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A taxonomic revision of *Desmodesmus* serie *Desmodesmus* (Sphaeropleales, Scenedesmaceae)

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Abstract: The revision of the serie *Desmodesmus*, based on light microscopy, TEM, SEM and ITS2r DNA, allowed us to distinguish among the taxa *Desmodesmus communis* var. *communis,* var. *polisicus*, *D. curvatocornis, D. rectangularis* comb. nov.*, D. pseudocommunis* n. sp. var. *texanus* n. var. and f. *verrucosus* n. f., *D. protuberans, D. protuberans* var. *communoides* var. nov., *D. pseudoprotuberans* n. sp., *D. schmidtii* n. sp. Keys were given for light microscopy, electron microscopy and ITS2r DNA.

Key words: *Desmodesmus*, morphology, cell wall ultrastructure, cell size, ITS–2, new *Desmodesmus* taxa, phylogeny, taxonomy, variability

Introduction

Members of the former genus *Scenedesmus* s.l. were common in eutrophic waters all over the world. Hence taxa of that "genus" were described early in the 19th century (e. g. Turpin 1820; 1828; Meyen 1828; Ehrenberg 1834; Corda 1835). Several of the early (before 1840) described taxa were insufficiently described and hence were often misinterpreted by later authors, especially the name *S. quadricauda* (Turpin) Bréb. was used for nearly every spiny "*Scenedesmus*" species (Hegewald 1979). In *Scenedesmus* s. l. morphological very different taxa were included: ovate or spindle–like cells with or without spines. Therefore the "genus" was subdivided e. g. by Chodat (1926) and more recently by Hegewald (1978), who recognized three subgenera. These were later elevated to genera. Based on DNA studies the subgenus *Desmodesmus* was raised to genus rank (An et al. 1999) and based on morphological characteristic (spindle–like cells) the subgenus *Acutodesmus* was elevated to genus level by Tsarenko et Petlevanny (2001). The species with obtuse cells but without spines and cell wall ultrastructure were left over and belong to *Scenedesmus* s. str. (Hegewald et al. 1988). While the genus *Desmodesmus* was verified by van Hannen et al. (2002), the genus *Acutodesmus* appeared to be polyphyletic (Hegewald & Wolf 2003) and was later accepted by Hegewald et al. (2010) although splitting the genus *Pectinodesmus.* Hegewald et al. (2013) separated additionally the genera *Chodatodesmus* E.Hegewald and *Verrucodesmus* E.Hegewald. *Acutodesmus* became recently a synonyme of *Tetrades- mus* (Wynne & Hallan 2016).

The subsection *Desmodesmus* as described by Hegewald (1978) was best characterized by the cell wall ultra–structure which consists of an outer cell wall layer with net–like structure, lifted by tubes (Pickett–Heaps & Staehelin 1975; Komárek & Ludvík1972; Hegewald 1978, 1997) and rosettes covered or surrounded by tubes. The cells were linearly arranged in 2–8 celled coenobia, single cells were never produced. The cell shape was variable as also the spination, however, a quadricaudate spination was predominant, in some taxa additional spines or coenobia without spines were observed.

The subsection *Desmodesmus* included two series: *Desmodesmus* with the species *D. communis* (E. Hegewald) E. Hegewald) and *D. protuberans* (F.E. Fritsch et M.F.Rich) E.Hegewald as the here newly described taxa and the serie *Maximi* with the species *D. maximus* (W. et G. S. West) E.Hegewald, *D. perforatus* (Lemmerm.) E.Hegewald and *D. tropicus* (Crow) E.Hegewald. Both series differed by the type of rosettes, which were covered by tubes in the serie *Desmodesmus* and surrounded by tubes in the serie *Maximi* (Komárek & Ludvík 1972; Hegewald & Schnepf 1979). In the subsection *Desmodesmus* are the largest species of the genus *Desmodesmus* are recorded: *D. maximus* according to type description up to 36 µm (serie *Maximi*) and *D. protuberans* and *D. communis* var. *polisicus* P.M.Tsarenko et E.Hegewald (both up to 34 µm) (serie *Desmodesmus*).

The type of the section and subsection *Desmodesmus* was the *Scenedesmus quadricauda* CHOD. (=*D. communis* (E.HEGEWALD) E.HEGEWALD (HEGEWALD 1978). The *Scenedesmus* (*Desmodesmus*) *communis* E.HEGEWALD was based on "*Scenedesmus quadricauda* CHODAT et auct. plur. p.p. an BRÉB." (CHODAT 1926) but not on *S. quadricauda* (TURPIN) BRÉB. The *Desmodesmus communis* differed from the *Scenedesmus quadricauda* significantly as was discussed by HEGEWALD (1977). COMPÈRE & KOMÁREK (1990) recommended the conservation of that name, which was done recently by conserving only the name and author of *Achnanthes quadricauda* TURPIN (= *Scenedesmus quadricauda* (TURPIN) BRÉB.) (TURPIN 1828) but excluding its type (description or illustration) as also the first publication of that species (TURPIN 1820), hence thus producing a nomen nudum which was filled with the type description and type illustration of *Scenedesmus* (*Desmodesmus*) *communis*, which was already validly published in 1977 (GREUTER et al. 2000). A not acceptable treatment. The correct citation should be *Achnanthes quadricauda* TURPIN sensu ICBN 2000 nom. illeg. because based on the type of *Scenedesmus communis* (HEGEWALD 1977).

Preliminary work for a revision of the section was done by HEGEWALD & SCHNEPF (1979) and HEGEWALD (1997). A recent revision of serie *Maximi* was done by JEON & HEGEWALD (2006). HEGEWALD (1984) reported on high temperature tolerating strains of the section. The studied species of the subsection *Desmodesmus* had high temperature tolerating strains and no high temperature tolerating strains, but if isolated from tropical climatic zones the strains were mainly tolerating high temperatures.

DNA studies for the subsection were first done by PASCHMA & HEGEWALD (1986), the ITS–2r DNA was analyzed for *D. communis* by KITSCHKE (2001, alignment unpubl.), HEGEWALD et al. (2001) and Bica et al. (2012). Complete18S DNA was available only for *D. communis* (KESSLER et. al. 1997).

We studied the taxa *Desmodesmus communis* (86 strains), *D. rectangularis* (10 strains), *D. communis* var. *curvatocornis* (2 strains), *D. pseudocommunis* (3 strains), *D. pseudocommunis* f. *verrucosus* (1 strains), *D. pseudocommunis* var. *texanus* (1 strains), *D. pseudoprotuberans* (2 strains), *D. protuberans* (5 strains), *D. protuberans* var. *communioides* (9 strains) and *D. schmidtii* (2 strains) (Table S1). *D. communis* var. *polisicus* described by TSARENKO et al. (2006) was not restudied here.

Although the species of that subsection were common in nature, they were rare in the strain collections (e. g. ACOI: 6 strains sub nom. *Scenedesmus communis* and *S. smithii*, AICB: 6, CCAP: 1, now after uptake of our strains: 34 and SAG: 1). A few strains of collections formerly identified as "*Scenedesmus quadricauda*" are misidentified taxa belonging to the *Desmodesmus armatus* group (HEGEWALD 1982; HEGEWALD 1989; HEGEWALD et al. 2005) or to *D. maximus* (strain collection UTEX) (HEGEWALD 1989).

Material and Methods

118 strains were studied, 22 of these were used for ITS–2 rDNA analyses (Tables S1, S2). Most of the strains were from the collection of the first author (including strains of AN, GROEHN, HOLTMANN, JEEJI BAI and STOJKOVICH), several of these were transferred to the collection CCAP (Oban, UK). Some strains were received from FELFÖLDI (Museum Budapest), HINDÁK (private collection, Bratislava), SAG (strains collection Göttingen), ACOI (strain collection Coimbra, Portugal) and AICB (strain collection Romania).

The isolates were cultured in batch cultures, in a shaking–apparatus–and/or in aerated tubes. As nutrition the modified medium of Bourrelly (HEGEWALD et al. 1994) or occasionally Chu X (VENKATARAMAN 1969), 0.2 × N8 (SOEDER et al. 1967) or Korn (KORN 1969) were used. The modified trace element solution and B vitamins as cited in HEGEWALD et al. (1994) were added to all media. The tubes were aerated with a 1% CO_2/air mixture and cultured at 30 °C (some additionally at 20, 25 or 38 °C) and 16:8 h light–dark cycle and diluted daily to an extinction of 0.02 at λ = 560 nm. The light intensity was about 200 $\mu mol.m^{-2}.s^{-1}$. The batch cultures and the shaken cultures (110 rotations per minute) were cultured at 21 ± 1 °C at a light–dark cycle 16:8 h at about 50 $\mu mol.m^{-2}.s^{-1}$. The shaken cultures were diluted 2 times all 5 days.

