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Redescription of Three Testate Amoebae (Protozoa, Rhizopoda) from a Caucasian Soil: *Centropyxis plagiostoma* BONNET & THOMAS, *Cyclopyxis kahli* (DEFLANDRE) and *C. intermedia* KUFFERATH

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Summary: The shell morphologies of *Centropyxis plagiostoma* BONNET & THOMAS, 1955, *Cyclopyxis kahli* (DEFLANDRE, 1929) and *C. intermedia* KUFFERATH, 1932 are redescribed using light and scanning electron microscopy and morphometry. The species are redefined, including literature data, and guide lines are suggested for species recognition in testate amoebae. High variability of most morphometric and morphological shell characters is evident, suggesting that the group is greatly oversplit; many species and varieties described are very likely based on alterations occurring during shell aging and decomposition. A variability of up to 100–150%, i.e. that the biggest individuals are twice as large as the smallest, is common if field populations from different biotopes and areas are compared. Thus, morphometric criteria are of very limited taxonomic value and should be used for species separation only if very distinct and/or accompanied by at least one reliable morphological character. The following synonymy is suggested for *C. kahli: C. kahli cyclostoma, C. kahli obliqua, C. dispar, C. dulcis, C. insolitus, C. profundistoma;* and for *C. intermedia: C. gigantea, C. bathystoma, C. kahli grandis.*

Key Words: Caucasia; *Centropyxis; Cyclopyxis;* Morphology; Rhizopoda; Soil protozoa; Testacea; Testate amoebae.

Introduction

Soil testate amoebae are increasingly used as bioindicators (FOISSNER 1987, 1994). However, unknown variability of most species and poor original descriptions often make a proper identification difficult. Thus, we continue our series of redescriptions of soil dwelling testaceans by means of morphometric analysis and scanning electron microscopy (LÜFTENEGGER & FOISSNER 1991; LÜFTENEGGER et al. 1988; SCHÖNBORN et al. 1983, 1987).

Material and Methods

Centropyxis plagiostoma, Cyclopyxis kahli and *C. intermedia* were collected on July 1989 from the upper soil layer (0–3 cm; mull humus) of a small deciduous forest in east Caucasus (Dagestan, Kurush district, surroundings of Mitzakh village), mainly composed of *Betula, Alnus* and *Salix* (= Krivolesje in Russian). The forest is located among high-grass meadows at the timberline (1800 m NN). The soil developed on limestone, pH = 6.6. See KORGANOVA (1994) for more detailed site description and complete list of species found in this area. Methods used for morphometric analysis, scanning electron microscopy and construction of the "ideal individuum" have been described in detail by SCHÖNBORN et al. (1983) and LÜFTENEGGER et al. (1988). All investigations were performed on empty shells of unknown age. A preliminary inspection of the sample revealed two rather distinct size classes in *C. plagiostoma* and three in *C. kahli.* These classes were sampled and investigated separately, paying particular attention to extreme specimens, i.e. especially large or small in size. The medium size class is thus underrepresented in the morphometric analysis. The largest size class (mean diameter 174 µm) of *C. kahli* was later recognized as a distinct species, *C. intermedia.* The ordinary (smallest) size class (mean diameter 89 µm) constituted the main portion of the *Cyclopyxis* specimens found, viz. about 95%.

Results

Centropyxis plagiostoma BONNET & THOMAS, 1955 (Figs. 1–16, Table 1)

The two size classes selected do not differ morphologically and are thus described together. All parameters measured vary isometrically, i.e. are about twice as large in the large size class as in the small one (Table 1).
Shell almost circular in ventral and dorsal view, usually slightly broader than long, about half as deep as broad, anterior portion more distinctly flattened than posterior; greyish or colourless, not transparent; composed of flat quartz particles more rough on posterior and dorsal than on ventral surface, which appears rather smooth and covered by thin organic layer (Figs. 13, 15). Pseudostome in anterior half of ventral surface, i.e. excentric, transverse-elliptical to almost circular, with irregular edge often completely or partially covered by knobby quartz particles ("dents"); distinctly invaginated, preoral portion apruptly curved, postoral surface flat and gradually inclined (Figs. 1, 3, 6, 12, 13, 15, 16).
Coefficients of variation low for characters 1 and 2, rather high for others, especially for characters 3 and 4, increase considerably, i.e. to 25– 37%, if both size classes are combined (Table 1).

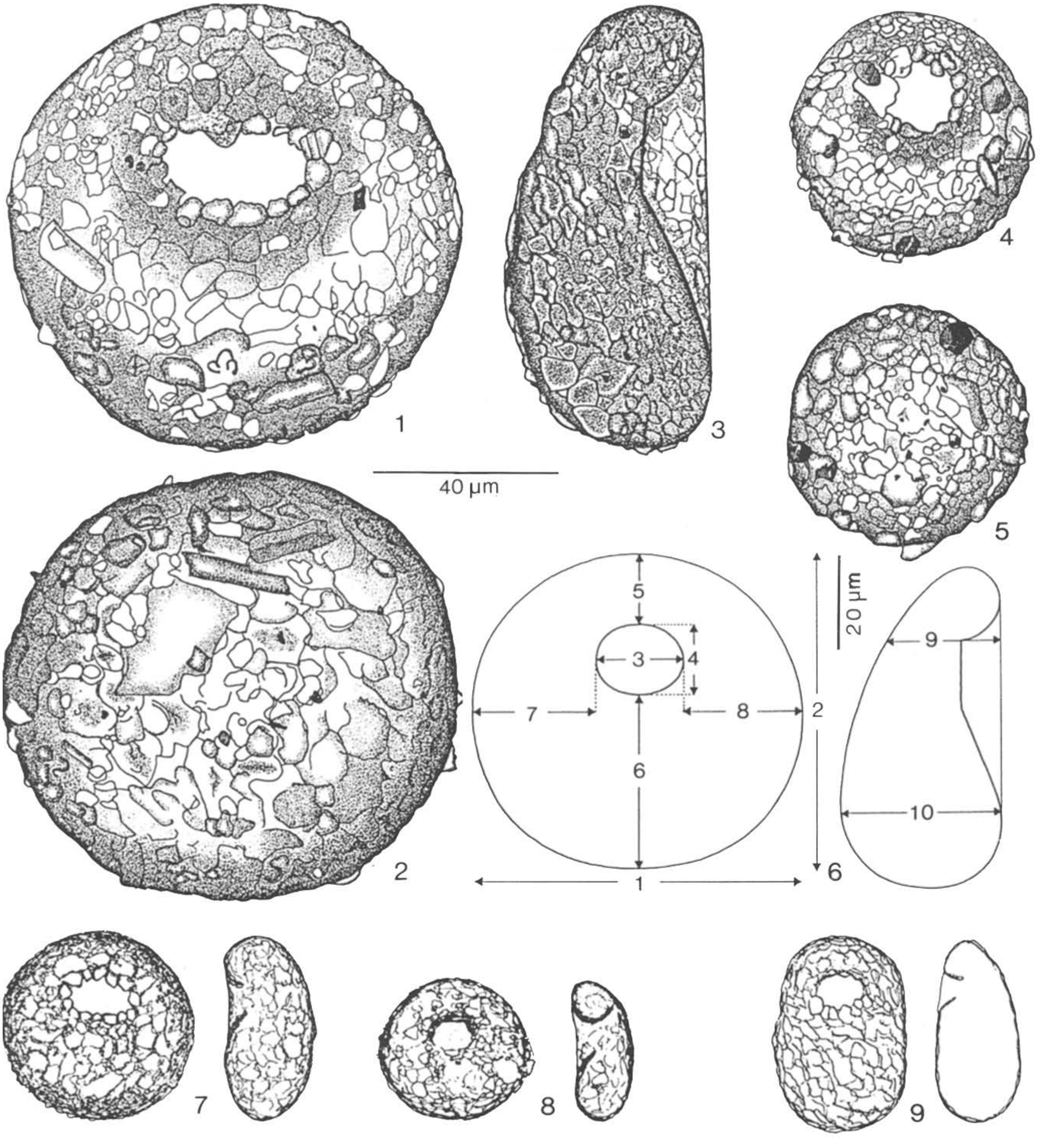
Cyclopyxis kahli (DEFLANDRE, 1929) DEFLANDRE, 1929 (Figs. 17–21, 23–29, 47–60, Tables 2–4)

