation of "form." They base their forms primarily upon the posterior spines. Variation in the posterior spines of *K. valga* seems to me to be "fortuitous." I do not in the least doubt that the progeny from a single female would in the course of several parthenogenetic generations produce individuals that varied greatly with regard to the length and proportions of the posterior spines. In other words the progeny would fall into several artificially delimited forms, yet to treat them as belonging to several forms seems illogical. For this reason I would hesitate arbitrarily to delimit "forms" in this species on the basis of posterior spines alone. There are two variants of *K. valga,* however, to which I think it desirable to give definite form names: f. *tropica* and f. *brehmi.*

Keratella valga f. **tropica** Apstein

Anuraea valga var. *tropica* Apstein, 1907, p. 210, Fig. F.

Anuraea longicornis Schmarda, 1850, p. 13, Pl. iv, fig. 3.

Anuraea scutata Thorpe, 1891, p. 306, Pl. vii, fig. 8.

?*Anuraea aculeata* var. *dumasi* Richard, 1894, p. 238.

Anuraea valga var. *asymmetrica* Barrois and Daday, 1894, p. 229, Pl. vii, fig. 11.

Anuraea valga var. *monstrosa* Barrois and Daday, 1894, p. 229, Pl. vii, fig. 12.

Anuraea aculeata var. *asymmetrica* Daday, 1894, p. 376, Pl. xii, fig. 2b.

Anuraea valga f. *monospina* Klausener, 1908, p. 400, Fig. 4.

Anuraea valga f. *heterospina* Klausener, 1908, p. 400, Fig. 5.

Keratella quadrata var. *tropica* Fadeev, 1927, pp. 145–147, Pl. ii, figs. 8–12 (f. *typica, heterospina, monospina* and *reducta*).

Keratella valga f. *asymmetrica* Edmondson and Hutchinson, 1934, p. 170, Fig. 4D; Hauer, 1937, p. 382, Fig. 30b–f; Ueno, 1938A, p. 141, Figs. 16–20; Ueno, 1938B, p. 17, Figs. 3, 4.

Keratella valga f. *monstrosa* Edmondson and

HUTCHINSON, 1934, p. 170, Fig. 4E; UENO, 1938B, p. 17, Figs. 1, 2.

Keratella valga f. *longicornis* EDMONDSON AND HUTCHINSON, 1934, p. 170.

Keratella valga f. *tropica* EDMONDSON AND HUTCHINSON, 1934, p. 170, Fig. 40; HAUER, 1937, p. 382, Fig. 30a; UENO, 1938A, p. 139, Figs. 14, 15.

Keratella valga f. *reducta* EDMONDSON AND HUTCHINSON, 1934, p. 170.

This form is characterized by having the right posterior spine usually well developed and in having the left spine of varying length from nearly as long as the right spine to rudimentary or completely wanting; the right spine also may be more or less reduced, especially on forms where the left spine is wanting.

The name of *tropica* is not the oldest name applied to this form; however, it is the generally accepted designation. Although the principle of priority is not binding in the case of *form* names, it has been followed elsewhere in this paper. The present instance is an exception. However, the description by Apstein is the first adequate description of the commonly occurring phase of this form. Moreover, most of the earlier descriptions referred to synonymy are highly unsatisfactory.

K. valga f. *tropica* is the only common form of the species encountered over most of the world wide distribution of this species. The form as here conceived would include the following forms of Edmondson and Hutchinson: f. *tropica*, f. *asymmetrica*, f. *monstrosa*, f. *reducta* and probably f. *longicornis*. The form on which the right posterior spine alone is developed may be termed for clarity f. *tropica-monospina*, although it must be emphasized that the name *monospina* has no taxonomic standing. I see no value in similarly using the names *asymmetrica*, *longicornis* or *reducta*.

There is not always a sharp line of demarcation between f. *tropica* and the typical species as described by Ehrenberg. The typical species is characterized by having both posterior spines present, both spines short though unequal, the right spine being longer; the posterior spines are usually quite divergent. In some South American habitats the variability of the posterior spines is so great that the distinction between the two forms entirely breaks down. The typical species apparently is uncommon. I have never seen material of either typical *valga* or f. *tropica* on which the left postero-spine was longer than the right; however, several investigators have reported observing specimens on which the left postero-spine was the longer.

Keratella valga f. **brehmi** (Klausener)

Plate XXXIX, figures 9–11

Anuraea curvicornis f. *brehmi* KLAUSENER, 1908, p. 400, Fig. 3.

Anuraea aculeata var. BREHM AND ZEDERBAUER, 1904, p. 52, Fig. 1.

Keratella quadrata var. *tropica* f. *aspina* FADEEV, 1927, pp. 145–147, Pl. II, fig. 14.

Keratella valga f. *brehmi* EDMONDSON AND HUTCHINSON, 1934, p. 171.

Keratella valga f. *aspina* EDMONDSON AND HUTCHINSON, 1934, p. 171, Fig. 4A.

This form lacks posterior spines. Form *brehmi* is often encountered in habitats where it is the only form of the species present; this fact has been commented upon previously. It rarely occurs in conjunction with other forms of *Keratella valga*. The form as here understood includes both f. *brehmi* and f. *aspina* of Edmondson and Hutchinson's analysis.