For the size measurements one inner cell of 20 coenobia was used and about 100 coenobia were used for measuring the spines.

For size measurement of the cell wall net structure we used a Zeiss Videoplan. For each culture type we measured 50 structures of 10 photos of two specimens, resulting in a total of 3000 measurements.

For the transmission electron microscope, empty cell walls were enriched by sedimentation or centrifugation (if not studied immediately, they were preserved with glutardialdehyde or formaldehyde), washed with distilled water, air dried and studied under the TEM with no further treatment or after shadow casting with Au/Pd (30°). For sectioning they were conserved with 1% $KMnO_4$.

For the scanning electron microscope the cells were fixed with glutardialdehyde or formaldehyde, dehydrated in acetone steps, critical–point dried and sputtered with gold.

The complete ITS–2 rDNA sequences were determined as described in HEGEWALD et al. (2001). The alignment editor of HEPPERLE (2002) was used.

The alignment for ITS2 was performed by hand according information on secondary structures (see also Figs S1–6) with a total of 235 bases in *D. communis* et var., *D. curvatocornis, D. rectangularis* and *D. pseudocommunis*) and 236 (*D. pseudoprotuberans, D. schmidtii, D. protuberans* et var.).

Results

We accepted the taxa *Desmodesmus communis,* its var. *polisicus* and *D. curvatocornis* comb. nov., *D. rectan-*

gularis comb. nov. and *D. protuberans*. We described as new the taxa *D. pseudocommunis, D. pseudocommunis* var. *texanus, D. pseudocommunis* f. *verrucosus, D. pseudoprotuberans, D. schmidtii* and *D. protuberans* var. *communioides*. In Fig. 1 is given a synoptic overview on the studied taxa, their cell size data, morphology and electron microscopical cell wall structures.

1. Accepted taxa

***Desmodesmus communis* (E.Hegewald) E.Hegewald var. *communis* (Figs 1I, 2, 3)**

A common species with wide range of cell length 9.0–23.1 µm (Tables 1,S2) but mainly stable cell wall ultrastructure (Figs 1, 3, 17c, d) and invariable ITS 2 data (GenBank: Table S1).

***D. communis* var. *polisicus* P.M.Tsarenko et E.Hegewald (Tsarenko et al. 2006) (Fig. 2c)**

A taxon with larger cell length 21.8–34.2 µm (Tables 1,S2) than *D. communis,* morphologically more resembling *D. maximus*. The cell wall ultrastructure is similar to *D. communis* and the variety had zero differences from *D. communis* var. *communis*. (GenBank: Table S1).

***D. curvatocornis* (Proshk.–Lavr.) E.Hegewald comb. nov. (Figs 1D, 4, 5)**

Basionym: *Scenedesmus curvatocornis* Proshk.–Lavr. 1925, Trudy Khar´kovsk. Obšč. Isp. Prir. 50: 36, fig. 8.

Characterized by the short spines, often strongly curved and sporadically additionally short spine or spines one of the outer cells (Hegewald 1979; Yamagishi & Hegewald 1998; Tsarenko et al. 2005). Strain Hegewald 1977–144 had scattered single tubes on the cell surface only visible under the EM. The net–like structure was regular and dense. The difference in ITS2 between the species and *D. communis* was zero (Fig. 21, Table S3).

Table 1. Synopsis of size measurements for all strains of the taxa of serie *Desmodesmus* and for *D. maximus* (serie *Maximi*).

taxon	cell length (µm) average	cell length (µm) min–max	cell length : cell width	spine length (µm) min–max
D. communis	9.6–19.3	7.6–23.1	2.5–3.5	8.2–15.2
var. *polisicus*	–	21.8–34.2	–	–
D. rectangularis	14.4–16.8	12.8–19.3	2.9–3.3	8.1–10.2
D. curvatocornis	23.5	18.3–28.1	3.1	<1
D. pseudocommunis	14.5–15.8	11.4–19.3	2.9	15.2
var. *texanus*	19.0	15.6–21.6	2.7	–
f. *verrucosus*	18.3–19.4	15.2–25.7	3.0	–
D. pseudoprotuberans	16.1–18.3	13.8–22.8	2.7–3.5	–
D. schmidtii	8.6/11.8	7.3–12.6	2.8/3.2	–
D. protuberans	18.2–27.1	15.0–31.7	3.1–4.4	10.7–21.2
D. maximus	20.0–31.8	17.4–36.9	2.5–3.7	–

Table 2. Compensatory base change (CBC) in section *Desmodesmus* compared with strains of section *Maximus* and with *D. pirkollei* as outgroup.

		1	2	3	4	5	6	7	8	9	10	11
1	*D. pirkollei* SAG2042	0	8	8	8	8	10	4	4	4	4	4
2	*D. maximus* Hegewald 1980–48	8	0	0	1	1	2	3	3	4	4	4
3	*D. maximus* UTEX 614	8	0	0	1	1	2	3	3	4	4	4
4	*D. perforatus* Hegewald 1997–12	8	1	1	0	0	1	3	3	5	4	4
5	*D. tropicus* Hegewald 1997–26	8	1	1	0	0	0	3	3	5	3	4
6	*D. tropicus* Hegewald 1998–18	10	2	2	1	0	0	5	5	6	5	5
7	*D. communis* Hegewald 1974–35	4	3	3	3	3	5	0	0	0	0	0
8	*D. rectangularis* Hegewald 1977–141	4	3	3	3	3	5	0	0	0	0	0
9	*D. protuberans* Hegewald 1997–2	4	4	4	5	5	6	0	0	0	0	0
10	*D. pseudocommunis* Hegewald 1976–43	4	4	4	4	3	5	0	0	0	0	0
11	*D. pseudoprotuberans* Hegewald 1981–51	4	4	4	4	4	5	0	0	0	0	0