The two size classes selected have a very similar morphology and are thus described together, the most conspicuous difference being the specialized xenosomes around the pseudostome, usually lacking in the large-sized specimens. All parameters measured vary isometrically, i.e. are larger in the large size class than in the small one (Table 2).

Shell usually circular in ventral and dorsal view, very rarely slightly elliptical, more than hemispherical (depth/diameter = 0.62 in the small and 0.71 in the large size class), lateral sides evenly rounded, in large size class sometimes almost parallel making shells barrel shaped (Fig. 29), dorsal side usually slightly flattened and often very uneven by large, protruding assortement of mineral particles (Figs. 19, 24, 25, 29); greyish to dark-brown, opaque; composed of xenosomes more distinct and rough on dorsal surface than on smoother ventral half, which appears covered by thin, organic layer (Figs. 26–28). Pseudostome in or near centre of ventral surface, distinctly and evenly invaginated, perfectly or roughly circular, with edge completely or partially covered by rather regularly arranged, roundish xenosomes ("dents") in about 60% and 10% of specimens from small and large size class, respectively (Figs. 17, 25–28); often plugged by detritus giving impression of very deep pseudostome invagination.
Coefficients of variation low for characters 1, 2 and 6, rather high for others, especially in large size class (Table 2).

Cyclopyxis intermedia KUFFERATH, 1932 (Figs. 22, 30–46, Tables 2, 3)

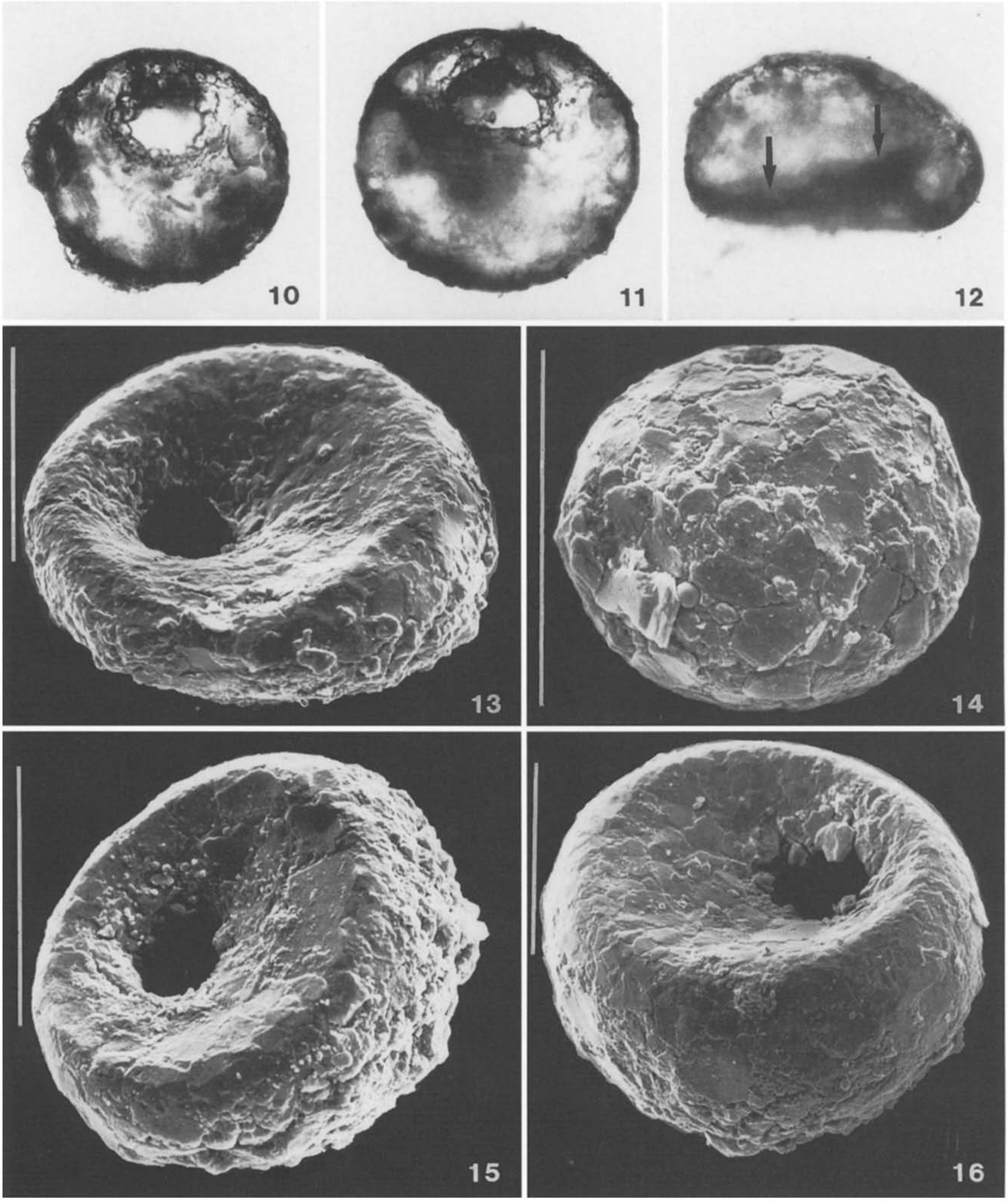
This species is very similar to *C. kahli* and distinguished from that species mainly by its large size. Thus, we provide only a drawing of the ideal individuum (Fig. 22) and some light and scanning electron micrographs (Figs. 30–35). The general aspect is shown in the original description (Figs. 36–38) and the figures of the synonyms (Figs. 39–46).
Shell circular in ventral and dorsal view, more than hemispherical (depth/diameter = 0.72), lateral and dorsal sides evenly rounded, rarely slightly irregular by protruding xenosomes; dark-brown to black at low magnification due to large size, opaque; composed of small to medium-sized quartz particles very flat and covered by thin organic layer in ventral half of shell which is thus usually very smooth (Figs. 30, 33, 34). Pseudostome in centre of ventral surface, distinctly and evenly invaginated, circular, edge irregular because formed by ordinary body xenosomes and never by specialized, knobby particles as in *C. kahli* (Figs. 30, 33, 36); often partially or completely closed by irregular, membranoid structure, possibly detritus and chitinoid material (Fig. 34), as described in *C. lithostoma,* very likely a junior synonym (see discussion).
Coefficients of variation low for characters 1, 2, 5 and 9, rather high (10–20%) for others. However, this is at least partially caused by measurement problems, especially for characters 5–8; the large shells are difficult to orientate because of the hemispherical dorsal surface.