Cyclomorphosis in this species apparently is not important. The cycle studied in culture by several investigators (Klausener, 1908; Hartmann, 1918) involved the addition of spines to the *brehmi* form. I rather suspect that if cyclomorphosis were studied on material of f. *tropica* it would be different from that found by the above investigators.

Keratella valga var. **procurva** (Thorpe)

Plate XXXIX, figure 8

Anuraea procurva THORPE, 1891, p. 305, Pl. VII, fig. 7.

My acquaintance with this variety is based upon a single specimen in the sample from Sohawa, Punjab, India, collected March 3, 1932. It differs from all other material of the species studied in that the postero-median plaque is pentagonal and terminates in a short median line. The ventral plate was pustulate for over two-thirds of its length, with the pustules diminishing in size posteriorward and laterally; the dorsal plate is rather heavily pustulate. The posterior spines were subequal (the right somewhat longer) and divergent, characters which led Edmondson and Hutchinson (1934, Fig. 4b) to call this specimen f. *valga*.

Also present in the same collection was *K. valga* f. *tropica*, which had the typical *valga* foundation pattern on the dorsal plate. The measurements of a specimen of f. *tropica* from this habitat are given in the table, and they will be seen to be much larger than for var. *procurva*.

This variety parallels var. *edmondsoni* of *Kerutella quadrata*, which has a similar foundation pattern and which likewise was found in material from India.

DIMENSIONS.—Total length, 155μ; width, 67μ; length body, 102μ; length posterior spines, 22, 27μ; length anterior spines, 19-17-30μ; width at base of anterior spines, 57μ; width at base of posterior spine, 46μ.

Thorpe first described this variety from the island of Ascension, where he collected it in a cattle trough with the expressive name of "God-be-thanked" tank. On his figure the left postero-spine is much shorter than the right.

Keratella cruciformis (Thompson)

Plate XXXVIII, figure 10

Anuraea cruciformis THOMPSON, 1892, p. 77; ROUSSELET, 1895, p. 125, Pl. VII, fig. 6; LEVANDER, 1901, p. 54, text fig. 2; LIE-PETTERSEN, 1905, p. 41, Pl. II, fig. 12.

Lorica lacks posterior spines. Lorica subovate and much compressed dorsoventrally. Width at widest point is about four-fifths of the length of the lorica exclusive of anterior spines. Anterior dorsal margin with six spines of about equal length, intermediates and laterals being slightly divergent, and laterals being recurved at tips. Lorica has the usual pattern of rather small interlacing areolations, which is not very pronounced. Ventral plate is not pustulate. The foundation pattern of the dorsum shows a cruciform marking. There is a longitudinal median line extending about the full length of the lorica which is crossed by two transversal lines, dividing the main portion of the dorsum into six large plaques, the posterior pair of which contains the greatest area; a number of smaller plaques occur at the margin and behind.

DISTRIBUTION.—A marine species originally described from off the coast of Norway. I have seen only a single slide of this species, Cat. No. 93 in American Museum collection, originally mounted by Rousselet from specimens obtained from type material (collected July, 1891, on cruise of S. Y. Argo).

DIMENSIONS.—Total length, 195μ; greatest width, 146μ; length of body without spines, 171μ; width at anterior points, 84μ; anterior spines, 21-21-22μ.

Keratella cruciformis var. **eichwaldi** (Levander)

Plate XXXVIII, figure 11

Anuraea eichwaldi LEVANDER, 1894, p. 62, Pl. III, fig. 41; LEVANDER, 1901, p. 51, text fig. 1.

Differs from the species chiefly in the details of the foundation pattern of the dorsum. In variety *eichwaldi* there are but two pairs of large plaques along the median line, while in the typical species there are three pairs of plaques.

In the material I have studied var. *eichwaldi* is smaller and proportionately less wide than the species; also the antero-intermediate spines and the antero-lateral spines are commonly curved or even hooked on the variety. As in the typical species the lorica is covered by a comparatively coarse areolate network but is not pustulate on either plate.

DISTRIBUTION.—Confined to brackish or marine habitats. Originally described from Norway, also reported from marine waters around Sweden, Esthonia and Danzig. I have seen material from several localities in British Columbia.

Keratella reducta (Huber-Pestalozzi)

Plate XXXIX, figures 15, 16

Anuraea reducta HUBER-PESTALOZZI, 1927, p. 353, text figs. 1–8 on p. 354.

Keratella tetracera HUTCHINSON, 1931, p. 564, Fig. 3.

