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A taxonomic revision of the peritrich ciliate genus *Pyxicola*

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ABSTRACT

The protozoan genus *Pyxicola* Kent, 1881 (Ciliata, Peritrichida, Vaginicolidae) has been critically revised. It is now considered to include the nominal genera *Pachytrocha* and *Caulicola*. An annotated list of the hitherto described nominal species is given. Eight species and two formae are recognized within the genus. A short description of each of these and a key to their identification are given. All recognized species are figured; many illustrations from the literature have been redrawn and brought together to facilitate comparison and to justify the taxonomical decisions which have been taken.

INTRODUCTION

"The literature of peritrichs is extensive". This statement by Chatton (1936) is quite true, especially forty years later. To search the literature of ciliates we have Kahl's impressive work (1935); but it is outdated. Still worse, it is not complete, and often lacks detail, because of its comprehensiveness. In protozoology there are almost no type specimens (see Corliss, 1972), and the taxonomist must work with descriptions; therefore, literature research seems to me more important than in other fields of zoology. In this paper, the accent lays on the revision of previously published works more than in presenting new data.

In the present paper a functional classification of the known species is devised. I have imitated Noland & Finley (1931) in making a checklist of nominal species. A more formal presentation of the literature is to be found under the headings of each species recognized, where full synonymies and references are given. Many drawings from the literature have been brought together. I believe this will help both the specialist and the general biologist who needs a simple and convenient identification guide.

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GENUS *Pyxicola*

Taxonomic position
Phylum: Protozoa Goldfuss, 1818, emend. Von Siebold, 1845
Subphylum: Ciliophora Doflein, 1901
Class: Ciliata Perty, 1852
Subclass: Peritrichia Stein, 1859
Order: Peritrichida Stein, 1859
Suborder: Sessilina Kahl, 1933
Family: Vaginicolidae De Fromentel, 1874
Genus: *Pyxicola* Kent, 1881

In the classification above, the paper by the Committee of the Society of Protozoologists (Honigberg et al., 1964) has been followed. The author considers the compromise of the Committee of the Society of Protozoologists a reasonable working arrangement which should be accepted by ciliate taxonomists until much more information (especially on ultrastructure) on peritrichs and related ciliates is available. Much has been written concerning the classification of ciliates in general (see Corliss, 1974 for a review), and often in disagreement (compare Raabe, 1964 with Corliss, 1977, for instance). The position of *Pyxicola* will change every time its family, the Vaginicolidae, is changed; and because a discussion on higher categories would be beyond the scope of this paper, the author has preferred to choose the classification of Honigberg et al. (1964) above some other more recent but more controversial one.

From its erection, *Pyxicola* has been included within the family Vaginicolidae (which Kent considered to be a sub-family called Vaginicolina). It has never been removed from that family. Matthes (1954) questioned the validity of the family because there are some loricate peritrichs which are not vaginicolids, but he did not propose to abolish the family. The Vaginicolidae remain a reasonably well-defined taxon, and a very convenient one to work with.

Diagnosis

Solitary peritrichs, with most of their body enclosed within a lorica or case, which stands on a stalk upon the substrate. Beneath the peristome, attached to the cell envelope, there is a kind of lid, the operculum, which closes the aperture of the lorica when the animal retracts; in some species it is too small for this purpose and then it is simply withdrawn within the case. The operculum of pyxicolas should not be confused with the elevated epistomial disc of some members of the Operculariidae (a related peritrich family) which is also sometimes improperly called an operculum, specially in the old literature.

General biology of the known species of the genus.

A modern account of the general biology of a representative species has been provided by Finley & Bacon (1965). It's therefore sufficient to summarize here the most important characteristics of pyxicolas, together with some particularities of the genus.

Like most peritrichs, pyxicolas have a sedentary and a free-swimming phase. When in the mobile phase, pyxicolas move rapidly in water; they are approximately cylindrical in shape, and swim with the aid of an aboral ciliary band. Such a larval organism is called a telotroch. It selects a place to settle down within a few hours. The telotroch then attaches to it and begins the construction of its case. This is secreted little by little, after the stalk has

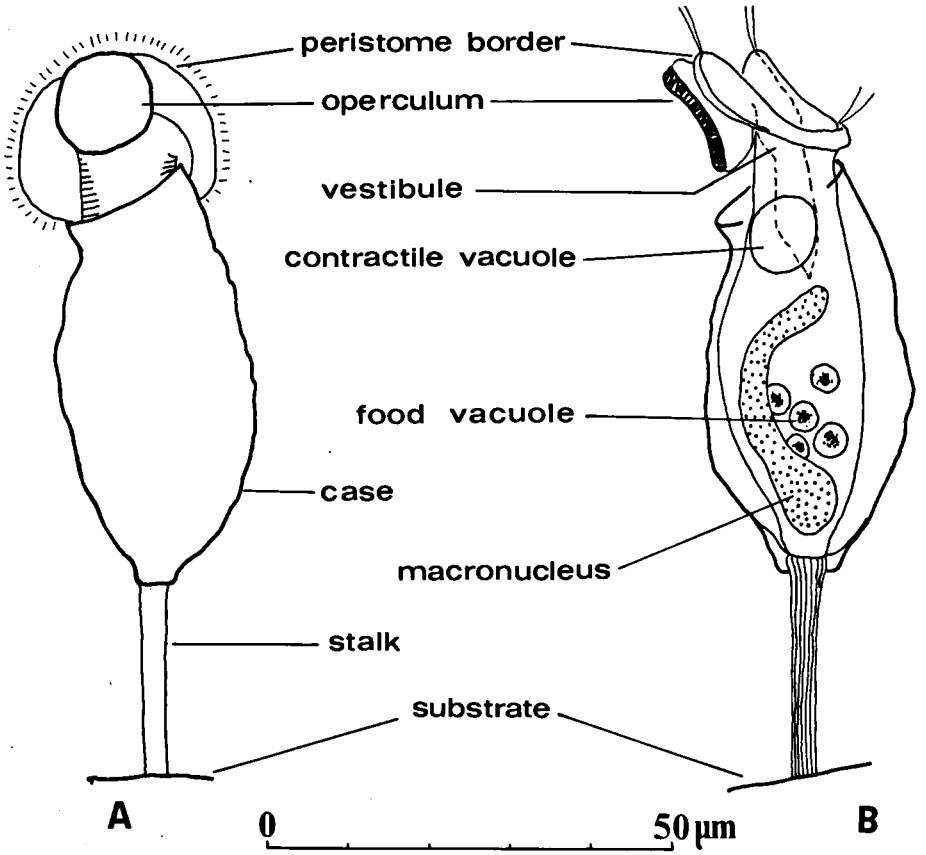

Fig. 1. *Pyxicola pusilla*, attached to a reed rootlet, illustrating some of the morphological terms used in this paper. A. Surface structures. B. The same individual, showing internal structures; the cell body has rotated ±90° in its lorica. The specimen was freshly mounted on a glass slide and drawn by means of a prism fixed to a Zeiss interference contrast microscope (Nomarski optics). All drawings by the author have been made in this way.

been completed. The form of the body changes in the process. According to Finley & Bacon (1965, p. 128), lorica building is interrupted by feeding periods. I once observed lorica building by *Pyxicola pusilla;* in this case no feeding took place before the lorica was finished and the operculum secreted. Moreover, the individuals of the *Cothurnia* spp. which most other authors and I observed while constructing their cases finished this activity before feeding. There is clearly some variation concerning this point.

The finished case (fig. 1) measures between 45 and 200 µm in length; the stalk varies from almost zero to 260 µm in length.

Feeding takes place by water currents which the adoral membranelles produce. Pyxicolas feed on bacteria and small algae. Cultures in defined growth media have not been achieved as yet, and even axenic cultures have not been reported.