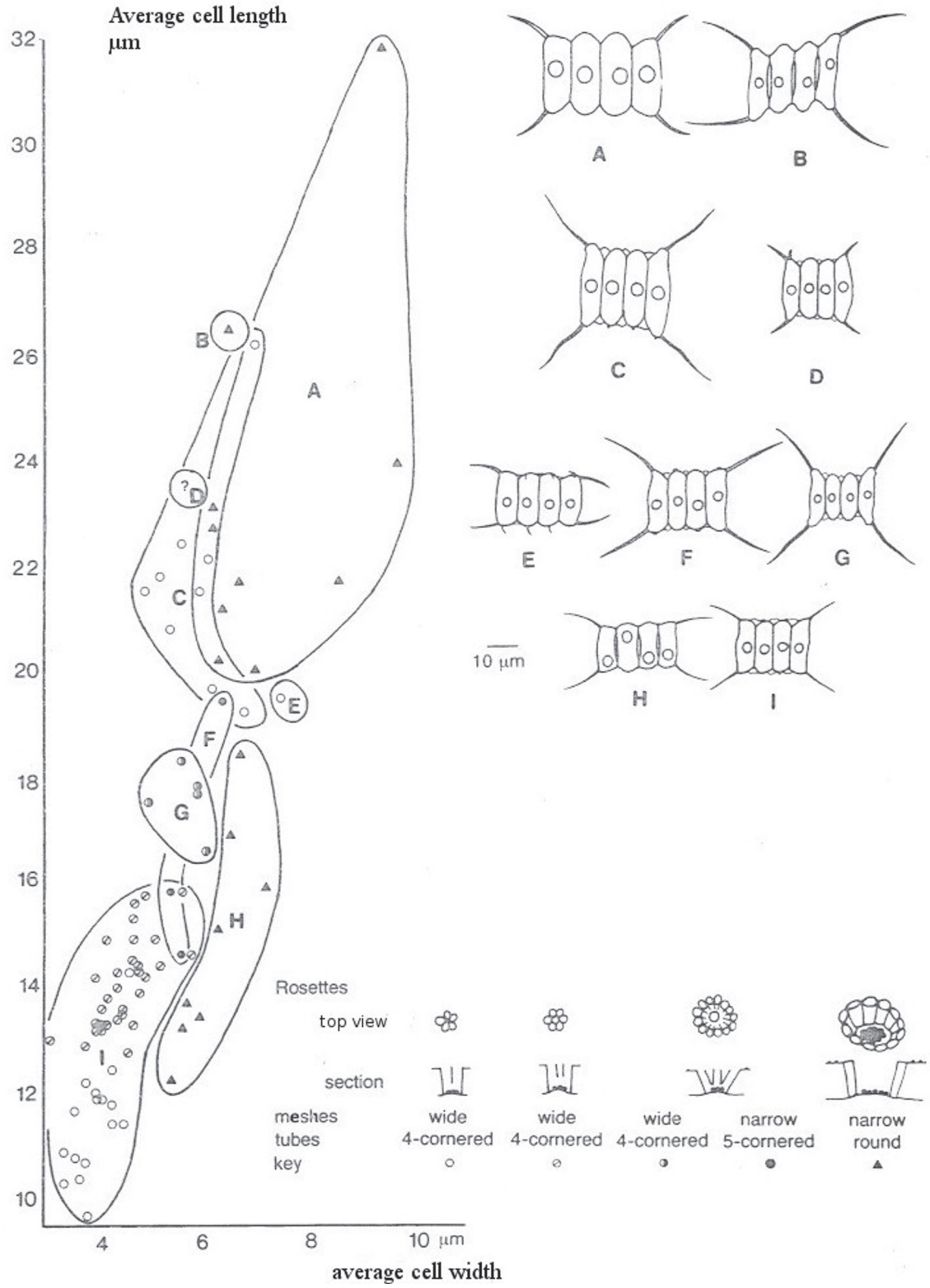

Fig. 1. Synoptical overview on the studied taxa of section *Desmodesmus*, cell size data (inner cells of coenobia), morphology and electron microscopic cell wall structures: (A) *D. maximus*; (B) *D. tropicus*; (C) *D. protuberans*; (D) *D. curvatocornis*; (E) *D. rectangularis*; (F) *D. pseudocommunis*; (G) *D. pseudoprotuberans*; (H) *D. perforates*; (I) *D. communis.*

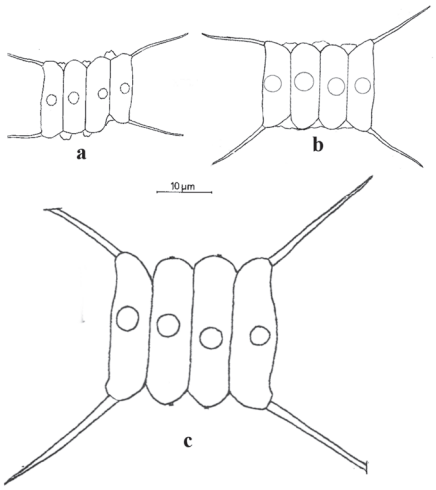

Fig. 2. *Desmodesmus communis*, light microscopic habitus: (a) small strain (Hegewald 1971–256, type strain); (b) large strain from Lake Titicaca, Peru (Hegewald 1977–170); (c) *D. communis* var. *polisicus* from Tsarenko et al. (2006).

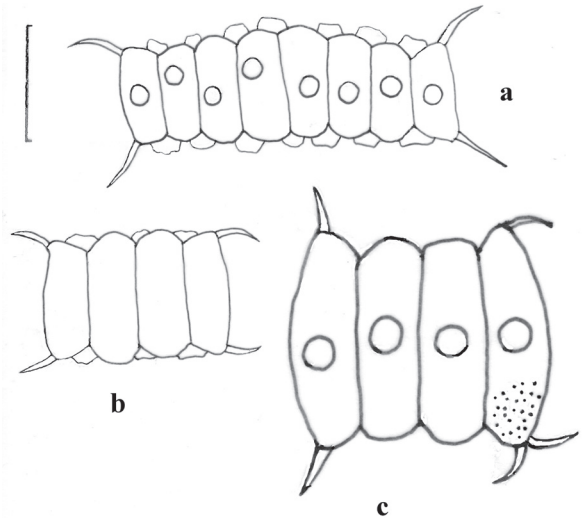

Fig. 4. *Desmodesmus curvatocornis,* light microscopic habitus: (a, b) strain Hegewald 1994–8; (c) specimen from Lake Steinhuder Meer (leg. Holtmann, 1977). Scale 10 µm.

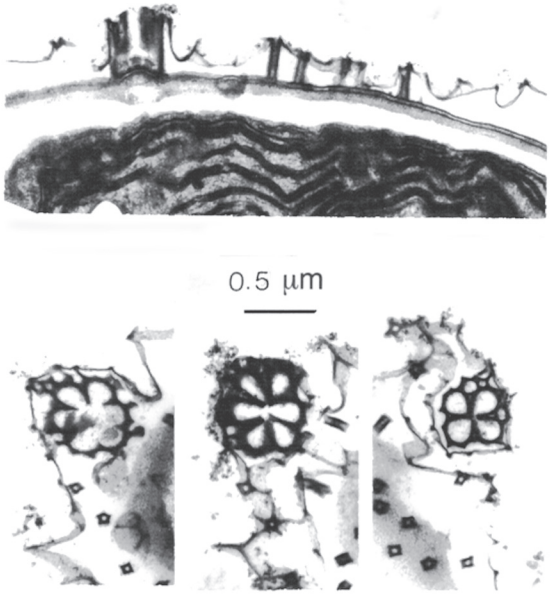

Fig. 3. *Desmodesmus communis*: (a) longitudinal section of a rosette; (b–d) serial section through a rosette basal to top (strain Hegewald 1975–135, India).

Although we weight ITS2 very high, the severe differences in morphology and cell wall ultrastructure forces us to keep the taxon at the level of a species (GenBank: Table S1). Cell size see Tables 1, S2.

***D. rectangularis* (G.S.West) E.Hegewald (Figs 1E, 6, 7)**

Basionym: *Scenedesmus quadricauda* var. *rectangularis* G.S.West 1914, Mem. Soc. Neuchátel. Sci. Nat. 5, 1025, pl. XXI, figs 14–21.

A species with slightly larger range of cell length than *D. communis*: 12.8–19.3 µm (Tables 1, S2), cells are more compact with obtuse angel between cells and usually additional spines on inner cells. Spines are as long as or often shorter than cell length. The cell wall ultrastructure as *D. communis* (Fig. 1) and in ITS 2 were two base exchanges compared to *D. communis* (Fig. S1). (GenBank: Table S1).

***D. protuberans* (F.E.Fritsch et M.F.Rich) E. Hegewald (Figs 1C, 8a, b, S3)**

Characterized by more elongated cells as well as by larger cell size (Tabs 1, S2) than the other members of the subsection *Desmodesmus,* and by longer outer cells than inner cells (except *D. pseudoprotuberans*), the smaller strains of the variety *communioides* (Figs 8c, d) were hardly to distinguish from *D. communis*. It differed in ITS2 from the other taxa discussed here by 5 to 7 base exchanges but the strains had a variability within themselves (Fig. S2). (GenBank: Table S1).

2. Description of new taxa

***Desmodesmus pseudocommunis* E. Hegewald sp. nov. (Figs 1F, 9a)**

Description: cells 11.4–19.3 × 4.1–6.4 µm (strain Hegewald 1976–43). Rosettes wider than high. Net–like structure of outer cell wall layer had regular and smaller meshes than *D. communis* (Figs 1I, 9)
GenBank access number KU359294 (ITS2).

Holotype: Fig. 9a.
Type strain: Hegewald 1976–43 (lost).
Paratype strains: Hegewald 1979–4 (Germany), Stojkovich 1998–2 (Serbia), AICB 1004 (Romania).
Type locality: Germany, Reservoir Halterner Stausee.
Habitat: Reservoir.
Etymology: Morphological similarity with *Desmodesmus communis*.