Lorica lacks posterior spines, shape is elongate pyriform and much compressed dorso-ventrally. The maximum width is about six-tenths the length of lorica exclusive of spines (0.60–0.65). The lorica

Keratella cruciformis var. *eichwaldi* (Levander)

Locality	Date	Total Length	Width	Length Body	Anterior Spines
Beaver Lake, Vancouver, B. C.	XI.—33	138μ	83μ	126μ	12-15-21μ
Lost Lagoon, Vancouver, B. C.	XI.—33	148μ	74μ	125μ	9-13-24μ
Rainy Bay, Barkley Sound, B. C.	VI.21.27	168μ	105μ	147μ	18-18-21μ

Keratella reducta (Huber-Pestalozzi)

Locality	Total Length	Width	Ant. Points	Length Body	Anterior Spines
Vley near Cakedon, S. Africa	132μ	61μ	39μ	98μ	30-16μ
Weltevreden, E. Pan, S. Africa	124μ	57μ	43μ	97μ	23-7μ
	135μ	64μ	53μ	106μ	28-9μ

is widest somewhat behind the middle and tapers gradually to the base of the anterior spines, where its width is about two-thirds of the maximum breadth. Anterior dorsal margin with four spines: laterals at least twice as long as medians and stouter, parallel or slightly divergent; medians are rather widely separated and are parallel or very slightly convergent, may be quite short. Lorica has the usual pattern of minute interlacing reticulations faintly developed on the ventral plate and more distinct on the dorsal. The ventral plate is not at all pustulate. The foundation pattern of the dorsum is usually hard to discern except in the posterior portion. Around the postero-lateral border there are six to eight small but well-defined plaques and immediately in front of these and alternating with them are five small facets; the principle dorsal plaques are three median polygons, the anterior one of which is small, while the posterior two are quite elongated; there are three pairs of lateral facets, the posterior pair of which extend half the length of the body.

DISTRIBUTION.—Known from a number of localities in South Africa.

This is the only species of *Keratella* having four anterior spines, and as such is readily distinguishable from all other *Keratella;* also it apparently never develops posterior spines as most species do. This species has the antero-lateral spines longer than the medians. *Keratella taurocephala* is the only other species having longer antero-lateral spines. As far as is known this species has a localized distribution.

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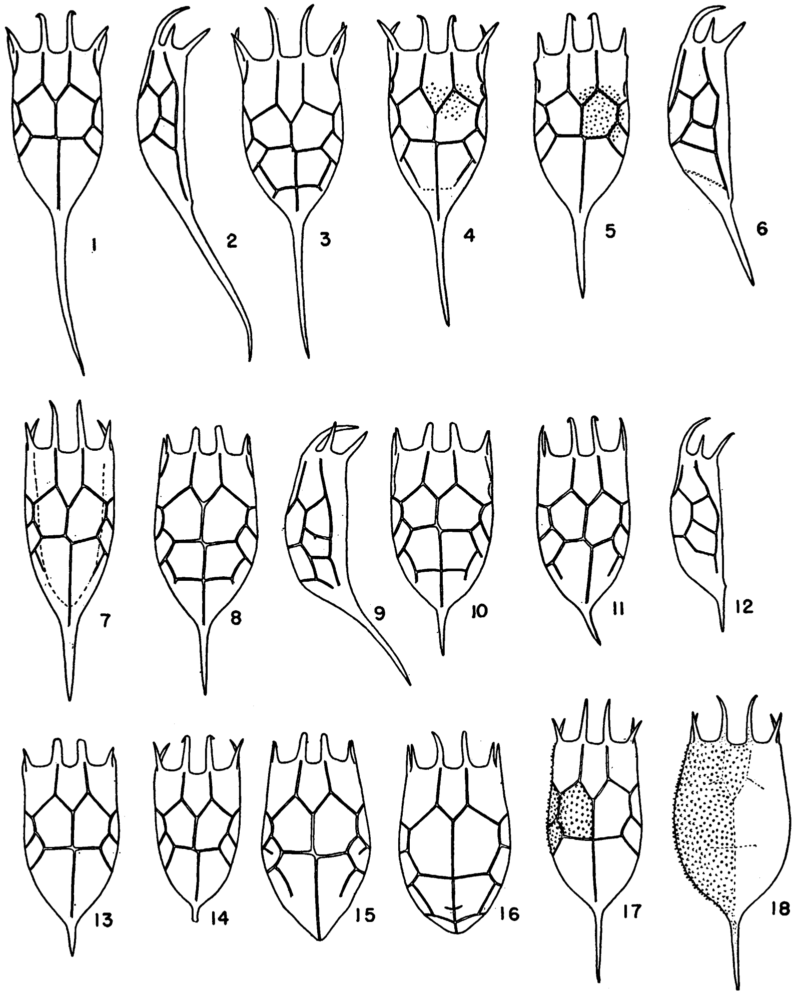
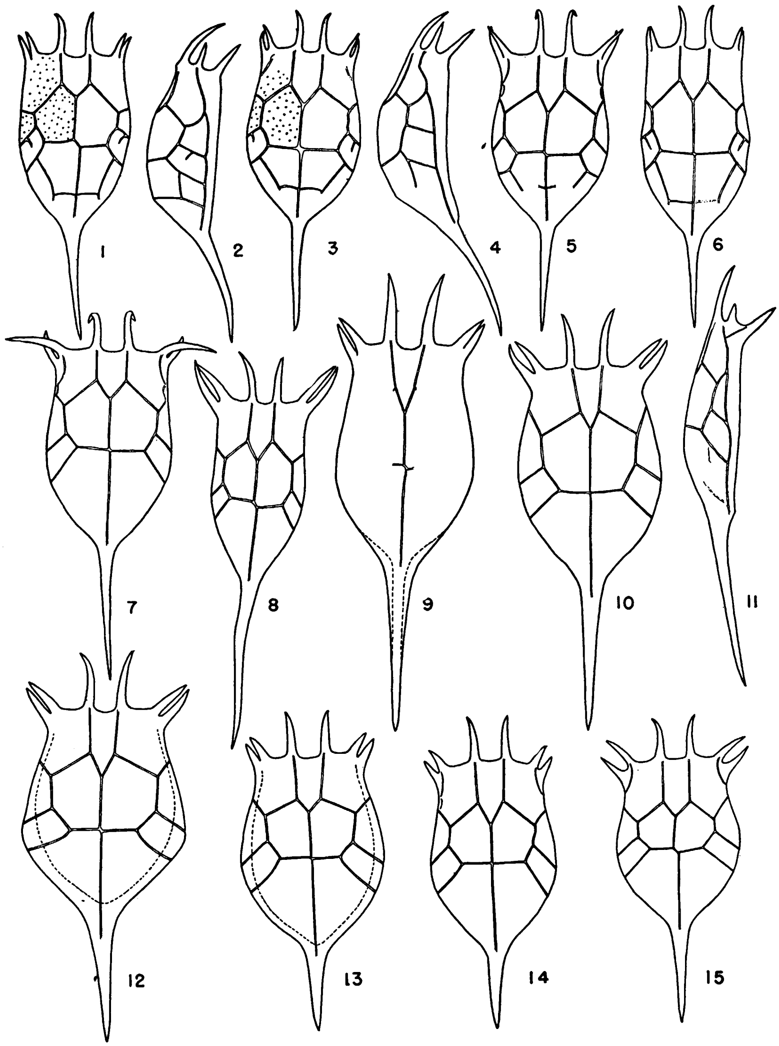