Figs. 1–6. *Centropyxis plagiostoma.* Figs. 1–5 drawn to scale to show differences between the two size classes selected. – **1–3.** Ventral, dorsal and lateral view of specimen from large size class. – **4, 5.** Ventral and dorsal view of specimen from small size class. – **6.** Ventral and lateral view of ideal individuum constructed from median values of all specimens from small and large size class. Numbers designate characters measured (cp. Table 1).

Figs. 7, 8. Ventral and lateral views of *Centropyxis plagiostoma* and *C. plagiostoma* var. *terricola* according to the original descriptions by Bonnet & Thomas (1955). Size 64–95 µm and 58–61 µm, respectively.

Fig. 9. Ventral and lateral view of *Centropyxis plagiostoma* var. *oblonga* according to the original description by Chardez (1962). Length 80–85 µm.



Figs. 10–16. *Centropyxis plagiostoma.* – **10–12.** Ventral and lateral light microscopical views of typical specimens having knobby xenosomes („dents") around shell aperture. Arrows mark flat and gradually invaginated postoral ventral surface. – **13–16.** Ventral and dorsal (Fig. 14) scanning electron microscope views of small (Figs. 14, 15) and large (Figs. 13, 16) sized specimens. Note that specimens shown in Figs. 13, 15 lack dents around oral aperture. The ventral surface is smoother than the dorsal. Bars 40 μm.

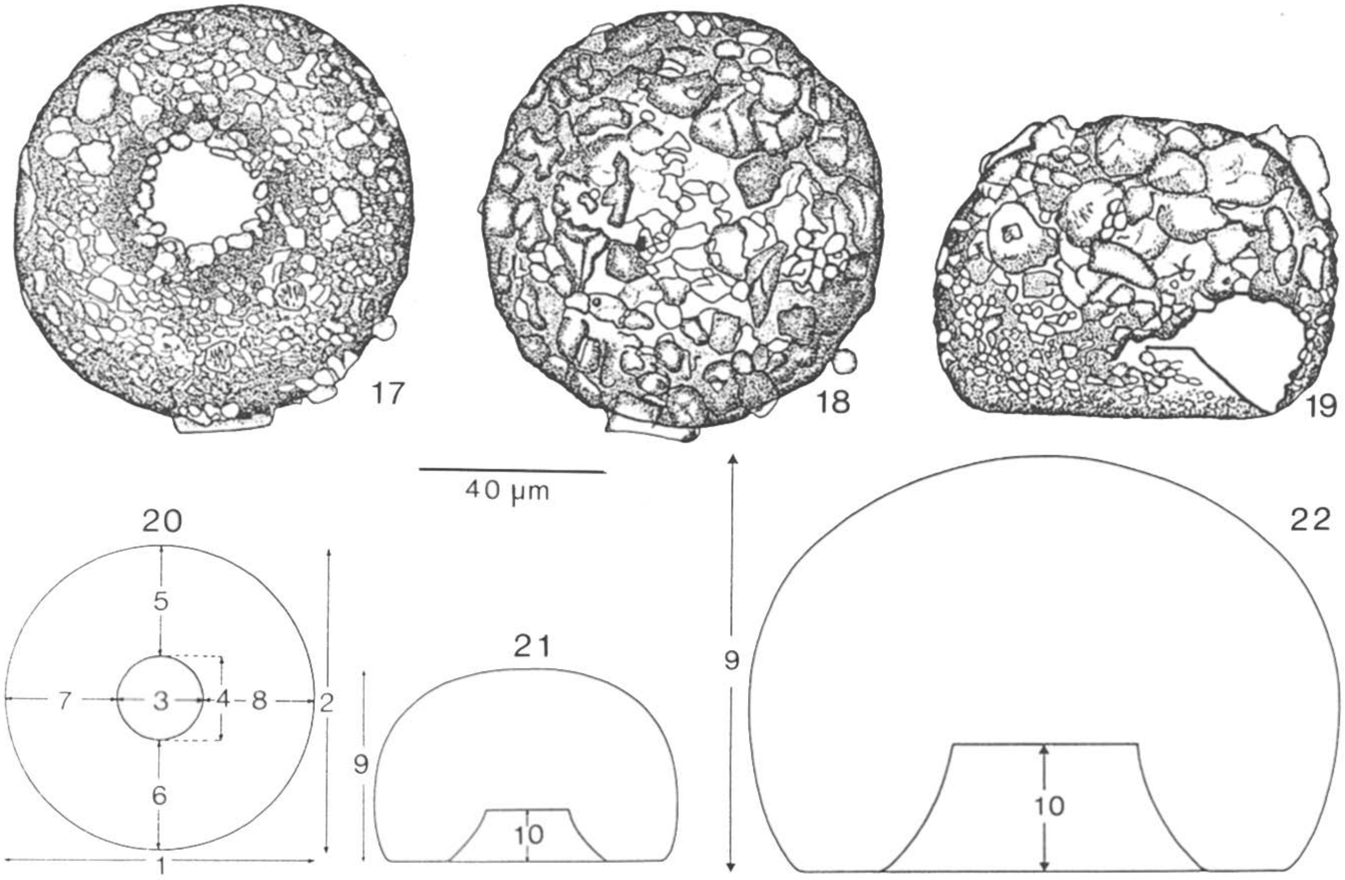
Table 1. Morphometric characteristics from *Centropyxis plagiostoma*. Upper line: large size class; middle line: small size class; lower line: large plus small size class. Measurements in µm. See Fig. 6 for character designation.

Character	$\bar{x}$	M	SD	$SE_{\bar{x}}$	CV	Min	Max	n
(1)	102.67	105	9.98	2.58	9.72	80	120	15
	56.93	55	5.33	1.38	9.35	50	70	15
	79.80	75	24.55	4.48	30.76	50	120	30
(2)	97.20	98	9.95	2.57	10.24	75	115	15
	54.93	55	4.88	1.26	8.88	45	65	15
	76.07	70	22.83	4.17	30.02	45	115	30
(3)	28.33	30	4.88	1.26	17.22	15	35	15
	15.93	15	1.79	0.46	11.24	15	20	15
	22.13	20	7.27	1.33	32.83	15	35	30
(4)	16.47	15	3.11	0.80	18.91	12	25	15
	11.73	10	2.19	0.57	18.64	10	15	15
	14.10	15	3.58	0.65	25.36	10	25	30
(5)	25.53	25	3.28	0.84	12.81	20	30	15
	12.53	12	2.53	0.65	20.20	10	17	15
	19.03	18	7.21	1.32	37.87	10	30	30
(6)	53.13	55	5.93	1.53	11.15	42	60	15
	30.00	30	3.27	0.85	10.91	25	35	15
	41.90	40	12.81	2.34	30.58	25	60	30
(7)	37.40	35	4.45	1.15	11.95	30	45	15
	19.47	20	3.16	0.82	16.23	12	25	15
	28.43	28	9.88	1.80	34.75	12	45	30
(8)	37.73	40	5.54	1.43	14.67	30	45	15
	22.13	20	4.96	1.28	22.39	15	35	15
	29.93	30	9.47	1.73	31.62	15	45	30
(9)	35.23	37	4.57	1.18	12.97	25	43	15
	19.15	18	2.00	0.55	10.41	18	25	13
	27.77	28	8.90	1.68	32.07	18	43	28
(10)	47.83	50	5.50	1.42	11.50	37	55	15
	27.15	25	3.21	0.89	11.82	23	31	13
	38.23	38	11.43	2.16	29.89	23	55	28