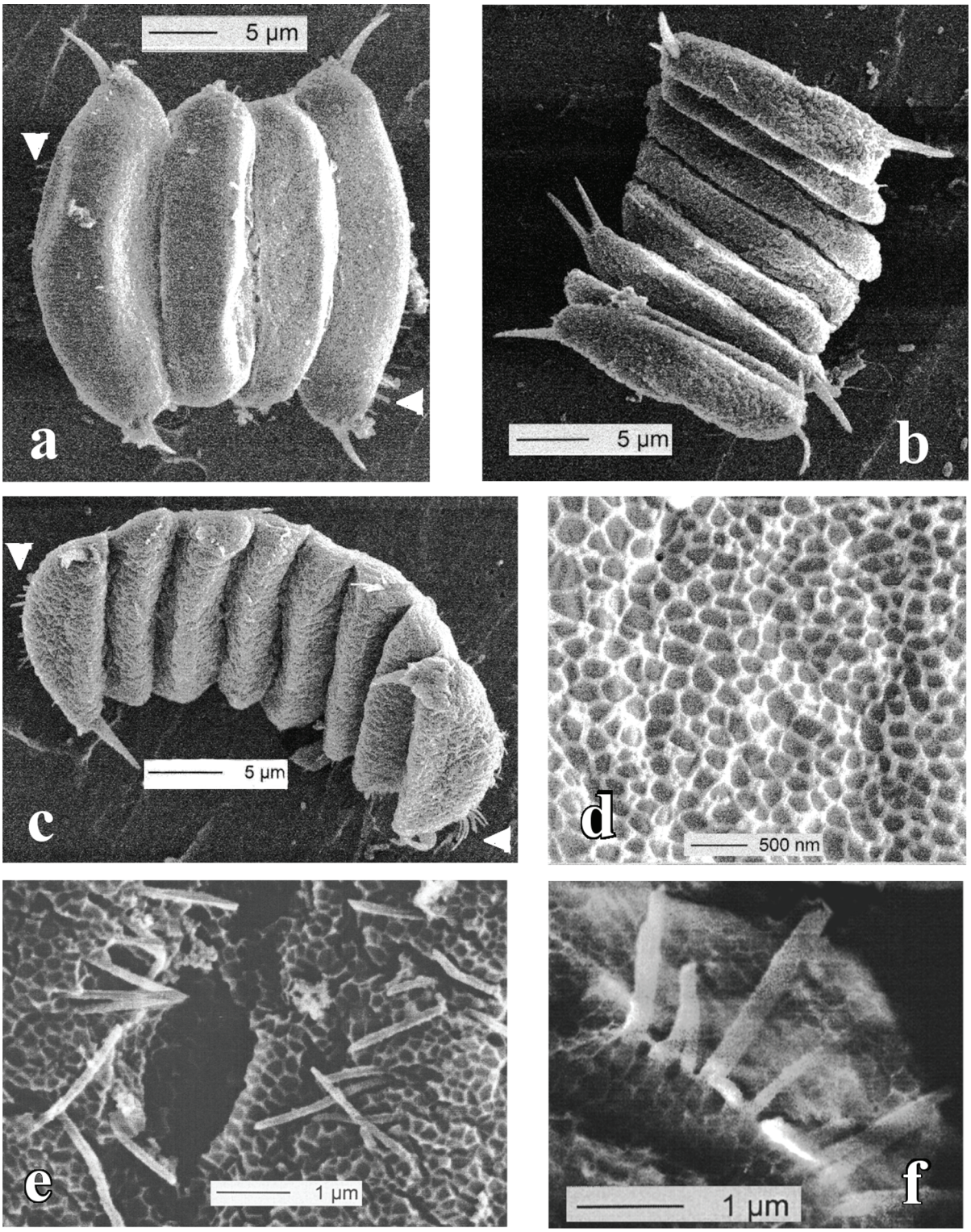

Fig. 5. *Desmodesmus curvatocornis,* strain Hegewald 1977–144 (strain from Lake Steinhuder Meer): (a) 4–celled coenobium (arrow heads in 5a and 5c: single tubes on the surface); (b) 8–celled coenobium with some additional spines; (c) 8–celled coenobium; (d) cell wall ultrastructure; (e) single tubes scattered on the surface; (f) single tubes and spines (bundles of tubes), arranged in a row.

***Desmodesmus pseudocommunis* var. *texanus* E. HEGEWALD var. nov. (Figs 10, 11)**

Description: coenobia usually with four cells, quadricaudate or additionally on the lateral walls of outer and inner cells with short spines or short ribs. Cells 15.6–21.6 × 5.6–8.4 µm (average: 19.0 ± 2.1 × 7.2 ± 0.9 µm). Outermost cell wall layer between cell poles often hardly visible. Rosettes wider than high. Bristles were freely produced.

Holotype: Fig 10.
Type strain: Hegewald 1986–24 (lost).

Fig. 6. *Desmodesmus rectangularis*, figs 16 and 18 of type figure (G.S.West 1914).

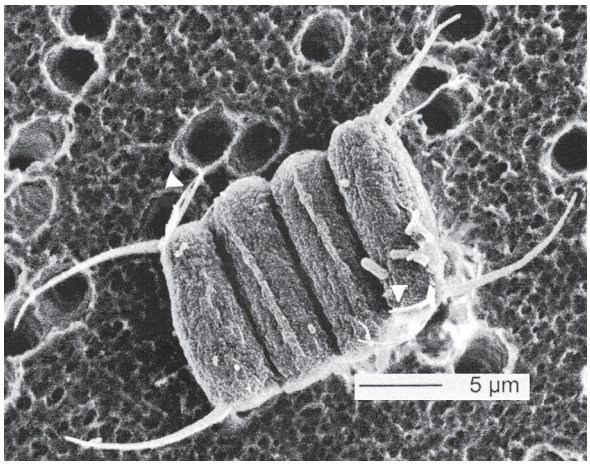

Fig. 7. *Desmodesmus rectangularis*, strain Hegewald 1977–141, habitus. Two arrow heads point to additional short spines.

Type locality: Lake Houston, Texas, USA.
Habitat: Plankton of a large Lake.
Etymology: The name was used because of the hitherto only known locality in the state of Texas.

***Desmodesmus pseudocommunis* f. *verrucosus* E. Hegewald f. nov. (Figs 9b, c, 12, 13)**
Description: differs from *Desmodesmus pseudocommunis* f. *pseudocommunis* by size (15.2–25.7 µm) and by groups of short tubes wider than the lifting tubes, scattered over the surface, visible only under the electron microscope.
GenBank access number KU359293(ITS2).

Holotype: Preserved sample of type strain (cultured in medium Pringsheim, harvested 4.7.1975), number B40 0041553 at herbarium of Botanical Garden and Botanical Museum, Berlin.
Type strain: Hegewald 1975–230 (lost).
Type locality: Lake Tegeler See, Berlin, Germany.
Habitat: Plankton of a stream lake.
Etymology: Name was given because of the granules which are visible under the electron mikroscope.

Remark: The invalid *Scenedesmus quadricauda* (var. *obtusospinosus*) f. *heterogranulatus* had some similarity especially fig. 1 of Hortobágyi (1971), and it was of similar size: 19.5–26 µm. However, the name could not be used, because it was invalid.

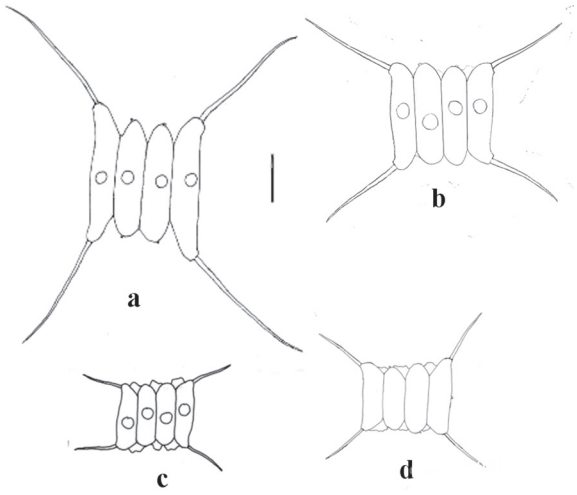

Fig. 8. *Desmodesmus protuberans*: (a–b) light microscopic habitus, (a) strain Hegewald 2001–4, (Germany, Berlin), (b) strain Hegewald 1979–6 (Germany, Dortmund), *Desmodesmus protuberans* var. *communioides*; (c) strain SAG 276/4b (UK, Cambridge); (d) strain Hegewald 1997–2 (Fiji). Scale 10 µm.

***Desmodesmus pseudoprotuberans* E. Hegewald sp. nov. (Figs 1G, 14 –16)**
Description: cells 12.0–22.8 × 3.6–7.8 µm (averages 14.0–18.3 × 4.7–6.9 µm), outer cells somewhat longer than inner cells.
GenBank access number KU359303.

Holotype: Preserved sample of type strain (cultured in medium Pringsheim, harvested 22.5.1978), number B40 0041554 at herbarium of Botanical Garden and Botanical Museum, Berlin
Paratypes: Preserved sample of type strain (cultured in medium Pringsheim, harvested 23.3.1975), number B40 0041554 at herbarium of Botanical Garden and Botanical Museum, Berlin Dahlem.
Strain Hegewald 1981–51 (=CCAP 258/81) Reservoir Seletar, Singapore.
Type strain: Hegewald 1973–293, strain lost.
Type locality: Lake Quistococha, Iquitos, Peru.
Habitat: Plankton of a reservoir.
Etymology: Morphological similarity with *Desmodesmus protuberans*.

Remark: This rare taxon had apparently a tropical distribution.