Binary fission is unequal: one of the daughter-cells retains the operculum and the lorica, the other one becomes a telotroch and swims away. Two mature zooids have never been observed within one case. Neither is there evidence of mature organisms leaving their loricas, as other vaginicolids sometimes do. By means of their opercula, pyxicola-cells protect themselves much better than other peritrichs do, and have therefore less need to escape.

Sexual reproduction has been described only by Finley & Bacon (1965); it is typically peritrichous, the microconjugant being absorbed by its larger partner.

The contractile vacuole, food vacuole, pellicula, macro- and micronucleus and ciliature (fig. 1) are typically vaginicolid. These structures resemble especially those of most *Cothurnia* spp. An annulus (the place on the pellicula where the telotrochal ciliary band might develop) is not distinguishable in mature individuals.

As a genus, *Pyxicola* is not abundant, but in some habitats great numbers of individuals belonging to certain species may be found. *P. socialis* is thus very common on the stalks of *Cordylophora* in fresh and brackish waters.

Synonymy

Pyxicola Kent, 1881, p. 725; Kahl, 1935, p. 787; Kudo, 1947, p. 691; Finley & Bacon, 1965, p. 123 129; Stiller, 1971, p. 218.
Pachytrocha Kent, 1881, p. 729.
Caulicola Stokes, 1894, p. 341; Kahl, 1935, p. 786; Kudo, 1947, p. 691; Stiller, 1971, p. 217.
Cothurnia sensu Entz, 1884, pp. 424-428 (in part); Lepşi, 1926, pp. 87, 94 (in part).

Kent (1881) created the genus *Pyxicola* because of the operculum possessed by its species. This is the essential difference between *Pyxicola* and *Cothurnia: Cothurnia* has no operculum. He did not know that some species have such a small operculum, that it cannot be used to close the lorica. Perhaps these small-operculated pyxicolas will be included in a new genus in the future, if many more species of their kind are discovered. All known pyxicolas have a stalk. Should some species be discovered without one, it will probably be better to create still another genus for that species.

Within *Pyxicola* is included, according to the author's opinion, *Pachytrocha* Kent, 1881. This monotypic genus was created for some (perhaps a single one) specimens found by Kent (1881, pp. 729-730). Dalla Torre (1891, p. 203) says he once found that organism. I have found no other records in the literature. The author has sometimes seen pyxicolas from which the operculum has somehow fallen off. Such organisms could easily have been taken for a *Pachytrocha.* Kahl (1935, p. 790) suggested also that *Pachytrocha* could be a mutilated or aberrant *Pyxicola.*

Caulicola Stokes, 1895, should also be considered a junior synonym of *Pyxicola.* Stokes' description is too short to be sure he did not make a mistake saying the operculum to be attached to the lorica instead than to the animal's body. Nobody has recorded other specimens of this nominal genus ever since.

I have observed many times pyxicolas at a position from which the operculum really seemed hinged to the border of the lorica, closing and opening it like a little door (see fig. 3E). Only careful observation convinced me that the operculum adheres to the animal itself. Some authors considered *Cothurnia pyxidiformis* D'Udekem to be a *Caulicola,* because the drawing of the original description shows the operculum contiguous with the animal's case, and not attached to the cell body. But the description itself leaves no doubt about this species being a normal *Pyxicola.* To me the description is much more conclusive than the drawing (see fig. 2 C). The same holds true for *Pyxicola nodosa* Vuxanovici.

Taxonomic characters within the genus

There is no reliable single character within the genus. A combination of several ones is needed to define infrageneric taxa. I have chosen the following ones: lorica size and shape, stalk length, kind of substrate and salinity of the water in which the organisms live. These characters are easy to record and measurable. The maximal length of the lorica divided by its maximal width is called "shape quotient" in the following. All the characters quoted above are quite variable. Fortunately, most species have characteristics which differ from the common ones: a small operculum, special shape of the macronucleus, etc.

No study on the "silver-line system" of any *Pyxicola* is available in the literature. Therefore, I have restricted myself to the use of the taxonomic characters indicated above which are among the classical ones in ciliate taxonomy. The techniques available today for making silver-impregnations of ciliates have been used with some peritrichs with promising results (see for instance Lom, 1964; Pätsch, 1974; Foissner & Schiffmann, 1975, 1976). It is possible that in the future they will be used to advantage with *Pyxicola* spp. Something similar may be said of the ultrastructure of pyxicolas.

Remark on nomenclature

According to article 30 (a) (2) of the International Code of Zoological

Nomenclature, *Pyxicola* should be treated as of feminine gender, because all users of the name have done such. No attempt should be made of changing the spelling of the old specific epithets. When giving names to new species feminine epithets should be used, too.

Key to species and forms

The eight species and the two varieties which are considered valid in this paper can be keyed out as indicated below. Most characters that have been chosen can be observed in fixed and retracted specimens.

1.a. Case shorter than 130 µm 3
b. Case longer than 150 µm 2
2(1)a. Case about 160 µm long, widest and symmetrical medially, roughly ovate, pointed at each end . . . . . *P. pyxidiformis*
b. Case about 200 µm long, ovate . . . . *P. pyxidiformis* forma *lacustris*
3(1)a. Case vertically elongate (shape quotient over 1.6) 4
Case more or less spherical (shape quotient under 1.5); attached to the crustacean *Ligia oceanica* (possibly to other marine animals as well) . . . . . *P. ligiae*
4(3)a. Operculum large enough to occlude the lorica's orifice; macronucleus elongate, more or less vertically situated . . *P. pusilla* complex: 5
b. Operculum far too small to close the lorica; macronucleus U-shaped, lying transversely near the middle of the animal's body . . . . . *P. entzii*
5(4) Note: the *P. pusilla* complex includes 5 very similar species; some individuals are very difficult to identify to the species level.
a. Case annulated; stalk usually longer than 70 µm; sea or brackish water 6
b. Case annulated or not; fresh or brackish water 7
6(5)a. Stalk up to 150 µm long; attached to algae or lifeless substrates . . . . . *P. socialis*
b. Stalk 140 to 260 µm long; attached to sessile invertebrates . . . . . *P. socialis* forma *longipes*
7(5)a. Case 75-85 µm long, shape quotient 2.4-3.3 (average 2.9), without rings; stalk 15-40 µm (average 27 µm); attached to the cave-dwelling isopod *Microlistra spinosissima* (possibly to other fresh-water animals as well) . . . . . *P. psammata*
b. Not as above 8
8(7)a. Stalk usually longer than the case, up to 150 µm; often attached to the hydroid *Cordylophora* sp., sometimes to aquatic plants . . . . . *P. operculigera*
b. Stalk not longer than the case; attached to aquatic plants or algal filaments 9
9(8)a. Stalk shorter than 15 µm, usually about 5 µm; case not opaque, slender (shape quotient about 2.5); in feeding position, the oper-

culum overhangs somewhat the aperture of the lorica . . *P. carteri*

b. Stalk 4-60 µm long; case often opaque; shape quotient about 2.0; in feeding position, the operculum is kept against the peristome, very near the edge of the case . . . . . *P. pusilla*

Descriptions of the recognized species

Pyxicola ligiae (Cuénot, 1891) Kahl, 1935

Synonymy

Cothurnia ligiae Cuénot, 1891, pp. 86-88, fig. 3 (fig. 2A of this paper); Hamburger & Von Buddenbrock-Heidelberg, 1911, p. 143, fig. 185.

Pyxicola ligiae Kahl 1935, p. 790, fig. p. 788, 4; Kahl 1933, p. 139, fig. 25, 15; Matthes & Wenzel 1966, p. 100, fig. 73 f (fig. 2B of this paper).