Discussion

Remarks on species separation in testate amoebae

The species problem in testate amoebae has been repeatedly and controversially discussed by, e.g. CASH et al. (1919), HOOGENRAAD & DE GROOT (1937), HEAL (1963), MEISTERFELD (1979), SCHÖNBORN & PESCHKE (1988, 1990) and MEDIOLI et al. (1990). The underlaying mechanisms of variation were updated by SCHÖNBORN (1992) and SCHÖNBORN & PESCHKE (1990). However, generally accepted conclusions were not reached, although all authors who did detailed morphometry emphasized the high variability of metric shell characters and thus doubted the validity of many species, varieties and forms described. Our former studies (LÜFTENEGGER & FOISSNER 1991; LÜFTENEGGER et al. 1988; SCHÖNBORN et al. 1983, 1987) and the present investigations follow this line and provide evidence for the view held by MEDIOLI et al. (1990) that "the vast majority of species used in the literature are hopelessly oversplit".



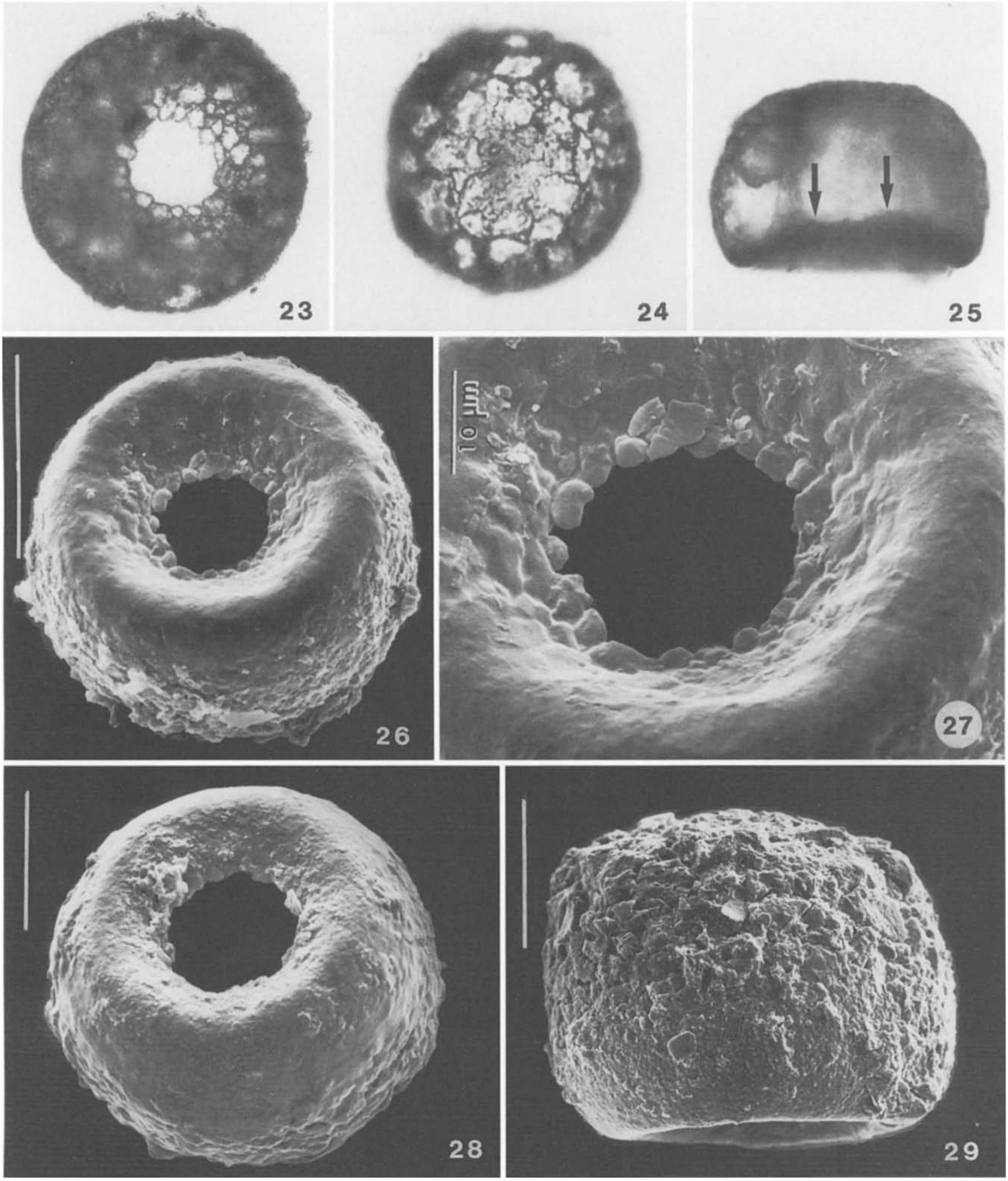
Figs. 17–21. *Cyclopyxis kahli.* – **17–19.** Ventral, dorsal and lateral view of specimen from small (ordinary) size class. – **20, 21.** Ventral and lateral view of ideal individuum constructed from median values of specimens from small size class. Numbers designate characters measured (cp. Table 2).

Fig. 22. *Cyclopyxis intermedia,* lateral view of ideal individuum constructed from median values shown in Table 2. Drawn to same scale as Figs. 20, 21 of *C. kahli* to show size differences.