Figs. 1–14. *Keratella cochlearis:* 1, dorsal view; 2, lateral view, from Wallace Lake, Isle Royale, Michigan; 3, dorsal view, Murray Lake, British Columbia; 4, dorsal view, from Lake Mendota, Wisconsin; 5, dorsal view, 6, lateral view, from lake near Wildwood, Florida; 7, dorsal view, from Lillington, North Carolina; 8, dorsal view, 9, lateral view, from Long Lake, British Columbia; 10, dorsal view, from Lake Warren, Pennsylvania; 11, dorsal view, 12, lateral view, from Riverview, Florida; 13, dorsal view, from Linnet Lake, Waterton, Alberta; 14, dorsal view, from Pocono Lake, Monroe County, Pennsylvania.

Figs. 15, 16. *Keratella cochlearis* f. *tecta:* 15, dorsal view, from Long Lake, British Columbia; 16, dorsal view, from canal, Riga, Latvia.

Figs. 17, 18. *Keratella cochlearis* var. *hispida:* 17, dorsal view, from Lake Windermere, England; 18, dorsal view, from Cheshire, England.

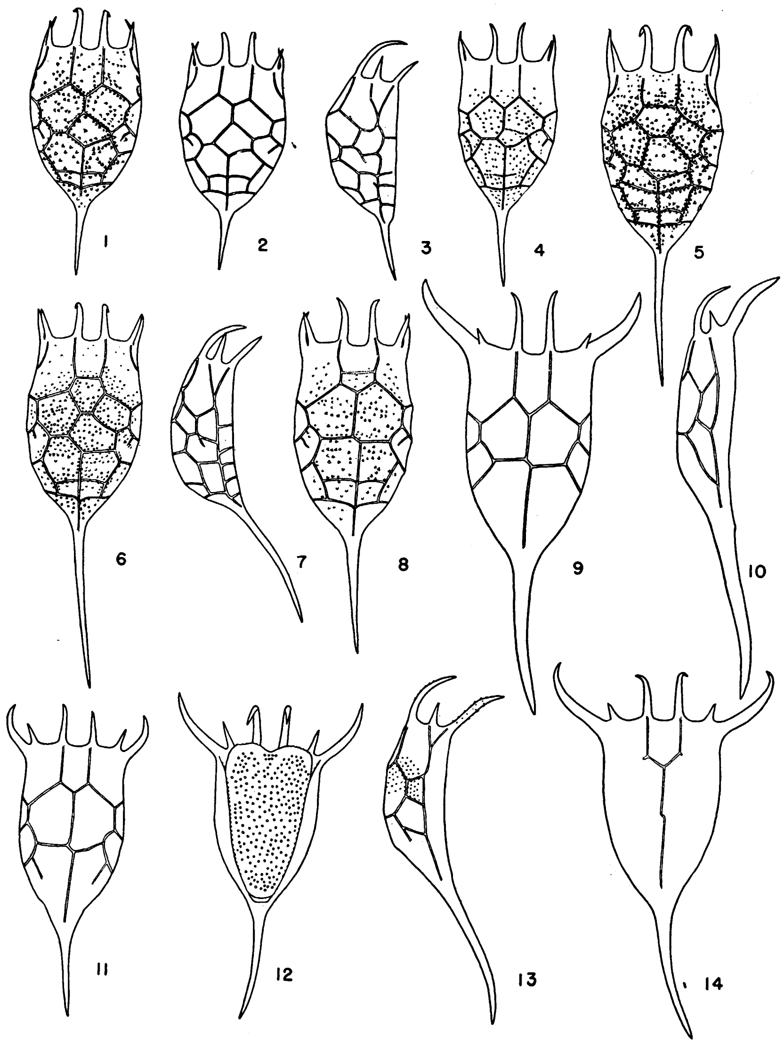


Figs. 1–6. *Keratella cochlearis* var. *robusta:* 1, dorsal view; 2, lateral view, from Lake Windermere, England; 3, dorsal view; 4, lateral view, from Cobin Lake, Jasper National Park, Alberta; 5, dorsal view, from Nicola Lake, British Columbia; 6, dorsal view, from Prospect Lake, Vancouver Island, British Columbia.