Remark on synonymy:

Kahl (1935, p. 790) refers to *P. ligiae* Cuénot 1811. This year is clearly misprinted, or it is a *lapsus calami* of Kahl.

Diagnosis

Lorica length about 55 µm, width about 36 µm, pear-shaped; operculum completely occluding the aperture of the lorica. Stalk 25 µm, peristome border thin.

Substrate: the crustacean *Ligia oceanica* (probably other marine invertebrates as well).

Habitat: marine. Found at Concarneau, Roscoff, Le Portel (France).

Remarks

This is a well characterised, epizoic species. Cuénot describes the vegetative division, which is of the normal kind among peritrichs.

Pyxicola pyxidiformis (D'Udekem, 1864) Kent, 1881

Synonymy

Cothurnia pyxidiformis D'Udekem, 1864, p. 27, pl. 5, fig. 1 (fig. 2C of this paper).

Pyxicola pyxidiformis Kent, 1881, p. 726; Kahl, 1935, p. 787, fig. p. 788, 7.

Caulicola pyxidiformis Kahl, 1935, p. 786, fig. p 7,88,7; Stiller, 1971, p. 217, fig. 132C.

Diagnosis

Lorica 160 µm long, widest medially, through which a plane of symmetry can be drawn. Stalk about 40 µm long.

Substrate: leaf of a water-lily

Habitat: a channel at Willebroeck (Belgium).

Remark

This species has been recorded only once, and from a single specimen. See also the comment under the next heading.

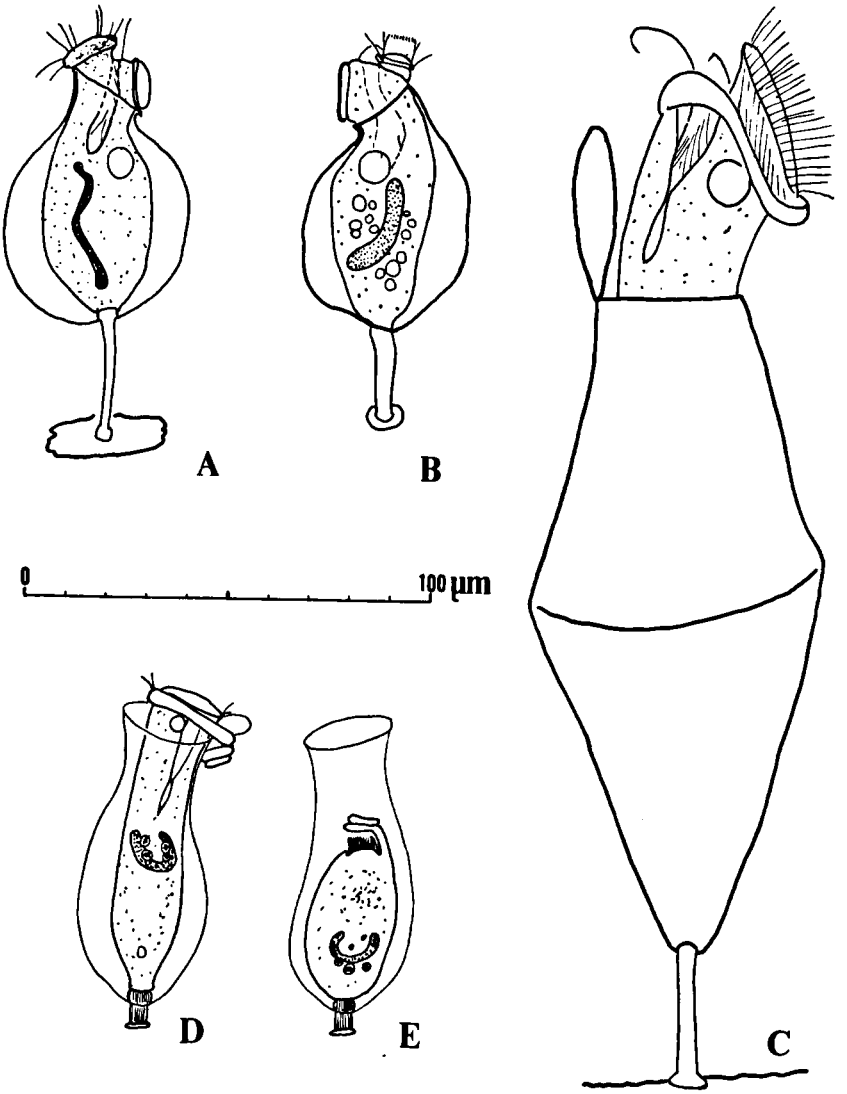

Fig. 2. Some pyxicolas drawn on the same scale, to facilitate comparison. Like all other figures from this paper, the original drawings have been copied on the same scale with the aid of a pantograph. The style of the original author is respected in each case; sometimes, the figures are simplified, but never "corrected".
A. Pyxicola ligiae (Cuénot), after Cuénot. B. *P. ligiae*, after Matthes. C. *P. pyxidiformis* (D'Udekem), after D'Udekem. D. *P. entzii* (Stiller) after Stiller (1931). E. The same, contracted, also after Stiller.

Pyxicola pyxidiformis forma **lacustris** (Maggi, 1879)

Synonymy
Cothurnia pyxidiformis var. *lacustris* Maggi, 1879, pp. 69-70, no figs.

Diagnosis
As *P. pyxidiformis*, but the lorica of more rounded forms, oval, about 200 μm long, of brick-red colour.
Habitat: found only once, on the leaf of a water-lily, in the freshwater lake of Brinzio (Italy).

Remarks
The length and somewhat different shape of the lorica seem to be sufficient to retain this variety, at least as a form. At the same time the paper of Maggi corroborates D'Udekem's description of *P. pyxidiformis*. It is scarcely probable that both D'Udekem and Maggi miscalculated the length of their animal's cases, which is their most distinctive character.

Because the term "varietas" is not to be used, according to the Code, I have had to change it to"forma"; the value of such infraspecific categories is very dubious until much more information on ciliate biology is available.

Pyxicola entzii (Stiller, 1931) Kahl, 1935

Synonymy:
Cothurniopsis Entzii Stiller, 1931, pp. 194-197, figs 16-17 (figs 2D-E of this paper).
Pyxicola entzi Kahl, 1935, p. 789, fig. p. 788, 9; Finley & Bacon, 1965, pp. 125 and 129.
Pyxicola Entzii Stiller, 1971, p. 219, fig. 133 C-D.

Note on nomenclature
Although the epitheton "entzi" is linguistically more correct, the original spelling and the last one (1971) from the author herself is "Entzii"; therefore, the (inadvertent?) correction of Kahl (and Finley & Bacon) should not be accepted.

The capital letter "E", according to the new rules, should nevertheless be changed into "e".

Diagnosis
Lorica 70—75 μm long, smooth, widest basally, stalk 4 μm long. Neck of the lorica much wider than operculum . Macronucleus short, U-shaped, lying transversally in the middle of the cell.
Substrate: the algal filaments of *Cladophora* sp., and the aquatic plant *Elodea canadensis*.
Habitat: the freshwater lake Balaton (Hungary).