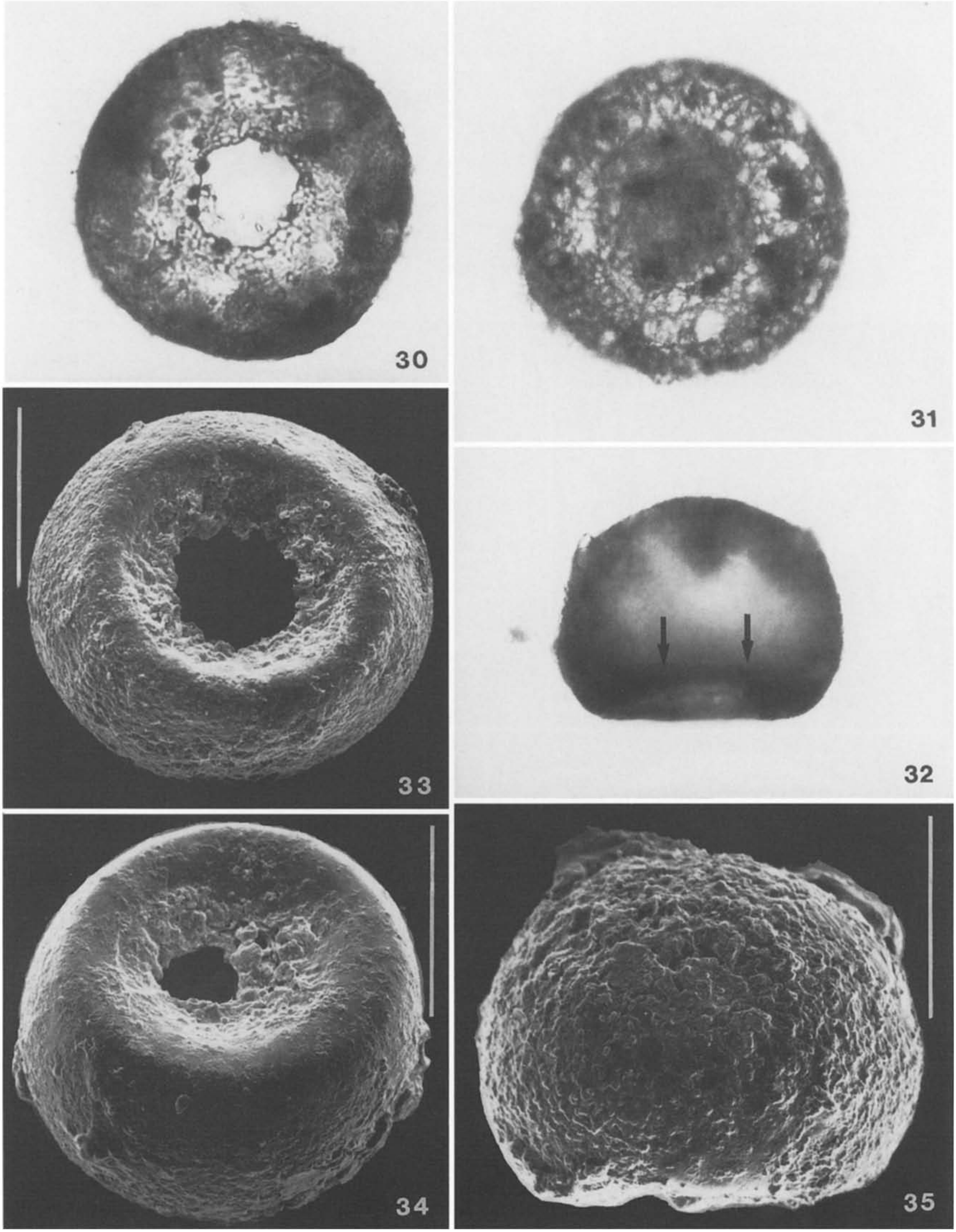
Recently, SCHÖNBORN & PESCHKE (1988) suggested a combination of ecological and morphometrical criteria for defining testate amoebae species, viz. that closely related forms possess species status if they are homotopic (belonging to the same taxocene), significantly different in quantitative characters, and the frequency analysis of different shell characters yields bell-shaped (normally distributed) curves.

However, later SCHÖNBORN (1992) relieved these strict criteria by demanding that they must be proved in clonal cultures: "The clones should not produce individuals of the other forms for over a year, otherwise the forms under investigation belong to a polymorphic species, especially if it is possible to alternate the forms". Unfortunately, the clonal criterion is difficult to apply because most testaceans, especially those from soil, are not easily cultivated.

We cannot provide the reader with a ready made solution to the problem. However, some practical advice might help do avoid oversplitting of taxa simply because of slight size and shape differences: (1) Never describe or redescribe a testacean taxon without providing detailed morphometric data; (2) If you separate taxa mainly by morphometric criteria, the distances between the main characters should be very distinct, as, e.g., in *Cyclopyxis kahli* and *C. intermedia* (Tables 2, 3). Study the literature carefully to be sure that intermediate populations have not (yet) been described. Keep in mind that it is impossible to prove a species mathematically (statistically); (3) Individuals of field populations very likely belong to the same species if the coefficients of variation of the main metric shell characters (e.g. shell and pseudostome size) do not exceed 30–50%, which equals a difference of about 100–200%, depending on the distribution of values. These limits were deduced from our previous and the present inve-



Figs. 23–29. *Cyclopyxis kahli.* – **23–25.** Ventral, dorsal and lateral light microscope views of specimens from small (ordinary) size class having knobby xenosomes („dents") around shell aperture and large quartz particles on dorsal surface. Arrows mark invaginated pseudostome. – **26, 27.** Ventral scanning electron microscope view of specimen from small size class. Note knobby xenosomes („dents") around shell aperture and smooth ventral surface. – **28, 29.** Ventral and lateral scanning electron microscope views of specimens from large size class. Dents around shell aperture are lacking and sides are almost parallel making shell barrel-shaped rather than hemispherical. Bars 40 µm, if not indicated otherwise.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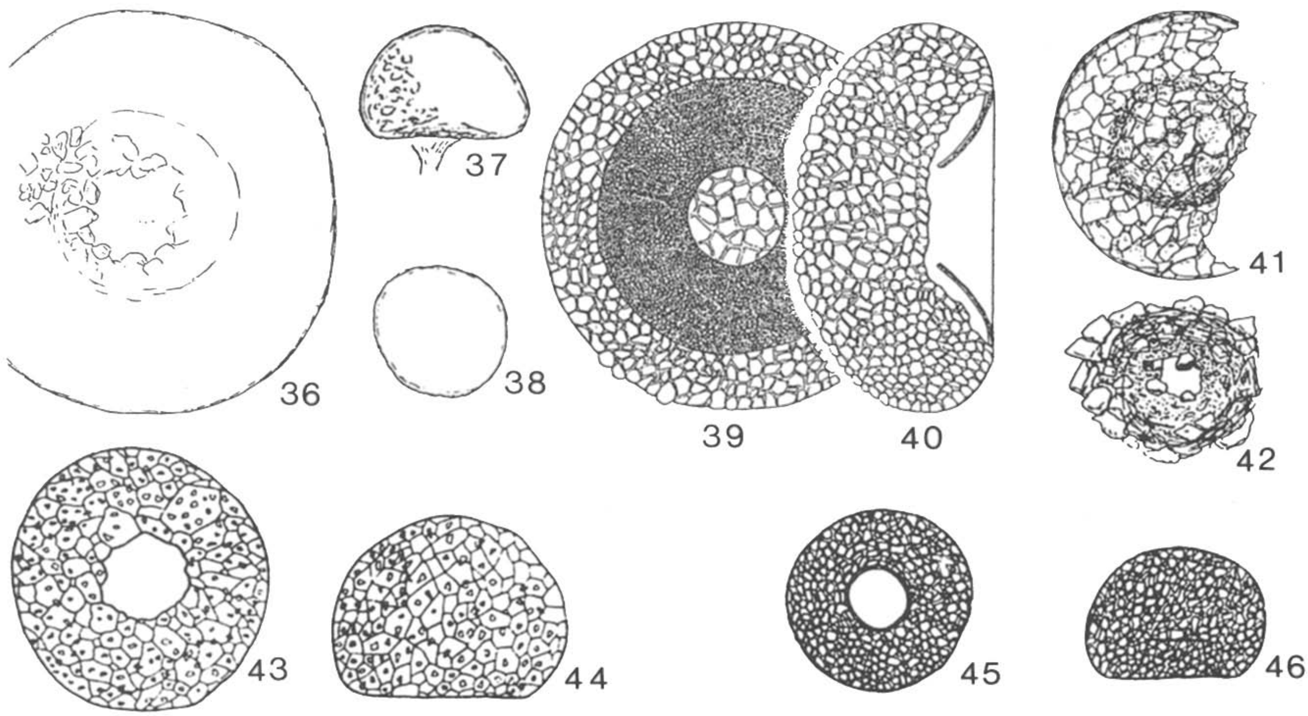


Figs. 36–46. *Cyclopyxis intermedia* and its synonyms. – **36–38.** Original figures of *C. intermedia* (from KUFFERATH 1932), showing specimens in ventral (Fig. 36), lateral (Fig. 37) and dorsal (Fig. 38) view; diameter 210–220 µm. The specimen shown in Fig. 37 has extended a lobopodium. – **39, 40.** Ventral and lateral view of *C. gigantea* (from BARTOS 1963); diameter up to 200 µm. Note that BARTOS figured the smooth and invaginated area of the ventral surface highly schematically, giving the shell a rather unusual appearance (cp. Figs. 55, 56). – **41, 42.** Ventral views of shell and pseudostome area of *C. lithostoma* (from BONNET 1974); diameter $\bar{x}$ 152 µm (n = 20). – **43, 44.** Ventral and lateral view of *C. kahli* var. *grandis* (from CHIBISOVA 1967); diameter 180–230 µm. – **45, 46.** Ventral and lateral view of *C. bathystoma* (from CHIBISOVA 1967); diameter 150 µm.