***Desmodesmus schmidtii* E. Hegewald sp. nov. (Figs 17a,b, 18, 19)**
Description: coenobia quadricaudate, bicaudate, heterocaudate or spineless. Cells in average 8.6/11.8 µm (two strains). Cell wall structures, rosettes and tube–like spacers were similar to those of *D. communis* but the number of spacers was greatly reduced and the net–like structure very delicate.
GenBank access number KU359297 (ITS2).
Holotype: Fig 19.

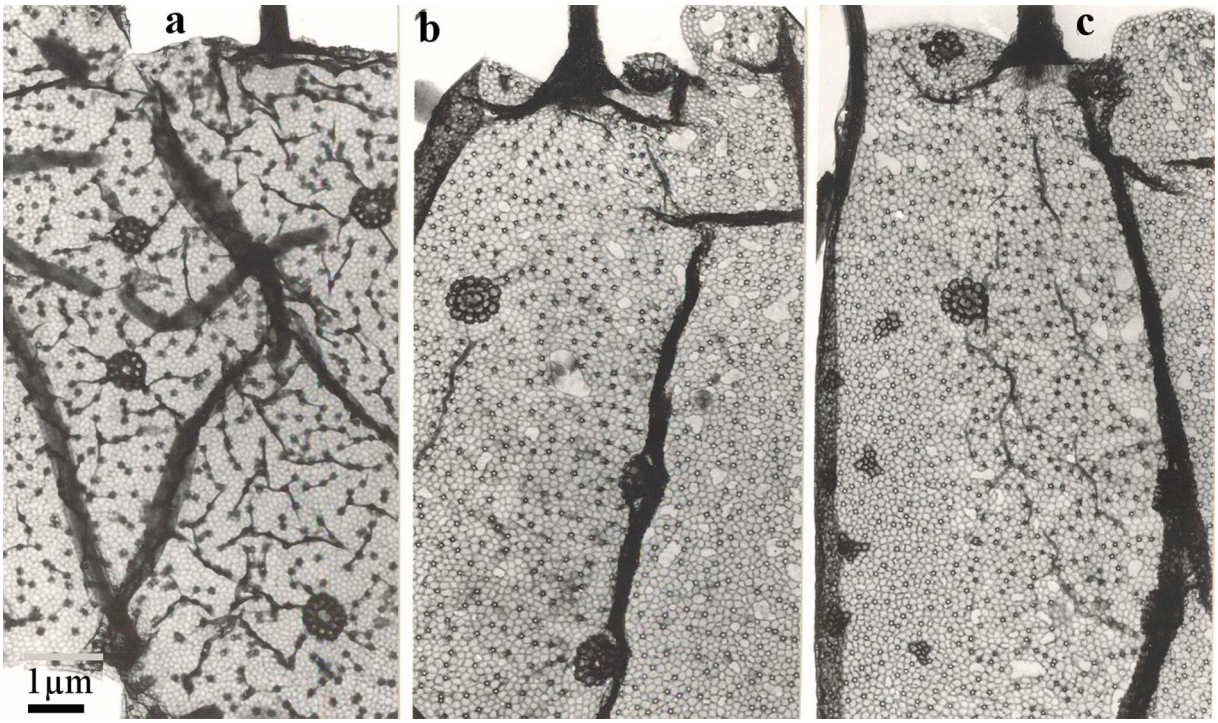

Fig. 9. *Desmodesmus pseudocommunis*, empty cell walls under the EM: (a) strain Hegewald 1976–43; (b, c) f. *verrucosus* strain Hegewald 1976–230, in (c) granules visible.

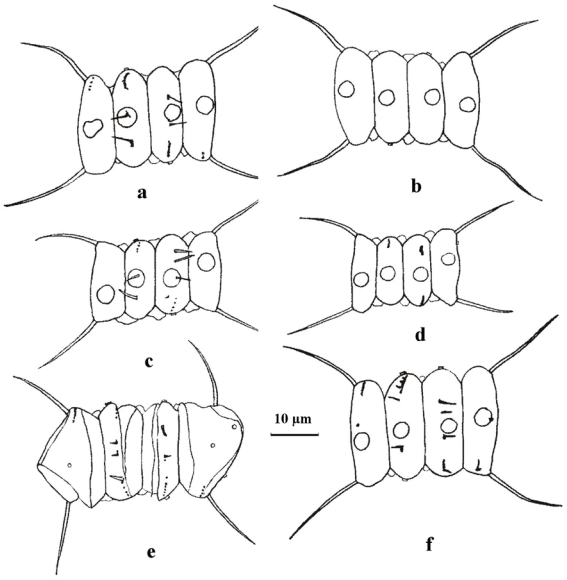

Fig. 10. *Desmodesmus pseudocommunis* var. *texanus*: (a–f) variability under the light microscope (strain Hegewald 1986–24); (e) empty cell wall.

Type strain: Hegewald 1971–257 (=CCAP 258/79).
Paratype strains: Hegewald 1981–14 (Indonesia). Chic 10/23P–17w (USA).
Type locality: Lake Belső–tó, Tihany, Hungary.
Habitat: Plankton of a lake and reservoir.
Etymology: The taxon was named in honor of the late Hungarian phycologist ANTAL SCHMIDT, a good friend and coauthor for several papers.

***Desmodesmus protuberans* var. *communioides* E. HEGEWALD var. nov. (Figs 8c, d)**
Description: coenobia quadricaudate. Cells of type strain 11.4–15.6 × 4.1–5.8 µm (average13.7 × 4.8 µm). Cell wall structures, rosettes and tube–like spacers were similar to those of *D. communis*. GenBank KU359302 (ITS2).

Holotype: Fig. 8d.
Type strain: Hegewald 1997–2 (=CCAP 258/132).
Syntype strains: CCALA 464 (as "*Desmodesmus quadricauda*"), UTEX 76 (= SAG 276–3b), EH 50, EH 52, EH 84, ET 85, ET93 (collection Vanormelingen, Belgium).
Type locality: Fiji, pond in Art Center in Pacific Harbour (island Vitu Levu)
Habitat: Plankton of a highly eutrophicated pond.
Etymology: Name was given because of a morphological similarity with *Desmodesmus communis*.

3. Morphology

The *Desmodesmus communis* strains had a very wide range of cell length, ITS2–sequenced strains: 9.0–23.1 µm and with averages between 10.3–19.3 µm (8 strains), that means, the averages of larger strains were nearly twice as large as the smaller strains. The *D. communis* var. *polisicus* strain was clearly larger with sizes between 21.8–34.2 µm. The *D. pseudoprotuberans* (6 strains), *D. rectangularis* (2 strains), *D. pseudocommunis* (2 strains), were within the range of *D. communis*. In average slightly larger was the strain of