The **Pyxicola pusilla** *species complex*

When studying pyxicolas, the author faced a two-sided problem: the literature is full of synonymies, and the pyxicolas themselves are too variable to recognize clear-cut species among them. A similar problem arose with

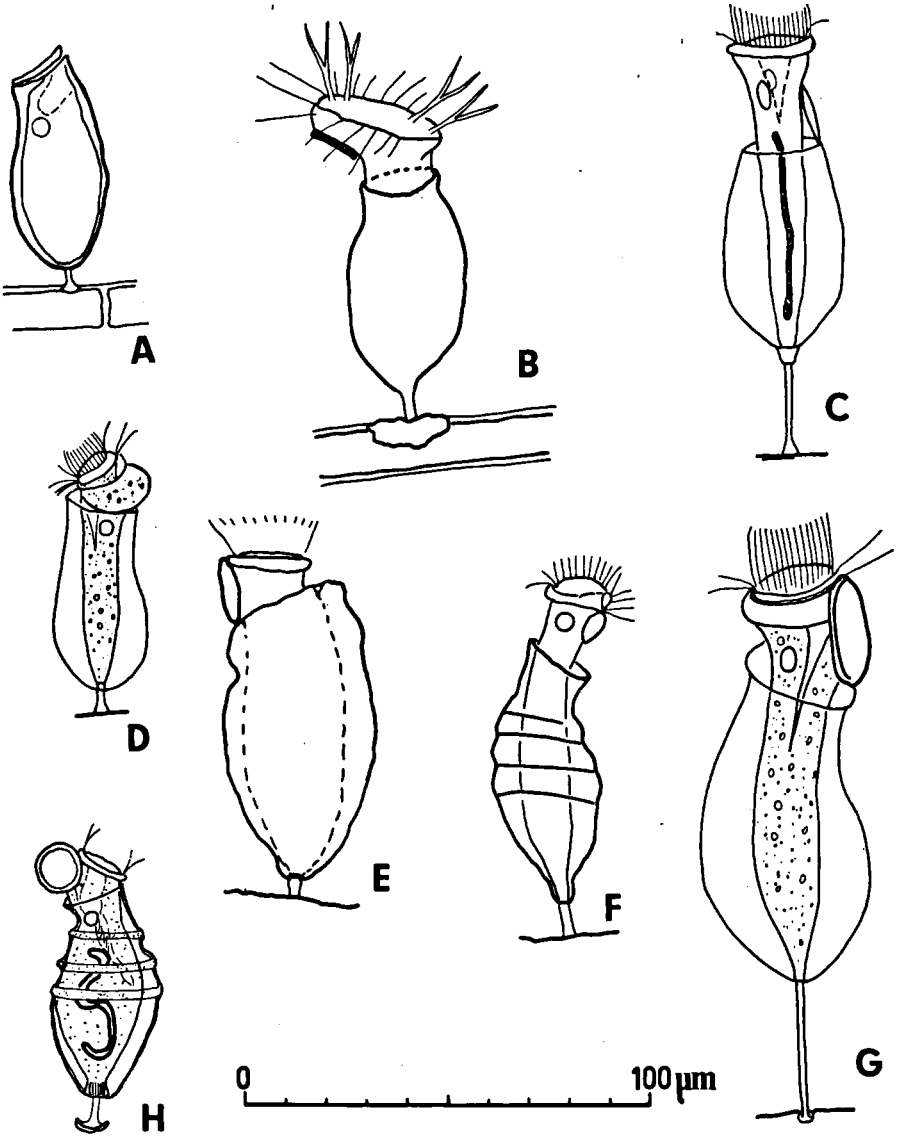

Fig. 3. Some pyxicolas drawn on the same scale, to facilitate comparison . All belong to the species *Pyxicola pusilla*, but they are here named with their original names for clarity. A. "*Cothurnia pusilla*", after Wrześniowski, 1870. B. "*Cothurnia furcifer*", after Hutton. C. "*Caulicola valvata*", after Stokes (1895). D. "*Pachytrocha cothurnoides*", after Kent (1881). E. An individual attached to a reed rootlet, drawn from an angle from which the operculum seems to be attached to the lorica. Note also the very thick wall of the case. F. "*Pyxicola annulata*", after Leidy. G. "*P. affinis*", after Kent (1881). H. "*P. eforiana*", after Tucolesco.

Platycola (Kralik, 1960), and of course with *Vorticella* (Noland & Finley, 1931). A taxonomic decision has to be taken if the bulk of the pyxicolas found both in nature and literature is to be classified within a consistent system.

In this study, five species are recognized to arrange the common pyxicolas in more or less discrete entities. When, some day, many detailed studies of the kind of that of Finley & Bacon (1965) are available, these five species could be split still further or unified under one name.

Pyxicola pusilla (Wrześniowsky, 1866) Kent, 1881

Synonymy:

Cothurnia pusilla Wrześniowsky, 1866, pp. 26—27, in part; Wrześniowsky, 1867, pp. 333—336 (but not pl. 6, fig. 3!), in part; Wrześniowski, 1870, pp. 469—471, in part, pl. 21 fig. 6 (fig. 3A of this paper), but not fig. 5!); Leidy, 1874, p. 140 (record only); Kahl, 1935, p. 789, fig. p. 788, 22.

Cothurnia furcifer Hutton, 1878, pp. 49—50, 1 fig. (fig. 3B of this paper).

Cothurnia affinis Blochmann, 1886, p. 84, fig. 205; Hickson, 1903, figs. 81-82.

Cothurnia cothurnoides Blochmann, 1886, p. 84.

Caulicola valvata Stokes, 1895, p. 341, pl. 21 fig. 9 (fig. 3C of this paper); Kahl, 1935, p. 786, fig. p. 788, 8; Kudo, 1947, p. 691, fig. 325, g; Kahl, 1933, p. 139, fig. 25. 23.

Pachytrocha cothurnoides Kent, 1881, pp. 729—730, pl. 40 fig. 32 (fig. 3D of this paper); Dalla Torre, 1891 (record only); Kahl, 1935, p. 790 fig. p. 788, 22; Noland, 1959, p. 294 (fig. 10. 32.e).

Pyxicola pusilla Kent, 1881, p. 726 (no figs.); Dalla Torre, 1891. p. 203 (record only); Stokes, 1888, p. 258 (record only); Kahl, 1935, p. 789, fig. p. 788, 21 (but not 20!).

Pyxicola affinis Kent 1881, p. 727, pl. 40, fig. 28—29 (fig. 3G of this paper); Dalla Torre, 1891, p. 203 (record only); Kahl, 1935, p. 787, fig. p. 788,1,2; Kudo, 1947, p. 691, figs. 325 h—i; Noland, 1959, p. 294, fig. 10.32.f; Finley & Bacon, 1965, p. 215, table 2 (dubious); Stiller, 1971, p. 218, fig. 133 A.

Pyxicola annulata Leidy, 1882, pp. 252—253, pl. 2 fig. 8 (fig. 3F of this paper), fig. 9 (dubious); Grenfell, 1884, pp. 134—135, fig. 3; Stokes, 1888b, pp. 259—260; Kahl, 1935, p. 787, (fig. p. 788, 19 is *P. striata*); Pätsch, 1976, p. 44, fig. 33.

Pyxicola eforiana Tucolesco, 1962, p. 36, fig. 56 (fig. 3H of this paper).

Pyxicola carteri sensu Sommer, 1951, pp. 416—417, fig. 42a.

Pyxicola carteri forma *constricta* sensu Nusch, 1970, p. 312 (this form could also be what in this paper is called *P. carteri*).

Diagnosis

Lorica 50—80 µm long (average 65 µm), 25—38 µm wide, transparent when young, deep chestnut brown and opaque when old, corrugated, slightly annulated or almost smooth. Shape quotient about 2.0 (1.6—2.4). Neck of the lorica sometimes very short, even absent. Stalk 4—60 µm long. The animal protrudes but little from its case, and holds the operculum tight against the peristome.

Substrate: aquatic plants and algae; lifeless objects.

Habitat: fresh waters from many places in the world; brackish water from Bulgaria (Tucolesco). Never found in sea water.