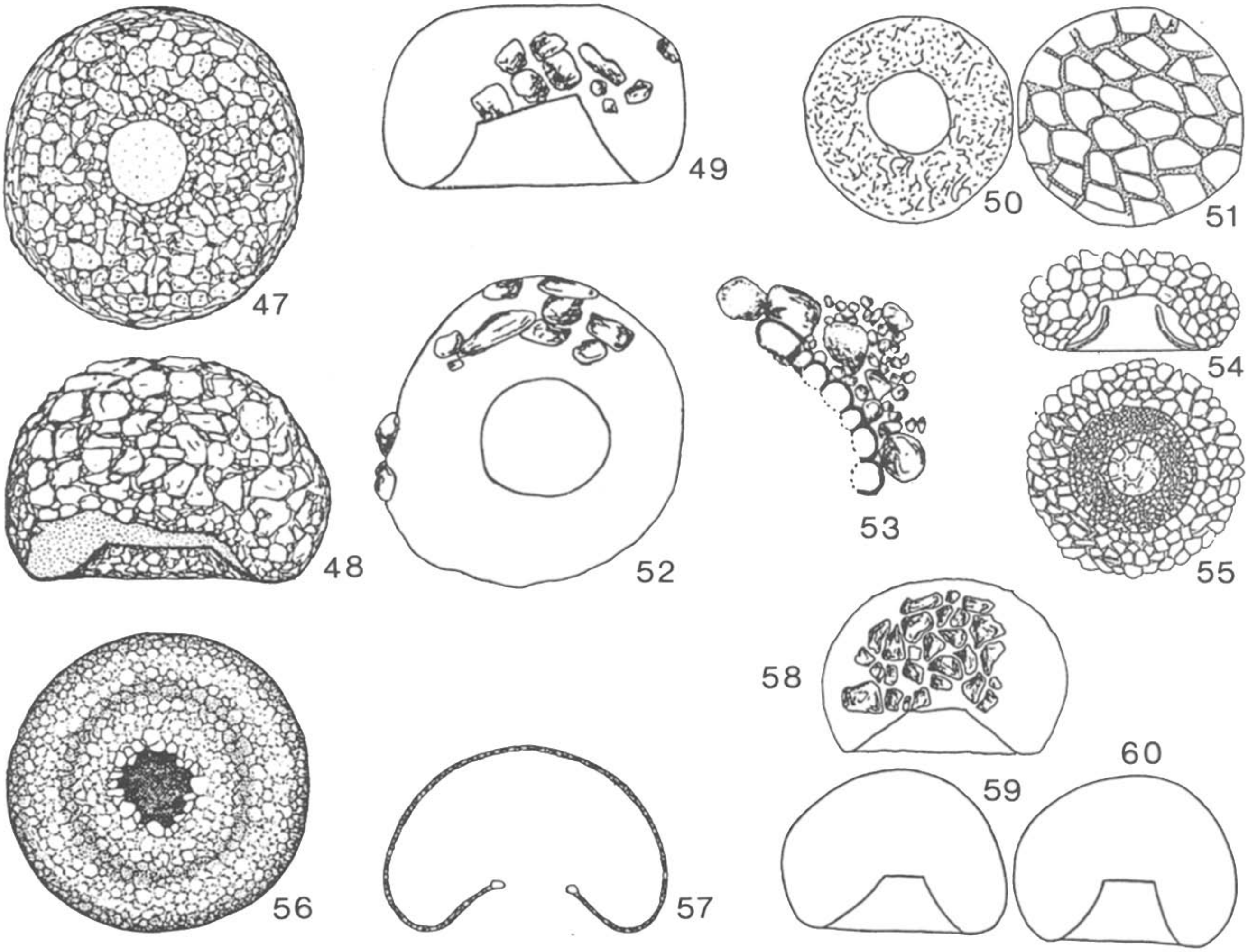
stigations (Tables 1,3) as well as from literature data (HEAL 1963; HOOGENRAAD & DE GROOT 1937; MEISTERFELD 1979, and others). They agree with data from loricate ciliates (e.g. KRALIK 1961); (4) Try to find and to quantify distinct qualitative characters (e.g. apertural bridges) which are still more reliable than morphometric characteristics.

Centropyxis plagiostoma

Centropyxis plagiostoma is most frequent in rich, calcareous rendzina soils and indicates circumneutral pH conditions and mull humus (BONNET 1989; FOISSNER 1987; SCHÖNBORN 1973). BONNET (1989) found it in 456 (22%) out of 2057 soil, litter and moss samples investigated, and AESCHT & FOISSNER (1989) recorded it from many soils in Austria. Despite its commonness and well studied ecology the morphology and variability of *C. plagiostoma* are poorly explored. The original description and later records provide, e.g., only extreme values for test and pseudostome size. The same applies to the two varieties described (BONNET & THOMAS 1955; CHARDEZ 1962).

Our observations agree largely with the original description. The most distinctive feature of *C. plagio-*

Figs. 30–35. *Cyclopyxis intermedia.* – **30–32.** Ventral, dorsal and lateral light microscope views of typical specimens. The shell aperture is irregularly circular and deeply invaginated (arrows). – **33–35.** Ventral and lateral scanning electron microscope views showing smooth ventral and rough dorsal half of shell. Note that pseudostome of specimen shown in Fig. 34 is almost closed by membranoid structure covered with irregular particles; such specimens closely resemble *C. lithostoma.* Bars 80 µm.



Figs. 47–60. Synonyms of *Cyclopyxis kahli.* – **47, 48.** Ventral and lateral view of *C. kahli* var. *cyclostoma* (from BONNET & THOMAS 1960a); diameter 80–100 µm. – **49.** Lateral view of *C. kahli* var. *obliqua* (from DECLOITRE 1969); diameter 75 µm. – **50, 51.** Ventral and dorsal view of *C. dispar* (from DECLOITRE 1965); diameter 55–60 µm. – **52, 53.** Ventral view of shell and pseudostome of *C. insolitus* (from DECLOITRE 1969); diameter 70 µm. – **54, 55.** Lateral and ventral view of *C. profundistoma* (from BARTOS 1963); diameter 85 µm. Note that BARTOS figured the smooth and invaginated area of the ventral surface highly schematically, giving the shell a rather unusual appearance (cp. Figs. 39, 40). – **56, 57.** Ventral and lateral view of *C. dulcis* (from COUTEAUX & MUNSCH 1978); diameter 108–117 µm. – **58–60.** Lateral views of *C. eurystoma* var. *stenostoma* (from DECLOITRE 1953, 1956); diameter 64–70 µm.

stoma is its almost centrally located pseudostome which lacks apertural bridges, in contrast to, e.g., *C. laevigata* which also occurs in soil, but less frequently (SCHÖNBORN et al. 1983). However, our morphometric extreme values considerably exceed those mentioned by BONNET & THOMAS (1955) and the postoral ventral side is smoother and flatter than indicated in the original figures (comp. Figs. 3, 7, 12, 13, 15). Furthermore, the knobby xenosomes around the shell aperture were often indistinct or even absent in our material (Figs. 13, 15). This character, which was emphasized in the original description, is highly variable in other species too, e.g. in *Cyclopyxis kahli,* and thus of very limited value for distinguishing species and subspecies. Possibly, these xenosomes are lost during shell aging and decomposition.