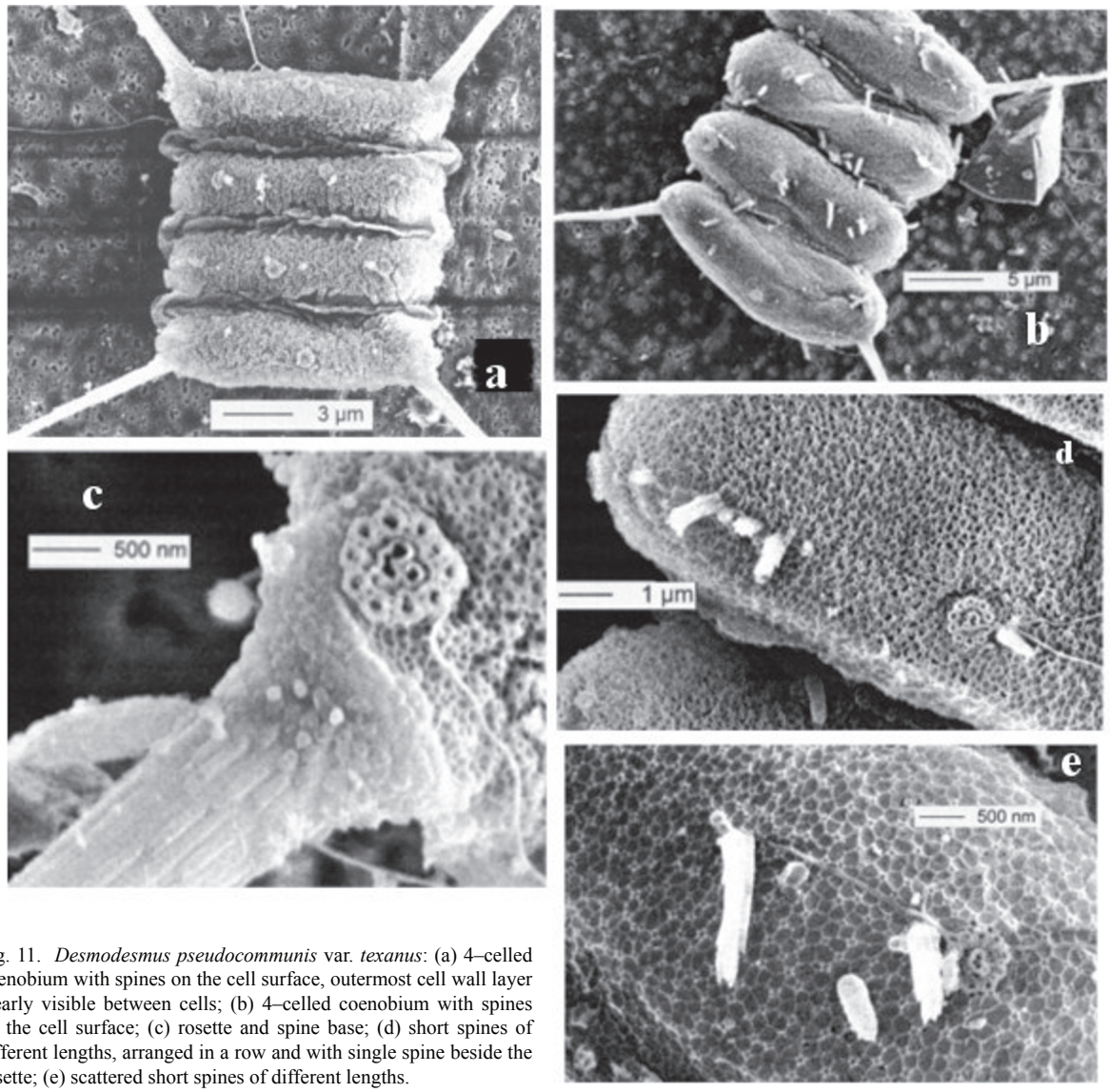

Fig. 11. *Desmodesmus pseudocommunis* var. *texanus*: (a) 4–celled coenobium with spines on the cell surface, outermost cell wall layer clearly visible between cells; (b) 4–celled coenobium with spines on the cell surface; (c) rosette and spine base; (d) short spines of different lengths, arranged in a row and with single spine beside the rosette; (e) scattered short spines of different lengths.

D. pseudocommunis f. *verrucosus* and the two strains of *D. curvatocornis*. The *D. protuberans* (12 strain) was mostly larger in cell size (inner cells of coenobium measured, the outer cells are larger): (11.0)15.0–31.7 µm and averages of sequenced strains between 20.3–27.1 µm, but the strains of *D. protuberans* var. *communioides* were smaller: averages 13.2–16.7 µm, smallest measured cell size 11.0 µm.

The cell shape was characterized by the ratio of cell length to cell width. The *D. communis* had a wide range (2.8–3.6:1), within this range were also all other studied taxa except *D. protuberans* var. *protuberans* (3.1–4.4:1). Hence this species had more elongated cells than the other taxa of the section (Figs 1, 8). This taxon was also characterized by the outer cells of the coenobia, which were longer than the inner cells. Size differences in cell length between inner and outer cells are also found in *D. pseudoprotuberans* (Fig. 14), however, these are usually much less pronounced.

The spines in most taxa in the serie *Desmodesmus* were about cell length or shorter, in *D. curvatocornis*, which had spines shorter than the cell diameter (Tabs 1, S2). Beside quadricaudate specimens, spineless, bicaudate and heterocaudate specimens were found in *D. schmidtii,* strain Hegewald 1971–257 (Fig. 19). While most of the studied taxa had a quadricaudate spination, the *D. rectangularis* had additionally short spines on one pole of the outer cells or more often short spines on one or several inner cells of the coenobia (Figs 6–7) and *D. curvatocornis* had sporadically an additional short spine on one pole of the outer cells (Figs 4c, 5b).The *D. pseudocommunis* var. *texanus* sporadically had spines scattered over the cells, sometimes connected with fragmented ribs, which are found in all taxa of the subsection only in this variety (Figs 10, 11). Spines are always bundle of tubes, but in var. *texanus* we observed a warty structure at the base of the spines (Fig. 11c).

Single tubes were observed on the cells of *D. curvatoronis* (Figs 5e–f).

4. Cell wall ultrastructure

We discussed following structures: nets, rosettes, and tube–like spacers.

Net–like structures: All studied taxa had an outer cell wall layer, carried by spacer tubes (Figs 3a, 11a, 15c). The outer cell wall layer had a reticulate net–like structure built of filaments attached on the outermost cell wall layer (Figs 5d, 9, 17d). This reticulate structures were different in different taxa. The *D. communis* and var. *polisicus*, *D. pseudoprotuberans, D. schmidtii* and *D. protuberans* and its variety had a structure with very irregular meshes (e.g. Fig. 17d), while *D. pseudocommunis* and *D. curvatocornis* had a very regular net–like structure with smaller mashes and stronger filaments (e.g. Fig. 5d). For two strains of different taxa the net–like structures were measured. The structure was characterized by mesh area or largest diameter of the meshes. In Fig. 20 is shown the mesh area distribution for these two taxa. The *D. pseudocommunis* f. *verrucosus* (strain Hegewald 1975–230) had a small mash area and regular net–like structure, hence it had a sharp distribution peak for the mesh area, while *D. communis* (strain Hegewald 1974–8) had an irregular net of very different mesh–sizes, hence a flat and wide distribution curve. For the screening of many strains we measured the smallest and largest mesh diameter only (Table S2).

Rosettes

The rosettes were special structures: openings in the outer cell wall layer for excretion of bristles (Fig. 16), which were produced from basal props (Figs 13a, f). We distinguished four types of rosettes:

- **type Ia** composed of 4 or 5 (rarely 6) tubes, which lose their central walls at the bottom (Figs 3a, b). Often one or several space holder tubes were attached (Fig. 3d, Table S2). These types of rosette were found in strains of *D. communis* with smaller cell sizes and in *D. protuberans* (Table S2).
- **type Ib** was similar to type Ia, but had additionally a central short tube. These types of rosette were found in strains of *D. communis* with larger cell sizes (Fig. 1). Often were found reduced or abnormal rosettes. In a few strains no rosettes were found.
- **type IIa** was more complex and had a larger number of outer (9–14) and central tubes (2–4). The central tubes had a reduced central wall, hence forming one central opening (13d, h). In the upper part of the rosette the outer tubes were connected to the central tubes by rods (Fig. 13h). This type is found in *D. pseudocommunis*.
- **type IIb** differs by connections of the outer tubes which were ladder–like (Fig. 15d). This type is found in *D. pseudoprotuberans*.

Tube–like spacers: Between the three inner cell wall layers and the outer layer were tube–like spacers. These tubes were in cross section 4– or 5–cornered, exceptionally 3–cornered or round. The *D. communis* has 4–corned tubes (rarely 5– or 3–cornered) as do also *D. protuberans* and *D. pseudoprotuberans*. The *D. pseudocommunis* has mainly 5–cornered and less common 4–cornered tubes. The section *Maximi* had circular tubes while *D. intermedius* (R.CHOD.) E.HEGEWALD (subgenus *Desmodesmus* Section *Intermedius*) had three–cornered tubes only.

5. ITS–2

The eleven sequenced strains of *D. communis* as additional data from GenBank (Table S1) were identical in ITS–2 base composition, but the strains Hegewald 1977–170 and AICB 989 differed in one base. The strain Hegewald 1977–170 had also four differences in the last 52 bases of 5.8 S DNA. All five differences were G instead of C or U. The two strains of *D. curvatocornis* and the strain of *D. communis* var. *polisicus* were identical in ITS–2 with the *D. communis* strains (Fig. 21). Two strains of *D. schmidtii* (Hegewald 1971–257, Hegewald 1981–14) were morphologically similar with *D. communis* but the outer cells could be a little bit larger than the inner ones. However, in ITS–2 (strain Hegewald 1981–14, Fig. S5) they fit into the *D. protuberans*–group (Fig. 21). The *D. schmidtii* strains differ from *D. protuberans* by 3–5 bases and from *D. communis* by 6 bases (Table S3). The *D. protuberans* differed from *D. communis* by 5–7 bases (Table S3). The *D. protuberans*–group (*D. protuberans/D. protuberans* var. *communioides,/D. pseudoprotuberans/D. schmidtii*) is characterized by several base exchanges in the top of helix II, especially by an exchange in position 81 (G or U) and an additional U between position 83 and 84. These changes result in a prolongation of helix II by one base pair.