Remarks

The author has observed pyxicolas during one year at different freshwater lakes of the Netherlands (Roos & Trueba, 1977), mostly attached to reed

rootlets. The stalk of one specimen measured 109 µm in length; all others (several hundreds in total) varied between 4 and 50 µm. Other characters varied as stated in the diagnosis of this species. I have segregated the long-stalked specimen in favour of *Pyxicola operculigera* (see below).

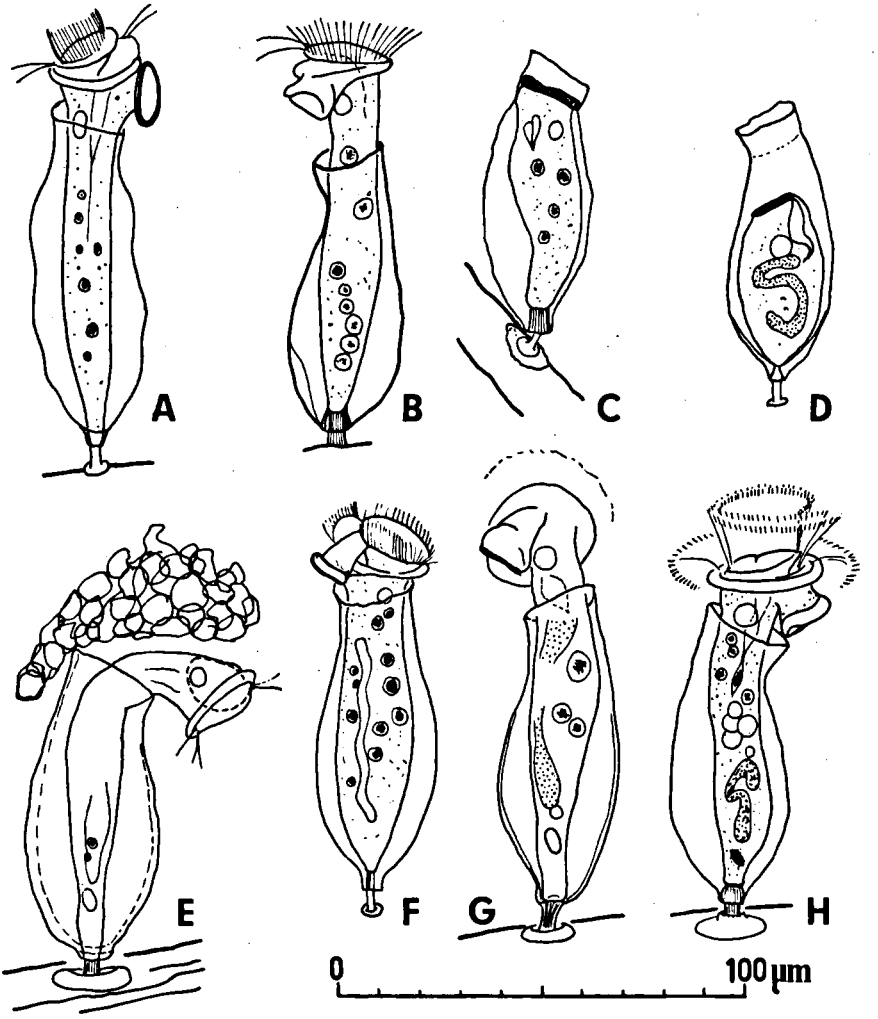

Fig. 4. Some pyxicolas drawn to the same scale, to facilitate comparison. All belong to the species *P. carteri*, but are here named by their original names for the sake of clarity. A. *P. carteri*, after Kent (1881). B. "*P. carteri* forma *constricta*", after Sommer. C. "*P. constricta*" after Stokes (1884). D. "*P. constricta*", after Stiller (1940). E. An individual which protrudes much from its case, due to some detritus. The macronucleus was only partly visible (like fig. G). F. "*P. limbata*", after Stiller (1939). G. An individual attached to a reed rootlet, with off-centered stalk, like "*P. limbata*". H. "*P. nolandi*", after Finley & Bacon.

Pyxicola carteri Kent, 1881

Synonymy:

Pyxicola carteri Kent, 1881, p. 729, pl. 40, fig. 40 (fig. 4A of this paper); Kahl, 1935, p. 787, fig. p 788, 6.

Pyxicola carteri forma *constricta* Sommer, 1951, p. 417, fig. 42b (fig. 4B of this paper), c—d; ? Nusch, 1970, p. 312 (no figs.).

Pyxicola constricta Stokes, 1884, pp. 24—25, fig. 5 (fig. 4C of this paper); Stokes, 1888a, fig. 16; Stokes, 1888b, p. 259, pl. 8 fig. 21; Kahl, 1935, p. 787, fig. p. 788, 18; Stiller, 1940, p. 285, fig. 14 (fig. 4D of this paper); Finley & Bacon, 1965, p. 125, table 2 (dubious); Stiller, 1971, p. 129, fig. 133B.

Pyxicola annulata Leidy, 1882, pro parte, pp. 252—253, pl. 2, fig. 9 (dubious) non 8; Finley & Bacon, 1965, p. 125, table 2.

Pyxicola limbata Kahl, 1935, p. 787, fig. p. 788, 10; Stiller, 1938, pp. 251—252, fig. 3 (fig. 4F of this paper); Finley & Bacon, 1965, table 2 (p. 215); Stiller, 1971, p. 219, fig. 133E.

Pyxicola nodosa Vuxanovici, 1961, pp. 439, 441-442, fig. 20.

Pyxicola nolandi Finley & Bacon, 1965, pp. 123—131, figs. 1A (fig. 4H of this paper), 2B—6.

Pyxicola striata Kellicott, 1884, p. 121, pl. 7 fig 3. See fig. 5B of this paper, taken from Kahl.

Diagnosis

Lorica 65—96 µm long, 20—33 µm wide, transparent when young, yellow-brown (but not opaque) when old, almost smooth, slightly ondulated, but without rings. Neck present, often quite marked, the operculum penetrating deeply into it. Shape quotient about 2.5 (2.2—3.0). Stalk quite short, 1—15 µm, mostly about 5 µm.

The adoral zone of the animal protrudes up to 30 µm from its case (more than *P. pusilla*). The operculum is connected to the body of the cell by means of a longer protoplasmic extension than other pyxicolas have.

Substrate: algal filaments

Habitat: freshwater. India and the Tropical Garden of London (Kent, 1881), lake Balaton (Sommer, 1951), Delaware Channel, U.S.A. (Stokes, 1895), and many other localities: Washington, D.C. (Finley & Bacon, 1965), Rumania (Vuxanovici, 1961), etc.