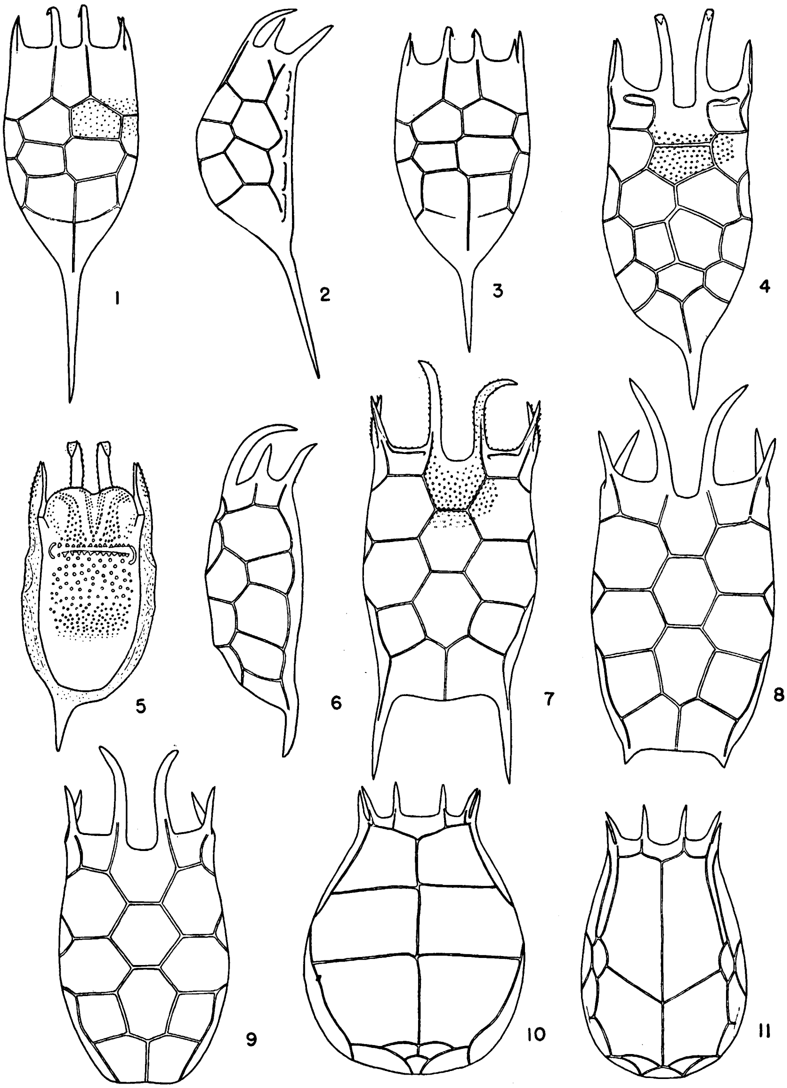
Fig. 7. *Keratella cochlearis* var. *recurvispina*, dorsal view, from Beaver Lake, British Columbia.

Fig. 8. *Keratella cochlearis* f. *macracantha*, dorsal view, from Penask Lake, British Columbia.

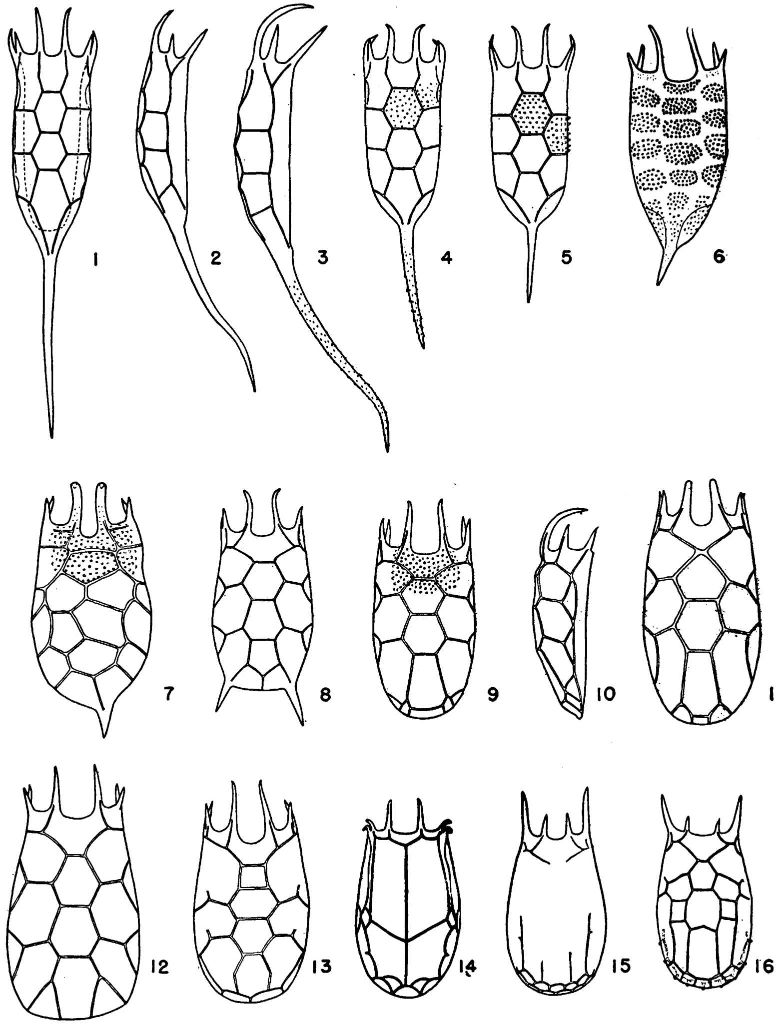
Figs. 9–15. *Keratella cochlearis* var. *faluta:* 9, dorsal view, from Pinantan Lake, British Columbia; 10, dorsal view; 11, lateral view, from Cobin Lake, Jasper National Park, Alberta; 12, dorsal view, from Beaver Lake, Okanagan, British Columbia; 13, dorsal view, from Isa Lake, Yellowstone Park, Wyoming; 14, dorsal view, from Forestry Bog, Wisconsin; 15, dorsal view, from Herbert Lake, British Columbia.