The *D. rectangularis* differs from *D. communis* by 2 bases only (Fig. S1, Table S3), the *D. pseudocommunis* by 5–6 (Fig. S3, Table S3) and the *D. pseudoprotuberans* by 8–9 (Table S3, Fig. S4). The members of the related serie *Maximi* differ by 25–29 bases from *D. communis*. All taxa of the serie *Desmodesmus* had no CBC (compensatory base change) between each other but they had 1–5 CBC´s compared to serie *Maximi* (Table 2).

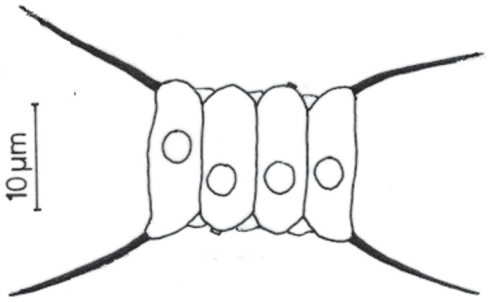

Fig. 12. *Desmodesmus pseudocommunis* f. *verrucosus*, strain Hegewald 1975–230, habitus. Scale 10µm.

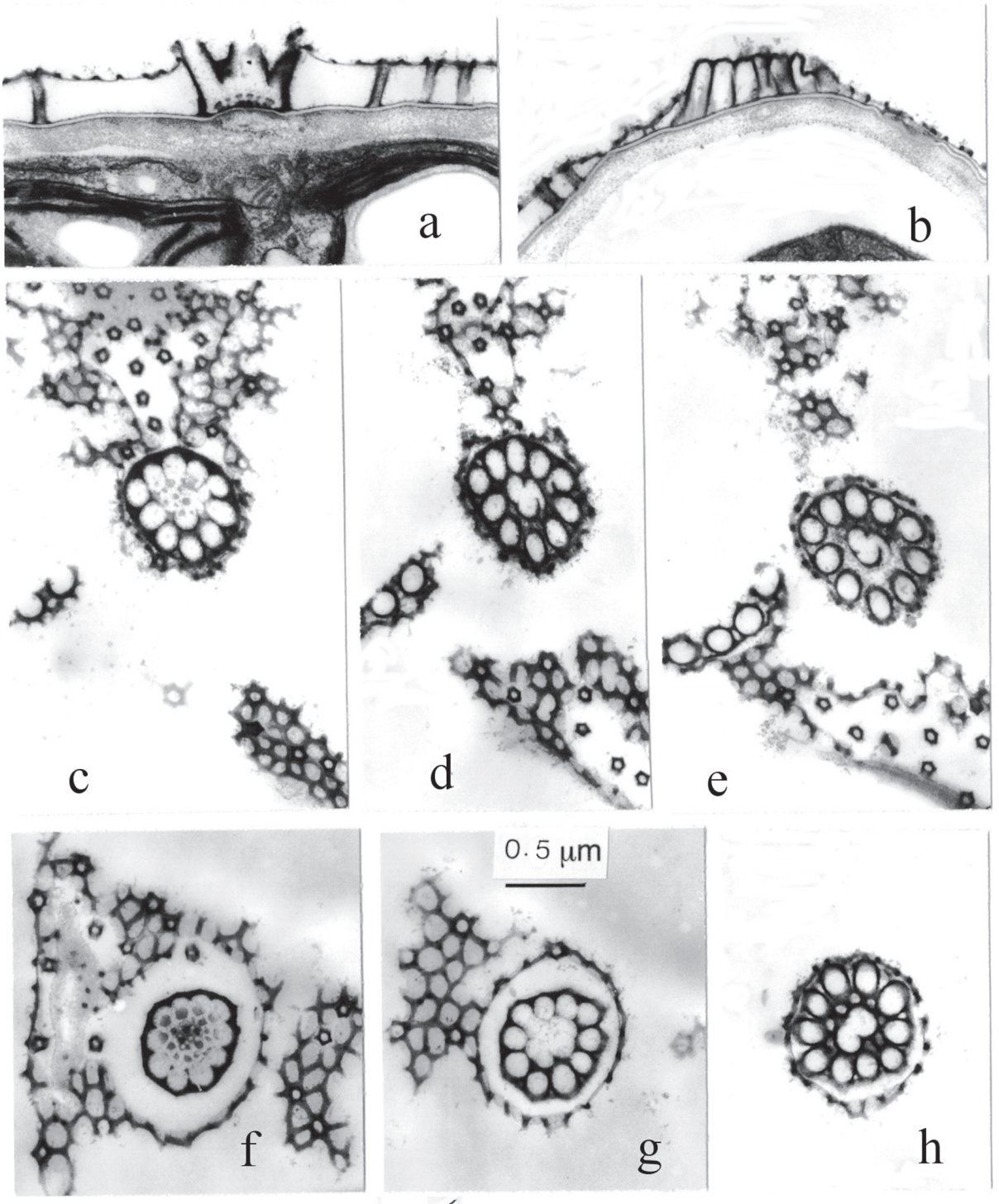

Fig. 13. *Desmodesmus pseudocommunis* f. *verrucosus*, strain Hegewald 1975–230: (a) longitudinal section through a rosette; (b) group of tubes, building the granules; (c–e) and (f–h) two series of serial cross–sections of rosettes from bottom to top.

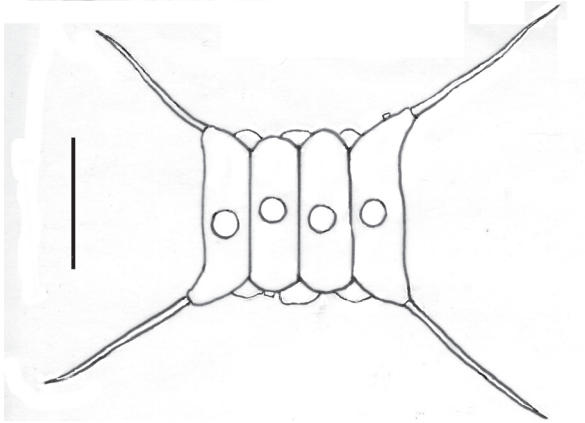

Fig. 14. *Desmodesmus pseudoprotuberans*, type strain: Hegewald 1973–293 (Peru, Rio Nanay). Scale 10 µm.