Remarks

Finley & Bacon (1965) have done a fine study on a population of pyxicolas in a shallow pond. They reared the animals in the laboratory and studied their life-cycle. In the abstract of their paper it is stated that they also cultured clones. Unfortunately, detailed information is given only of *P. nolandi*. The other "species" remain therefore taxonomically indistinguishable from *P. pusilla* and *P. carteri* as defined in this paper. I consider *P. nolandi* itself a synomym of *P. carteri*. The only difficulty in so doing is its reported variation which is exceedingly small. It is not specified whether they represent a variation within clonal organisms, in the laboratory aquaria or in the pond where they came from; neither it is stated how many individuals were measured. Therefore, I am not able to discuss why such a small variation was found. I have not studied the preserved specimens which are said to be the type material of the species. According to Carpenter (Smithsonian Institution, Washington) (in agreement with Corliss: personal

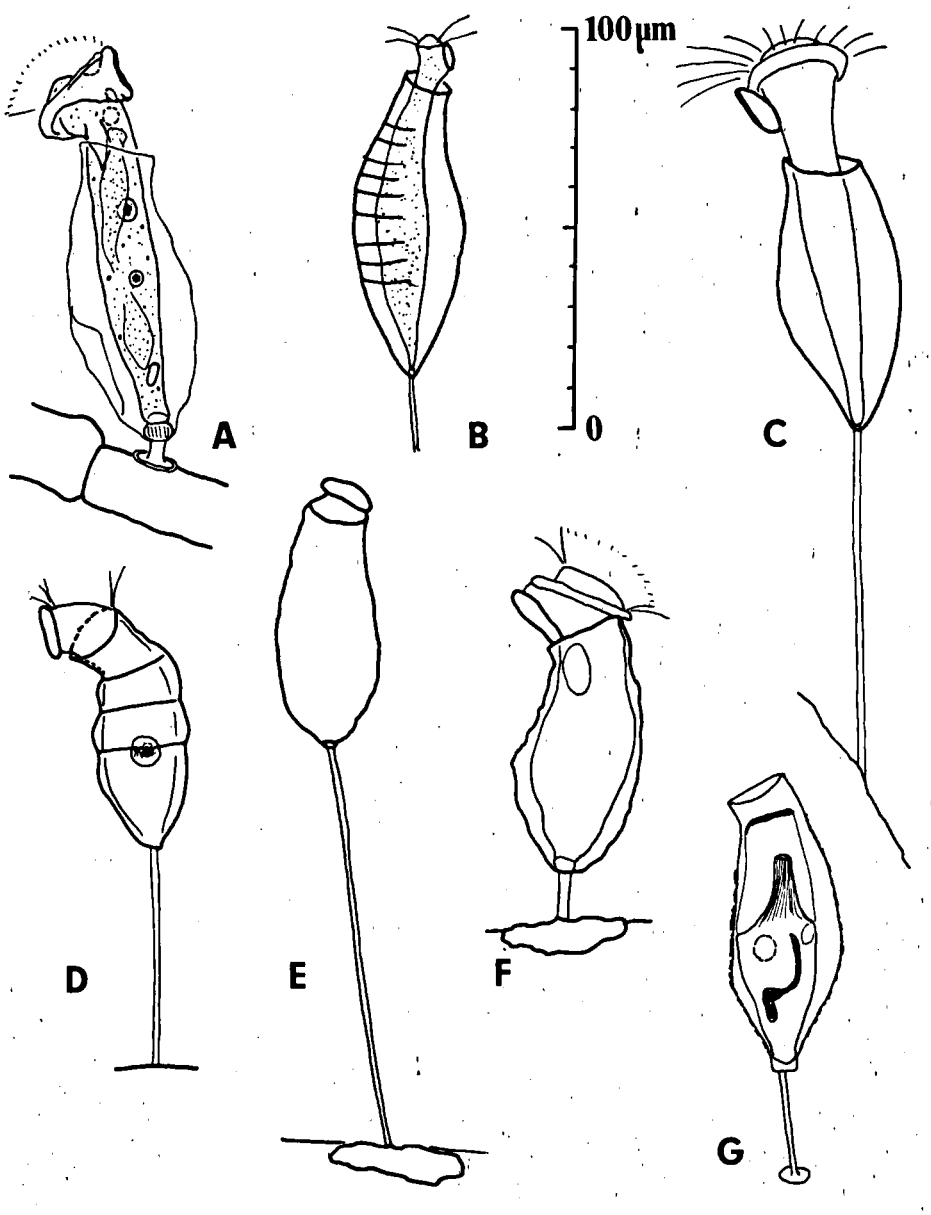

Fig. 5. Some pyxicolas drawn to the same scale, to facilitate comparison. A. *Pyxicola carteri*, found attached to *Cladophora* sp. B. "*P. striata*", after Kellicott, from Kahl, a synonym of *P. carteri*. C. "*Cothurnia operculigera*", now *Pyxicola operculigera*, after Kent (1869). D. *P. operculigera*, after Caspers. E. Individual of the same species, found attached to *Cordylophora* sp. F. Another pyxicola, found near the preceeding one. Note that this second specimen could both be classified as *P. operculigera* or *P. pusilla*, if the substrate is not taken into consideration. G. *P. psammata*, after Hadži.

communication), Finley "never actually got around to depositing his types in the collection".

P. carteri, as defined above, is distinguished from *P. pusilla* by its longer and slender case, and other subtle differences. The organisms seem to prefer algal filaments above other substrates. The author has observed about 20 individuals, attached to *Cladophora* sp., or reed rootlets, from the shallow lake "Naardermeer", in Central Netherlands, and from a park pond in Amsterdam. At this point, the question immediately rises: are the animals selective for the substrate, or does the substrate somehow influence the morphology of the animals? As far as peritrichs are concerned, both questions may be positively answered, depending on the particular case in question. In fact, this is a major taxonomical problem concerning especially botanists, but even more students of sessile animals. Going back to *Pyxicola,* considering the paper of Finley & Bacon, as well as my own observations, it seems that *P. carteri* is really different from *P. pusilla.*

Pyxicola operculigera (Kent, 1869) Kent, 1881

Synonymy

Cothurnia operculigera Kent, 1869, pp. 289—291, pl. 12, figs. 1—4 (from which fig. 5C of this paper is taken).

Pyxicola operculigera Kent, 1881, pp. 725—726, pl. 40, fig. 39; Kahl, 1935, p. 789, fig. p. 788, 5; Kahl, 1933, p. 139, fig. 25.22 (non fig. 20); Caspers, 1950, pp. 256—257, fig. 7 (from which fig. 5D of this paper); Streble & Krauter, 1973, p. 250, fig. p. 251, 4.

Diagnosis

Lorica 45-70 µm long (average 61 µm), 22-35 µm wide, shape quotient 1.7-2.6 (mostly 2.1), transparent when young, brown and opaque when old; corrugated, never clearly annulated, often smooth. Stalk 12-130 µm long (average 80 µm), rectilinear or slightly curved. Adoral zone protruding little from the lorica (10-20 µm); the operculum is held tightly against the cell body.
Substrate: On *Cordylophora* it grows abundantly, but it also has been found on aquatic plants and algae, and sometimes on other vaginicolids.
Habitat: Fresh and brackish waters. Reported from England and Germany.

Remarks

The only distinctive characters of this species are its long stalk and a somewhat smaller lorica than found in related species. The long stalk is the rule, as far the pyxicolas are concerned that are found on *Cordylophora* (Roos, personal communication). I have measured 22 individuals on *Cordylophora* sp., and the variation of stalk length was great, 12 to 105 µm, but in most cases the lorica is shorter than the stalk; the opposite is found in *P. pusilla.*

Pyxicola socialis (Gruber, 1879) Kent, 1881

Synonymy

Cothurnia socialis Gruber, 1879, p. 519 (preliminary presentation); Gruber, 1880, pp. 457—462, pl. 26 figs. 24—27 (fig. 6A of this paper); Mereschkowsky, 1881, pp. 210—211, pl. 12 fig. 3;

Bütschli, 1889, pl. 75 fig. 3; Hamburger & von Buddenbrock-Heidelberg, 1911, p. 141, fig. 181a; Dons, 1922, pp. 67—68, fig. 17 (fig. 6B of this paper); Rhumbler, 1923, fig. 268; Lepsi, 1926, p. 94; Wiersma-Verschaffelt, 1936, p. 37 (record only).

Cothurnia corrugata Davis, 1879, pp. 653—655, pl. 20, figs. 1 (fig. 6E of this paper), 2, 3 in part (not figs. 4—5).

Pyxicola socialis Kent, 1881, p. 728, pl. 40 figs. 16, 30—31; Kahl, 1935, pp. 789—790, fig. p. 788, 3; Kahl, 1933, p. 139, fig. 25.19; Kudo, 1947, p. 691, fig. 325 j; Biernacka, 1963, p. 63, fig. 141 a—b? (misspelled *Pixicola*); Felinska, 1965, p. 238, fig. 26.