The size of our small individuals matches that of *C. plagiostoma* var. *terricola* BONNET et THOMAS, 1955 well: 50–70 and 58–61 µm, respectively. The main character of this variety is the more pronounced anterior contour of the aperture giving the impression of being doubled (Fig. 8). This effect is caused by the inner part of the apertural wall which almost touches the inner dorsal wall of the shell. The outer and the inner edge of the pseudostome thus overlap in plan view and appear as a thickened line. This feature is lacking in our small sized

Table 2. Morphometric characteristics from *Cyclopyxis kahli* (first line: ordinary size class; second line: large size class) and *C. intermedia* (third line). Measurements in µm. See Figs. 20–22 for character designation.

Character	$\bar{x}$	M	SD	$SE_{\bar{x}}$	CV	Min	Max	n
(1)	89.20	90	3.93	1.02	4.41	82	95	15
	113.50	115	4.90	1.31	4.31	105	120	14
	174.07	175	8.79	2.27	5.05	162	187	15
(2)	90.27	90	3.94	1.02	4.36	85	97	15
	111.14	111	5.43	1.45	4.89	100	117	14
	174.10	175	8.45	2.18	4.86	150	187	15
(3)	24.67	25	3.31	0.85	13.42	20	30	15
	36.71	35	6.55	1.75	17.83	27	50	14
	54.10	56	9.68	2.50	17.88	33	62	15
(4)	24.73	25	2.55	0.66	10.30	20	30	15
	34.64	33	6.52	1.74	18.83	27	50	14
	54.90	56	10.32	2.66	18.80	31	68	15
(5)	33.40	35	2.72	0.70	8.15	30	37	15
	35.14	35	4.59	1.23	13.06	30	45	14
	58.20	62	5.17	1.34	8.89	50	62	15
(6)	31.87	32	2.13	0.55	6.70	30	35	15
	39.07	40	6.06	1.62	15.50	30	50	14
	61.40	62	6.98	1.80	11.37	50	75	15
(7)	31.67	30	2.44	0.63	7.70	30	35	15
	37.07	36	4.58	1.23	12.36	30	45	14
	61.97	62	6.58	1.70	10.61	50	75	15
(8)	31.80	30	2.40	0.62	7.54	30	35	15
	38.29	36	7.40	1.98	19.31	30	50	14
	61.13	62	8.90	2.30	14.56	50	75	15
(9)	55.20	56	5.34	1.38	9.67	50	68	15
	81.18	81	7.36	1.97	9.06	62	87	14
	128.20	125	6.77	1.75	5.28	118	137	15
(10)	–	15	–	–	–	–	–	3
	37.50	37	–	–	–	37	37	9

Table 3. Selected statistics from *Cyclopyxis*. Upper line: small and large size class of *C. kahli* combined; lower line: small and large size class of *C. kahli* and *C. intermedia* combined. Measurements in µm. See Figs. 20–22 for character designation.

Character	$\bar{x}$	SD	CV	Min	Max	n
(1)	100.9	13.1	13.0	82	120	29
	125.8	36.9	29.3	82	187	44
(3)	30.5	7.9	26.0	20	50	29
	38.4	14.0	36.5	20	62	44
(9)	67.6	14.5	21.4	50	87	29
	88.2	31.5	35.7	50	137	44

Table 4. Morphometric comparison of different populations of *Cyclopyxis kahli.*

References	Shell diameter (µm)		Pseudostome diam. (µm)		Shell depth (µm)	
	Extremes	x̄	Extremes	x̄	Extremes	x̄
LÜFTENEGGER & FOISSNER (1991)[1])	58–89	70.1	13–22	18.0	35–54	44.3
OGDEN & HEDLEY (1980)[2])	77–105	?	24–36	?	43–61	?
OGDEN (1988)[3])	72–82	77.3	36–57	42.5	37–53	41.3
OGDEN (1988)[4])	75–94	86.1	20–26	24.2	50–63	55.4
RAUENBUSCH (1987)[5])	80–125	?	24–32	?	60–70	?
WANNER & MEISTERFELD (1994)[6])	73–110	81.6	25–67	39.0	not measured	
WANNER & MEISTERFELD (1994)[7])	71–104	86.8	12–40	26.4	not measured	
WANNER[8])	67–116	88.6	not measured		not measured	
Present data, small size class	85–97	90.3	20–30	24.7	50–68	55.2
Present data, large size class	100–117	111.1	27–50	36.7	62–87	81.1

[1]) Field population from meadow soil in Austria; n = 23–28.
[2]) Source of material not indicated; n = 7.
[3]) Clone from soil in France, cultured without mineral particles. Number of individuals investigated not given, possibly ≥ 20.
[4]) As above, but cultured with mineral particles.
[5]) Field material from spruce forest in Germany. Number of individuals investigated not indicated.
[6]) Clone from forest soil in Germany, cultured with mineral particles (see Table 2 in WANNER & MEISTERFELD 1994 and pers. comm.); n = 75.
[7]) As above, buth another experiment (see Table 3 in WANNER & MEISTERFELD 1994); n = 560.
[8]) Clone culture from forest soil in Germany; 6126 (!) individuals were measured; paper in preparation.

specimens of *C. plagiostoma.* We thus include them into the phenospectrum of this species. Certainly, the variety *terricola* has to be studied more accurately before ist can be recognized as a reliable infraspecific taxon. The same is true for the variety *oblonga* described by CHARDEZ (1962). It differs from the nominal taxon by the more oblong shape (Fig. 9).

There are at least two other species which resemble *C. plagiostoma* and *C. plagiostoma terricola,* namely *C. minuta* DEFLANDRE, 1929 and *C. obscurus* CHARDEZ, 1990. *Centropyxis minuta* has a size of 35–60 µm and is less flattened than *C. plagiostoma.* However, both characters have not yet been quantitatively analysed and the 60 µm sized specimen depicted by HOOGENRAAD &

De Groot (1940) looks very much like a small individual of *C. plagiostoma*. The same holds true for *C. obscurus*, which is similar to an ordinary *C. plagiostoma* in size but lacks specialized xenosomes around the shell aperture in all stages of the life cycle. Furthermore, the organic matrix of the shell is apparently more distinct than in *C. plagiostoma*.