Figs. 1–3. *Keratella irregularis:* 1, dorsal view, Karluk Lake, Kodiak Island, Alaska; 2, dorsal view; 3, lateral view, from Buspielezers See, Kurzeme Province, Latvia (pustulation not shown).
Fig. 4. *Keratella irregularis* var. *angulifera,* dorsal view, from Lake Windermere, England.
Figs. 5–7. *Keratella earlinae:* 5, dorsal view, from Linsley Pond, North Branford, Connecticut; 6, dorsal view, from Talbot Lake, Jasper National Park, Alberta; 7, lateral view, from Benedict Lake, Wisconsin.
Fig. 8. *Keratella earlinae* var. *nesiotica,* dorsal view, from Bear Lake, Vancouver Island, British Columbia.
Figs. 9–14. *Keratella taurocephala:* 9, dorsal view; 10, lateral view; 11, dorsal view, from Forestry Bog, Wisconsin; 12, ventral view, from Keystone Lake, Florida; 13, lateral view, from Page's Lake, Raleigh, North Carolina; 14, dorsal view, from Tamaque Lake, Lutherland, Pennsylvania.



Figs. 1–3. *Keratella crassa:* 1, dorsal view; 2, lateral view, from Fox Lake, Fox Lake, Illinois; 3, dorsal view, from quarry, Stony Ridge, Ohio.
Figs. 4–6. *Keratella mixta:* 4, dorsal view, from Lenape Lake, New Jersey; 5, ventral view; 6, lateral view, from pool, Morehead City, North Carolina.
Figs. 7, 8. *Keratella serrulata:* 7, dorsal view, from Parvin State Park, New Jersey; 8, dorsal view, from Killarney Lake, Bowen Island, British Columbia.
Fig. 9. *Keratella serrulata* f. *curvicornis*, dorsal view, from lake near Apopka, Florida.
Fig. 10. *Keratella cruciformis*, dorsal view, from off west coast of Norway.
Fig. 11. *Keratella cruciformis* var. *eichwaldi*, dorsal view, from Rainy Bay, Barkley Sound, British Columbia.



Figs. 1–5. *Keratella gracilenta:* 1, dorsal view, 2, lateral view, from Lillington, North Carolina; 3, lateral view, from Lake Chascomus, Chascomus, Argentina; 4, dorsal view, from Graham Lake, Maine; 5, dorsal view, from Pocono Lake, Monroe County, Pennsylvania.

Fig. 6. *Keratella paludosa*, dorsal view, from Lake Hartridge, Polk County, Florida.

Fig. 7. *Keratella mixta*, dorsal view, from Morehead City, North Carolina.

Fig. 8. *Keratella valga* var. *procurva*, dorsal view from Sohawa, Punjab, India.