Note on synonymy

The paper on *Cothurnia corrugata* was published in October 1879; Gruber's primary report on *Cothurnia socialis* was published more or less simultaneously. Since the name *C. corrugata* has not been used for over 50 years (excluding a brief comment by Kahl, 1935), and *C. socialis* has been used many times since, this last name is to be preferred.

Diagnosis

Lorica 55-120 µm (most authors give values around 70 µm long), 26-36 µm wide. Form factor 1.7-2.6 (usually about 2.2). Rings usually well marked, sometimes just present, rarely absent; neck present. Lorica transparency changes with age from hyaline to opaque brown. Stalk length varies usually between 70 and 150 µm. A short internal stalk is sometimes present. Other characters like *P. pusilla.*

Substrate: algae.

Habitat: sea water. Reported from the North Sea, at a variety of localities.

Remarks

Biernacka (1963) found pyxicolas within the salinity margins 3-35‰, and named them altogether *P. socialis.* His two drawings show short-stalked specimens. It is difficult to classify them, because the figures are not explained. Caspers (1950) reports on *P. operculigera* with clearly annulated cases, and therefore synonymizes it with *P. socialis.* Something similar has been done by Precht (1935). The question of how pronounced the annulation is remains of course partly subjective; I have prefered to retain both *P. operculigera* and *P. socialis* as species, mainly on the basis of my own observations.

Pyxicola socialis forma **longipes** Stiller, 1939

Synonymy

Pyxicola socialis var. *longipes* Stiller, 1939, pp. 449—450, fig. 24 (fig. 6C of this paper).

Diagnosis

As *P. socialis,* but with longer stalk (140—260 µm), and attached to *Hydralmania falcata* (then the longest stalks are found) or to *Mytilus edulis.*

Pyxicola psammata Hadži, 1940

Synonymy

Pyxicola psammata Hadzi, 1940, pp. 133—135, figs. 2 and 8 a—s (fig. 5G of this paper); Stiller, 1971, p. 220, fig. 133F.

Diagnosis

Lorica 75—85 µm long, 23—35 µm wide; shape quotient 2.4—3.3 (average 2.9), smooth or very slightly ondulated; no constriction beneath the lorica's aperture, or a very slight one. Stalk 15—40 µm long (average 27 µm); operculum diameter about 7 µm.

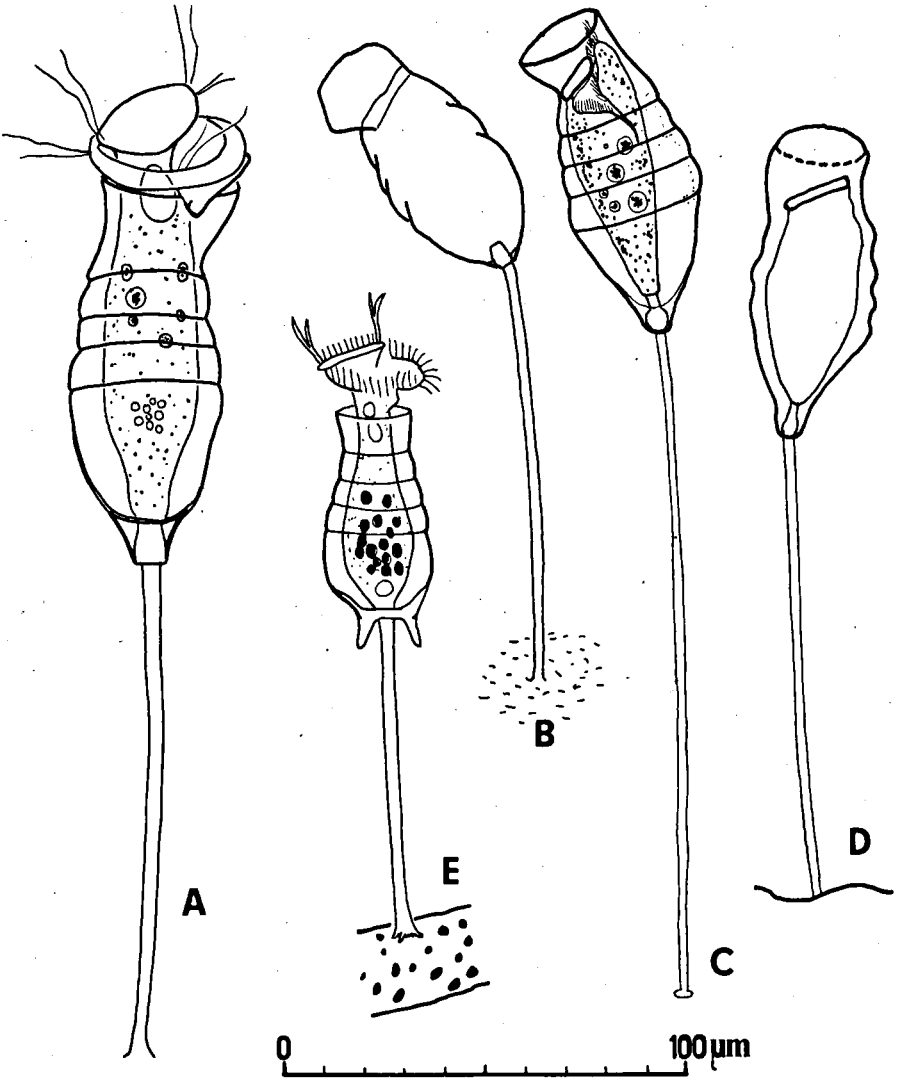

Fig. 6. Some pyxicolas drawn on the same scale, to facilitate comparison. All belong to the species *Pyxicola socialis*, but they are named here by their original names for the sake of clarity. A. "*Cothurnia socialis*", after Gruber. B. "*C. socialis*", after Dons. C. "*P. socialis* var. *longipes*", after Stiller, 1939. D. An individual attached to *Enteromorpha* sp. Note the short stalk inside the lorica. E. "*Cothurnia corrugata*", after Davis.

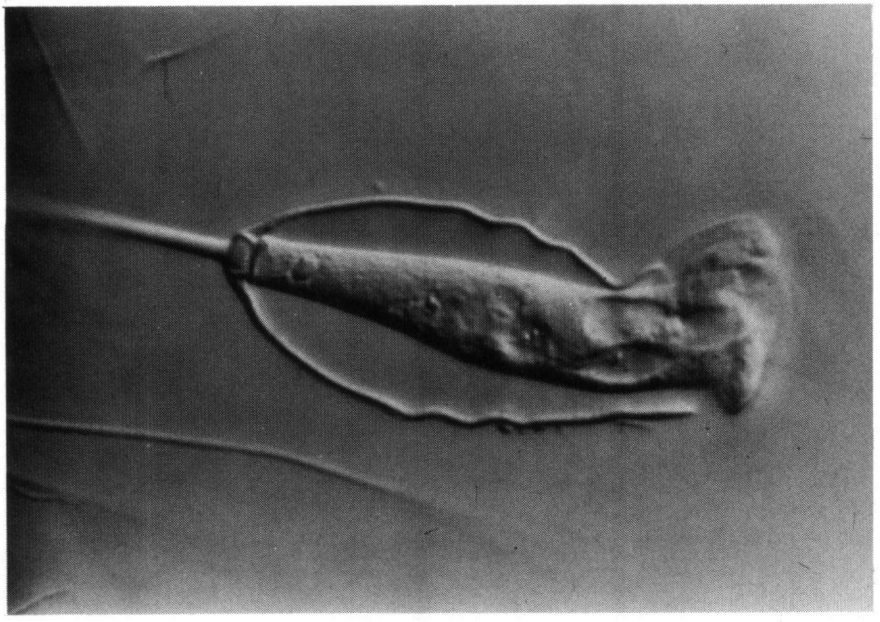

Fig. 7. *Pyxicola pusilla*, attached to a reed rootlet, photographed while feeding. The lorica (66 µm long) is thin and transparent. Contractile vacuole and operculum may be seen at the right side of the animal. The eytopharinx and some feeding vacuoles, at its left. The micronucleus can be seen at the aboral end of the cell body.