Cyclopyxis kahli

Cyclopyxis kahli is a very widespread, euryoecious species occurring in many biotopes worldwide, especially in mosses and soils (Aescht & Foissner 1989; Bonnet 1989). Bonnet (1989) found it in 1120 (54%) out of 2057 soil, litter and moss samples investigated.
There is a considerable amount of morphological and morphometrical data available on *C. kahli*, the most detailed of which are summarized in Table 4. This compilation shows that our size limits match literature data well, and the shell diameter ranges from about 60–120 µm with clearly different means, however (70–111 µm). These limits hardly change if other, less detailed measurements and the synonyms suggested (see below) are included: shell diameter 70–80 µm, shell depth 55–60 µm, pseudostome diameter 24–25 µm (Deflandre 1929, mosses in France); shell diameter 90–108 µm, pseudostome diameter 30 µm (Golemansky 1966a, mosses in Yugoslavia); shell diameter 66–92 µm, shell depth 46–67 µm, pseudostome diameter 14–24 µm (Golemansky 1966b, mosses and soils in Bulgaria); shell diameter 92 µm, shell depth 58 µm (Golemansky 1967, *Sphagnum* in Bulgaria); shell diameter 64 µm, shell depth 41 µm, pseudostome diameter 15 µm (Golemansky 1970, single specimen from littoral cave in Poland); shell diameter 50–65 µm, shell depth 40–45 µm (Guru & Dash 1983, soil in India); shell diameter 87–90 µm, shell depth 55–60 µm, pseudostome diameter 28 µm (Kufferath 1932, mosses in central Africa); shell diameter 91 µm, shell depth 62 µm, pseudostome diameter 24 µm (Ogden 1984, lake in Yugoslavia); shell diameter 69–103 µm (Opravilova 1974, river in Moravia); shell diameter 100 µm, shell depth 70 µm, pseudostome diameter 40 µm (Oye 1958, *Sphagnum* in central Africa).
Clonal and field populations are very similar in shell diameter but markedly different in pseudostome diameter under certain not yet defined conditions (Table 4). It is obvious that, if such populations should occur in the field (see values by Oye 1958 cited above!), they easily could be mistaken for other species, like *C. eurystoma* or *C. arcelloides* (Ogden 1988). Generally, the pseudostome size shows higher coefficients of variation than the shell size (Tables 1, 2; Lüftenegger & Foissner 1991; Lüftenegger et al. 1988).
The rim of dent-like xenosomes around the shell aperture is widely considered an important character of *C. kahli* (Bonnet & Thomas 1960b; Deflandre 1929; Ogden 1988; Rauenbusch 1987). Rauenbusch (1987) showed that the dents contain more K and Fe than the rest of the shell, indicating that these particles are in fact specialized. However, Lüftenegger & Foissner (1991) showed that the dents are often indistinct or even lacking in field material. This is fully confirmed by the present results. It seems reasonable to assume that specimens without dents have lost them during aging and decomposition of the shell.
Even more unreliable characters of *C. kahli* (and of many other xenosome bearing testaceans!) are the colour of the shell and the size and arrangement of the xenosomes used for shell building. Ogden (1988) showed that in cultures the colour of the shells changed with age from light yellow to deep brown, sometimes becoming almost black. The size variability of the xenosomes has not yet been measured exactly; however it is obvious from the descriptions available and our own experience that the variability in size and arrangement of the (usually) quartz particles is great and cannot thus be used to distinguish species or varieties. Usually, they are largest near and on the dorsal surface (Figs. 24, 29).
Based on these data, we suggest synonymizing with *C. kahli* the following species and varieties, most of which are poorly described: *C. kahli cyclostoma* Bonnet & Thomas, 1960a (Figs. 47, 48; shell diameter 80–100 µm, shell depth 50–60 µm, pseudostome diameter 12–30 µm; pseudostome edge without specialized xenosomes); *C. kahli obliqua* Decloitre, 1969 (Fig. 49; shell diameter 75 µm, shell depth 50 µm, pseudostome diameter 25 µm; pseudostome obligue; possibly described from single, terratogenic specimen); *C. dispar* Decloitre, 1965 (Figs. 50, 51; shell diameter 55–60 µm, shell with large xenosomes on dorsal surface); *C. dulcis* Couteaux & Munsch, 1978 (Figs. 56, 57; shell diameter 108–117 µm, shell depth 59–67 µm; xenosomes small); *C. eurystoma stenostoma* Decloitre, 1953, 1956 (non Decloitre 1949; Figs. 58–60, shell diameter 64–70 µm, shell depth 50 µm, pseudostome diameter 10–12 µm, pseudostome invagination 16–20 µm); *C. insolitus* Decloitre, 1969 (Figs. 52, 53; shell diameter 70 µm, shell depth 60 µm; pseudostome diameter 25 µm; pseudostome edge with small specialized xenosomes); *C. profundistoma* Bartos, 1963 (Figs. 54, 55; shell diameter 85 µm, shell depth 40 µm; without specialized xenosomes around pseudostome).

Cyclopyxis intermedia

As far as we know this species has rarely been mentioned in the literature since the original description, which is not very detailed: "Cette grande forme, la plus grande que nous ayons rencontrée dans les échantillons congolais, provient d'Eala. Elle mesure 110, 210 à 220 µ de diamètre. La coque grisâtre est constituée par de petits grains de sable ne faisant pas saillie. L'ouverture buccale, irrégulièrement délimitée par des grains de sable, a environ 50 µ de diamètre. Le rapport H/D est 0.6 à 0.62. Latéralement la coque est arrondie, un peu conique. Dans un exemplaire nous avons vu l'organisme émettre un large pied formé d'une colonne un peu conique (Figs. 36–38)".

All shell characters mentioned by KUFFERATH (1932) perfectly match not only our specimes but also the following species, which we consider as junior synonyms of *C. intermedia: C. gigantea* BARTOS, 1963 (Figs. 39, 40), *C. bathystoma* CHIBISOVA, 1967 (Figs. 45, 46), *C. kahli* var. *grandis* CHIBISOVA, 1967 (Figs. 43, 44) and *C. lithostoma* BONNET, 1974 (Figs. 41, 42). The synonymy suggested is also supported by other matters: (1) All authors overlooked KUFFERATH'S description or at least did not compare the new species with *C. intermedia;* (2) All descriptions are rather poor, i.e. lack any detailed morphometry and micrographs; (3) The descriptions do not contain any character which would separate the species unequivocally from *C. intermedia;* all differences mentioned concern size and structure of shell, which are highly variable and/or difficult to quantify.

Another possible synonym of *C. intermedia* is *C. pirini* GOLEMANSKY, 1974. This large species (diameter 330–380 µm) was described from a lake sediment but later found also in soil (GOLEMANSKY & TODOROV 1985), where it was considerably smaller (diameter 155–280 µm; pseudostome 100–200 µm). Both populations used not only sand grains but also diatoms for shell building, which is unusual in soil testaceans. Furthermore, the pseudostome was larger and less distinctly invaginated. Thus, *C. pirini* might be indeed a distinct species or at least not synonymous with *C. intermedia.*

Taking all observations, i.e. including the synonyms and excluding *C. pirini* and the small (110 µm) sized specimen (possibly a misidentified *C. kahli*) mentioned by KUFFERATH (1932), the size range of *C. intermedia* runs to 150–230 µm, and that of the pseudostome diameter to 33–72 µm. Furthermore, all observations agree that the pseudostome is not reinforced by specialized xenosomes as (usually) in *C. kahli.* However, the similarities between *C. intermedia* and *C. kahli* are striking and conspecifity cannot thus be excluded. At the present state of knowledge the size gap of 60 µm (Table 2) seems sufficient for maintaining both taxa as valid species.

Centropyxis intermedia is distributed worldwide in soils and mosses if the synonyms are included (DECLOITRE 1977, 1979, 1982).

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