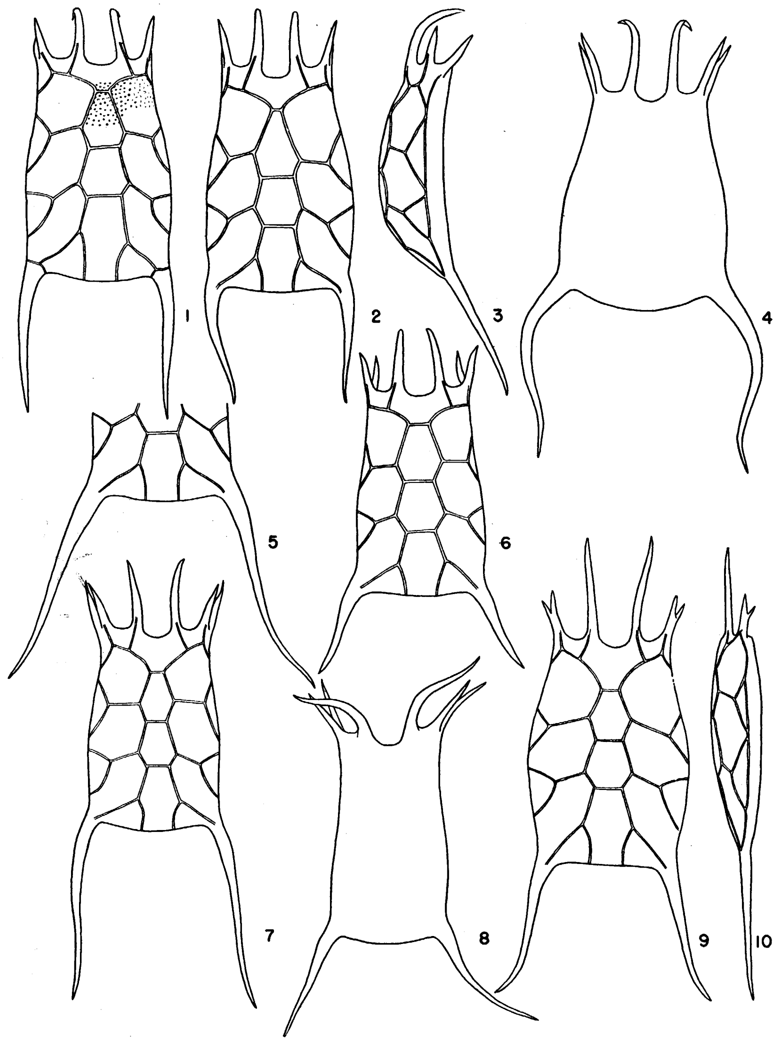
Figs. 9–11. *Keratella valga* f. *brehmi:* 9, dorsal view, 10, lateral view, from near Myakka City, Florida; 11, dorsal view, from pond at Monterey, California.

Fig. 12. *Keratella quadrata* f. *araneosa*, dorsal view, from pond, Los Angeles, California.

Fig. 13. *Keratella quadrata* var. *curvicornis*, dorsal view, from Totteridge, England.

Fig. 14. *Keratella cruciformis* var. *eichwaldi*, dorsal view, from Beaver Lake, Vancouver Island, British Columbia.

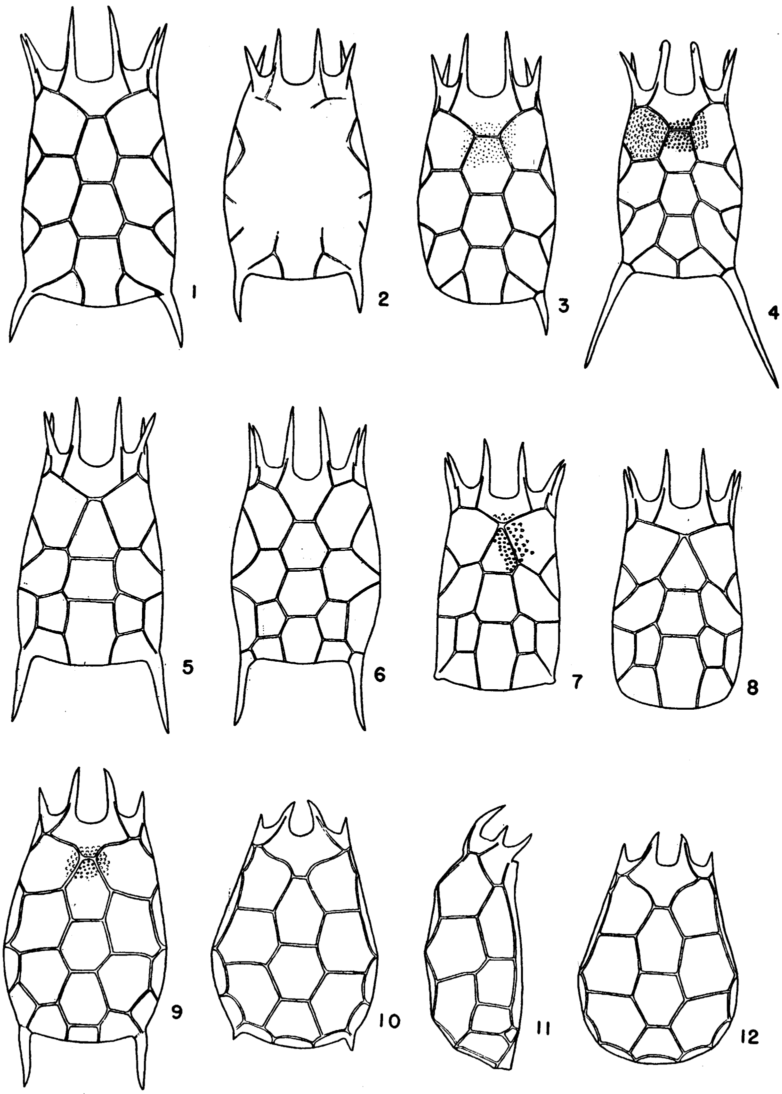
Figs. 15, 16. *Keratella reducta:* 15, dorsal view, from Cakedon, South Africa; 16, dorsal view, Weltevreden, East Pan near Lake Chrissie, South Africa.