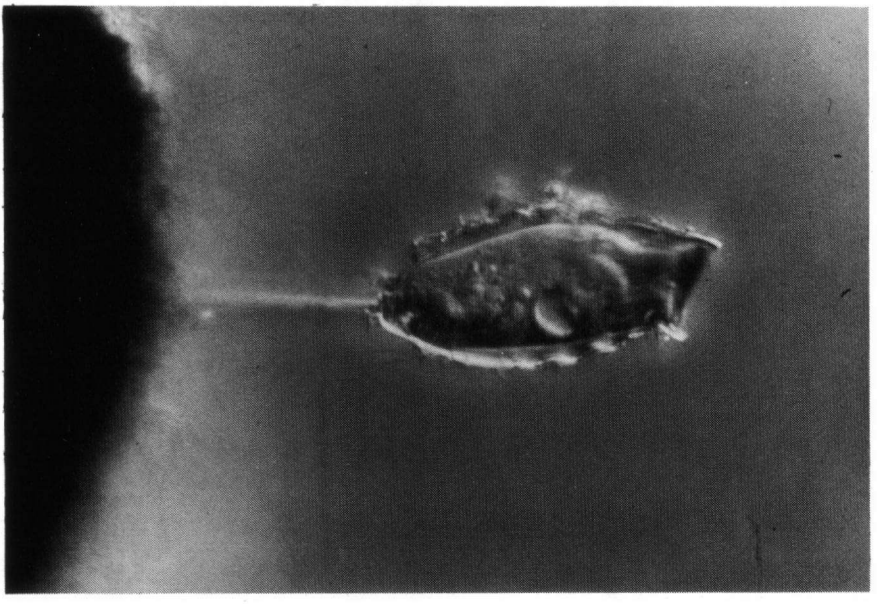

Fig. 8. Another specimen of *Pyxicola pusilla*, also attached to a reed rootlet, photographed while contracted. The case (77 µm long) is thick and yellow-brown. The contractile vacuole can be distinguished.

Substrate: the cave-dwelling *Microlistra spinosissima* (Isopoda, Crustacea).
Habitat: found only once, in Yugoslavia.

Remarks

This species is distinct mainly because of its substrate. The original description is extensive, and it is accompanied by one photograph and one drawing, figuring together 20 individuals. The study was made on fixed specimens all retracted in their cases.

ANNOTATED LIST OF NOMINAL SPECIES

The following list contains the described "species" with their original names. An effort has been made to make the list complete, and the references accurate. After each nominal species a reference is given to the name of the species of which it is considered to be a synonym by the author. More information about the nominal species in question is to be found there.

Caulicola valvata Stokes, 1895 is, in the author's opinion, a synonym of *P. pusilla* (see the comments on the genus *Pyxicola* and its limits).
Cothurnia corrugata Davis, 1879 is a reasonably well described and figured species. From the figures of the original paper (plate 20), only ns. 1—2 and part of 3 are pyxicolas; the other drawings represent some species of *Cothurnia.* Kent (1881, pp. 728—729) and Bütschli (1880, p. 185) deprecate Davis' paper on grounds that I cannot understand. Both Kent and Butschli refer correctly to the paper in question (Kent spells Davies instead of Davis) but they write, among other criticisms, that Davis considered his animals to be rotifers. But the name rotifer is not used once in Davis's paper. I assume therefore that there has been a misunderstanding. See further *P. socialis*, of which I believe *C. corrugata* is a synonym.
Cothurnia furcifer Hutton, 1878 is a synonym of *P. pusilla.*
Cothurnia ligiae Cuénot, 1891 is a well-defined taxon. See *P. ligiae.*
Cothurnia operculigera Kent, 1869 is often considered to be the first described pyxicola-species, but it is not. *C. pyxidiformis* was the first one, and *C. pusilla* the second. See further *P. operculigera.*
Cothurnia pusilla Wrześniowski, 1866 has been described three times by the same author. The first one is only a Latin diagnosis. The second (1867) gives an extensive description in Polish, and a figure, which is not of a pyxicola. The third one (1870) is a German translation of the second paper, but includes a figure (fig. 3A of this paper) which had not been published previously. In all three papers the pyxicolas are considered to be old cothurnias which have grown an operculum and therefore they are lumped together with real cothurnias. See further *P. pusilla.* Kent (1881) writes about *P. pusilla* without any reference to its original author. I do not understand why he did not; he just could not have overlooked the original publication, using as he did the epitheton "pusilla".

Cothurnia pyxidiformis D'Udekem, 1864 is possibly a distinct species. See under *Pyxicola pyxidiformis.*
Cothurnia socialis Gruber, 1879 was first named and shortly described; the full description came a year later (Gruber, 1880). See further *P. socialis.*
Cothurniopsis Entzii Stiller, 1931 is a well-defined species. See under *Pyxicola entzii.*
Pachytrocha cothurnoides Kent, 1881 is in my opinion a *Pyxicola pusilla* with fallen operculum. For a discussion see under the headings "Synonymy" (of the genus *Pyxicola*) and *"Pyxicola pusilla".*
Pixicola socialis as written by Biernacka, 1963, is a misspelling.
Pyxicola affinis Kent, 1881, is most probably a synonym of *P. pusilla.*
P. annulata Leidy, 1882 is a synonym of *P. pusilla.* See also *P. carteri. P. annulata* Leidy is synonym and homonym with *P. annulata* Grenfell, 1884.
P. carteri Kent, 1881 is in this paper considered a distinct species.
P. carteri forma *constricta* Sommer, 1951, was regarded by its author as an extreme variation of *P. carteri.* Nusch (1971) names with the same name some pyxicolas found by him. They are probably *P. pusilla.*
P. eforiana Tucolesco, 1962 is a synonym of *P. pusilla.*
P. limbata Kahl, 1935 was described shortly before *P. limbata* Stiller, 1938. Stiller regarded it as a new species mostly because of its excentrically situated stalk. Otherwise it resembles very much *P. carteri* and the like. I do not recognize it as a distinct species.
P. nodosa Vuxanovici, 1961 is described and figured from a single specimen. The figure is bad, and the description too short. It is a synonym of *P. carteri,* most probably.
P. nolandi Finley & Bacon, 1965 is the only pyxicola extensively described in the literature. Life-cycle, variation, morphological details, all are explained and figured. Nevertheless, *P. nolandi* is probably a junior synonym of *P. carteri* (see there); anyway, it is identical with *P. constricta* Stokes, though perhaps somewhat larger.
P. psammata Hadži, 1940, is an epizoic, freshwater species.
P. striata Kellicott, 1884 is regarded by Stokes (1888b, p. 259) as a synonym of *P. annulata.* Note that Kahl's text figure (1935, p. 788, fig. 19, fig. 5B of this paper) is provided with a wrong footnote. I consider it a synonym of *P. carteri.*

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escaped my attention. Since I have not followed all the suggestions they made to me, the full responsibility remains mine. I am grateful also to the Laboratory for Electron Microscopy, University of Amsterdam, for the facilities given to me while preparing the manuscript, and to Mrs. Appel-Rijfkogel for typing it.

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