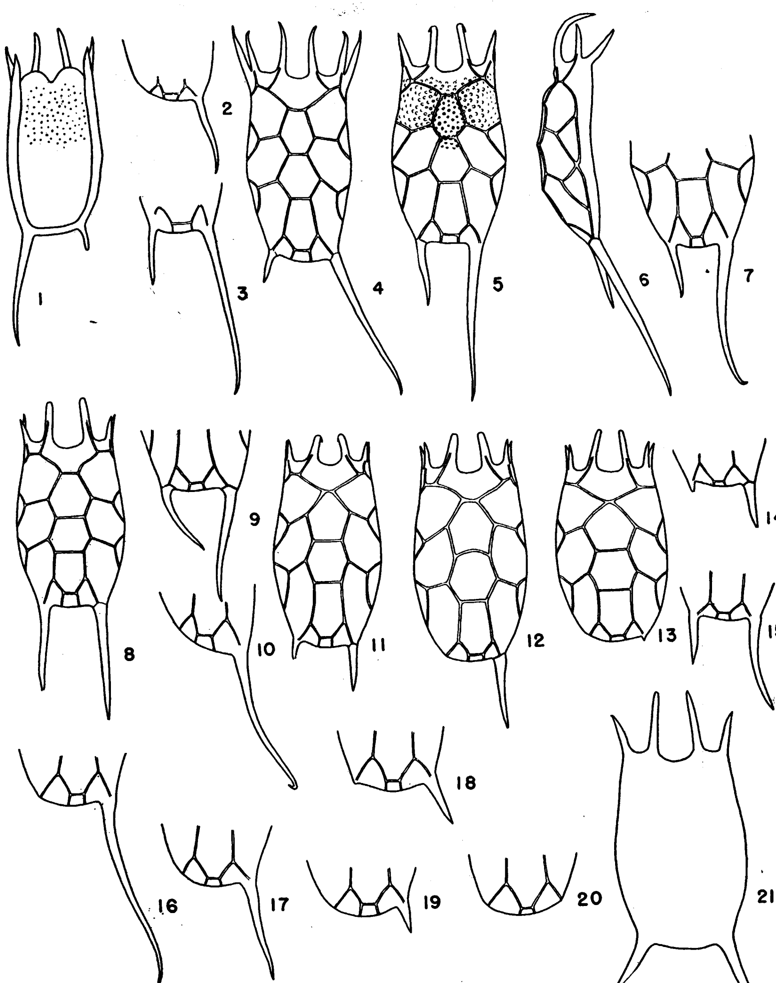
Figs. 1–7. *Keratella quadrata:* 1, dorsal view, from Lake Windermere, England; 2, dorsal view, from Westlake, Los Angeles, California; 3, lateral view, from Deadman's Lake, Okanagan, British Columbia; 4, dorsal view, from Clark Lake, Saskatchewan (sculpture indistinct); 5, posterior portion of lorica, from Westlake, Los Angeles, California; 6, dorsal view, from swamp, Phashakuri. Kashmir Valley, India; 7, dorsal view, from Westlake, Los Angeles, California.

Fig. 8. *Keratella quadrata* var. *platei*, dorsal view, from Baltic Sea (sculpture indistinct).

Figs. 9, 10. *Keratella quadrata* var. *adnata:* 9, dorsal view, 10, lateral view, from Christine Lake, Jasper National Park, Alberta.



Figs. 1–3. *Keratella quadrata* f. *testudo:* 1, dorsal view, from Westlake, Los Angeles, California; 2, 3, dorsal views, from pond, Los Angeles, California.
Fig. 4. *Keratella quadrata* var. *edmondsoni*, dorsal view, from lake, Ootacamund, Nilgiri Hills, Madras Presidency, India.
Figs. 5–8. *Keratella quadrata* var. *brevispina:* 5, dorsal view from Ororotse Tso, Indian Tibet; 6, dorsal view, from Bear Lake, Vancouver Island, British Columbia; 7, 8, dorsal views, from Mystic Lake, Banff, Alberta. (Fig. 8 is f. *gossei.*)
Figs. 9–12. *Keratella quadrata* var. *pyriformis:* 9, dorsal view, from Ororotse Tso, Indian Tibet; 10, 12, dorsal views, 11, lateral view, from Sta-rtsak-puk Tso, Rupshu, Indian Tibet. (Figs. 11 and 12 are of f. *hutchinsoni.*)



Figs. 1–21. *Keratella valga:* 1, ventral view, 2, 3, posterior portions of lorica, from Colombo Lake, Ceylon; 4, dorsal view, from Sohawa, Punjab, India; 5, dorsal view, 6, lateral view, 7, posterior portion of lorica, from Brakpan, Transvaal, South Africa; 8, dorsal view, from pool, Glew, near Buenos Aires, Argentina; 9, 10, posterior portions, from Lagunes Julia and Soven, respectively, San Luis Province, Argentina; 11, 13, dorsal views, from Encadenadas Oeste, San Luis Province, Argentina; 12, dorsal view, 14, 15, posterior portions of lorica from Lagune Plateado, San Luis Province, Argentina; 16–20, posterior portions of lorica, from Bear River Refuge, Utah (showing variations in posterior spines found in a single collection); 21, dorsal view, from Clare Island, Ireland (pattern indistinct).