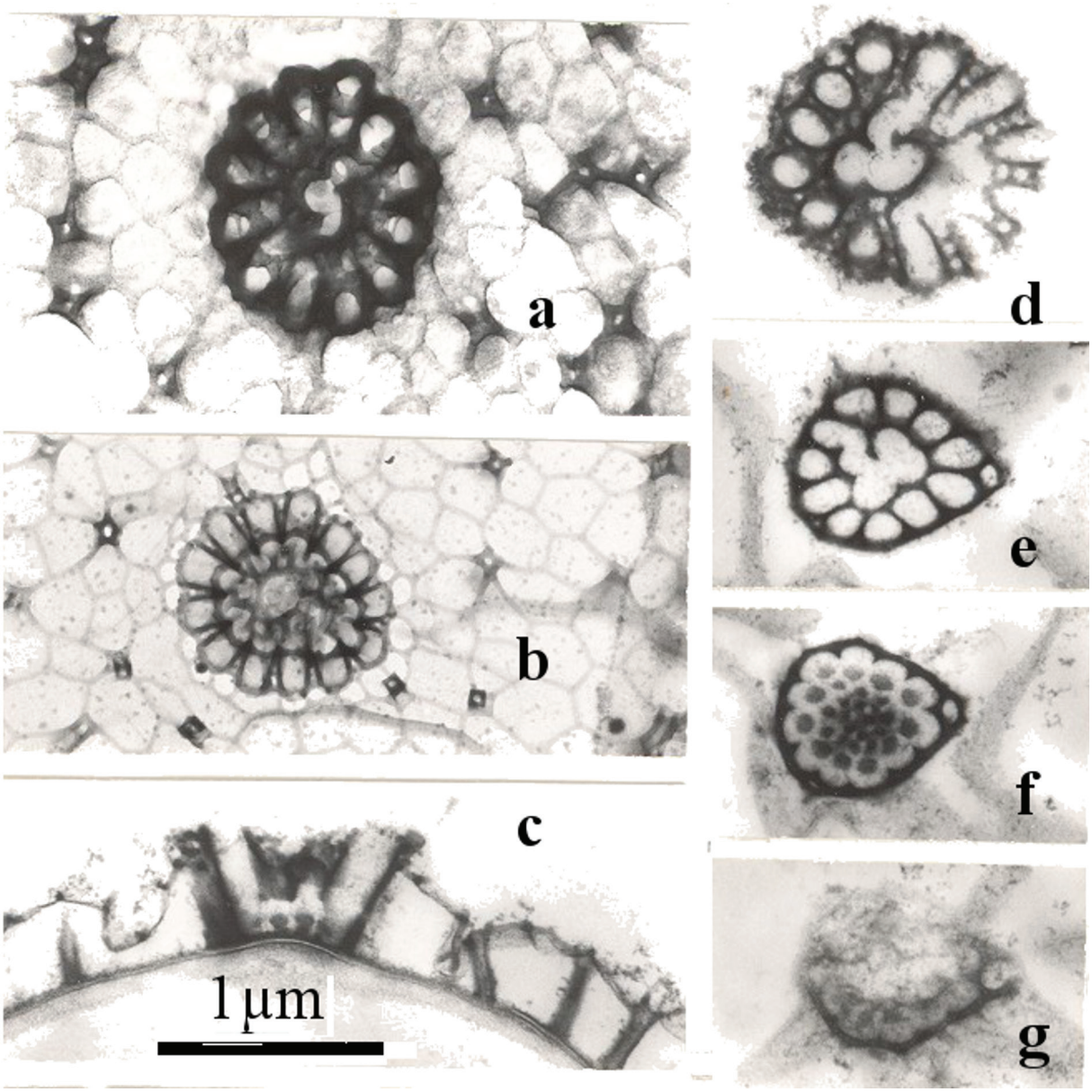

Fig. 15. *Desmodesmus pseudoprotuberans* strain Hegewald 1973–293 under the EM: (a, b) top view on rosettes; (c) longitudinal section of a rosette; (d–g) serial sections through a rosette from top to bottom.

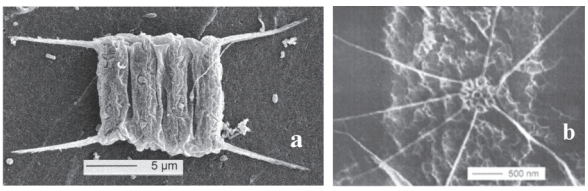

Fig. 16. *Desmodesmus pseudoprotuberans* strain Hegewald 1981–51 under the EM: (a) habitus; (b) rosette with excreted bristles.

For all studied taxa most base exchanges were in helix I and II: 21, in helix III there were two and in helix IV there were three (Fig. S6).

For the serie *Desmodesmus* most of the base exchanges were in loops. If we count the changes in helices only, the *D. communis* is distinguished from *D. rectangularis* and from *D. pseudocommunis* by one base only, from *D. protuberans* by two and from *D. pseudoprotuberans* and *D. schmidtii* by three.

DISCUSSION

The recent unforced conservation of the species name *Achnanthes* (*Scenedesmus*) *quadricauda* TURPIN in the ICBN (Greuter 2000) should be followed. However, we do not recommend doing it, because this conservation has to be reconsidered. Beside the fact, that *A. quadricauda* is related to the *Desmodesmus armatus*–group, but different from *Desmodesmus communis* (HEGEWALD 1977), it makes no sense, to retain a name

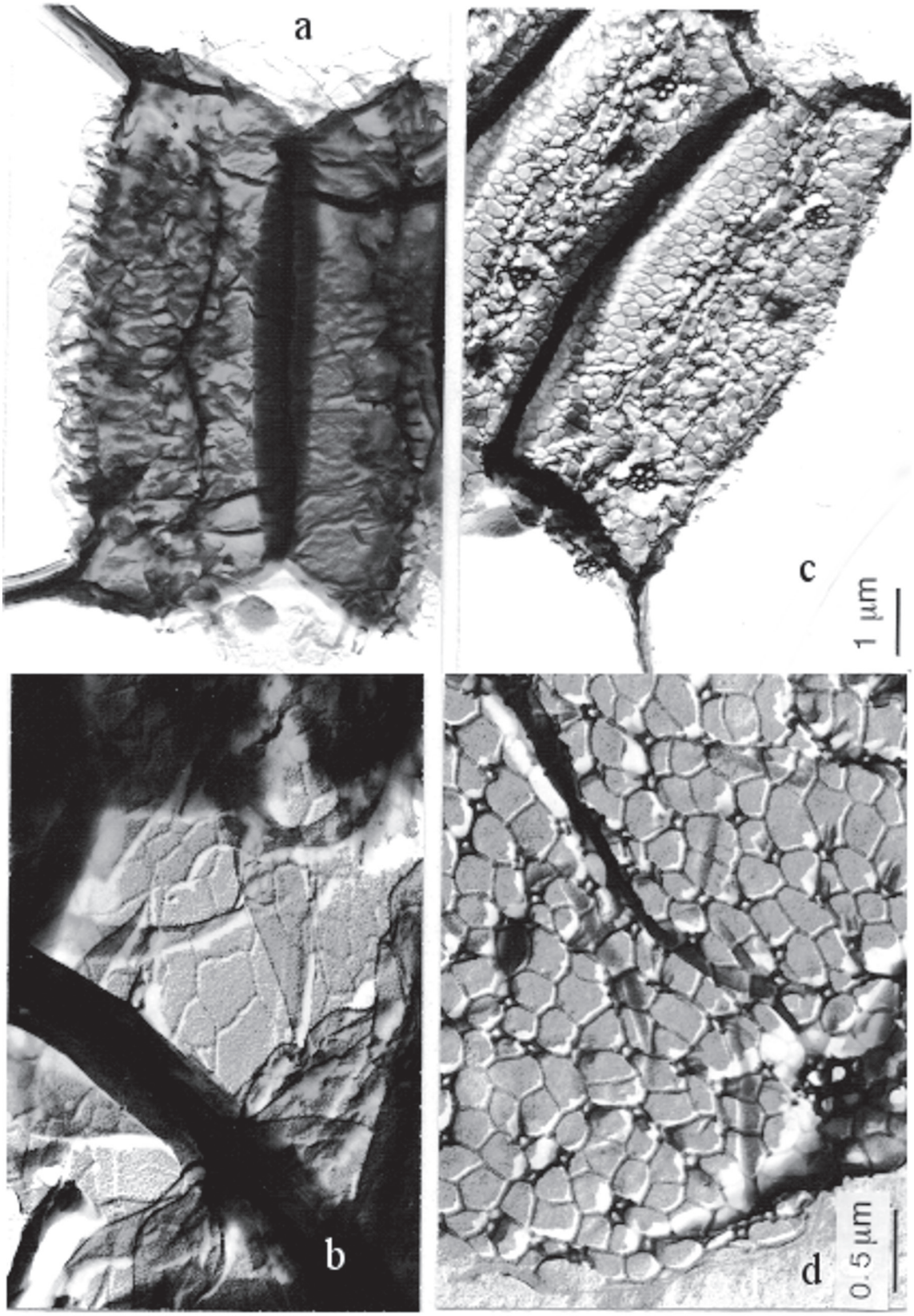

Fig. 17. *Desmodesmus schmidtii*, strain Hegewald 1971–257: (a) cell wall ultrastructure; (b) detail; *Desmodesmus communis* strain Bai 1971–26; (c) cell wall ultrastructure; (d) detail. Both strains are isolated from the same pond (Belsõ–tó, Hungary). Scale in b also for a, scale in d also for c.

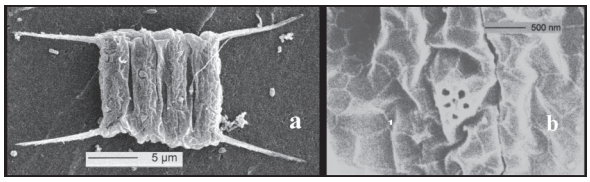

Fig. 18. *Desmodesmus schmidtii*, strain Hegewald 1981–14: (a) habitus; (b) rosette and delicate cell wall structures under the SEM.

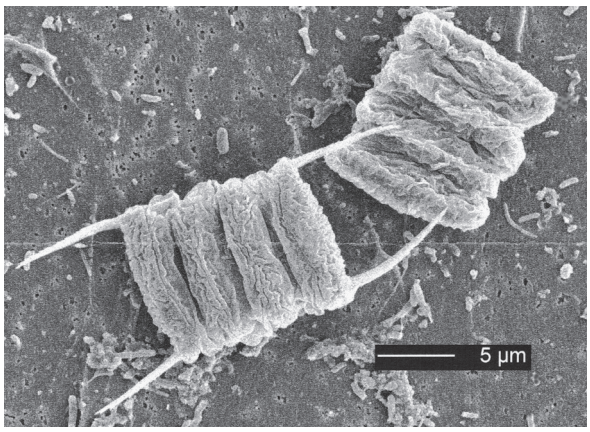

Fig. 19. *Desmodesmus schmidtii*, strain Hegewald 1971–257: a spiny and a spineless coenobium under SEM.

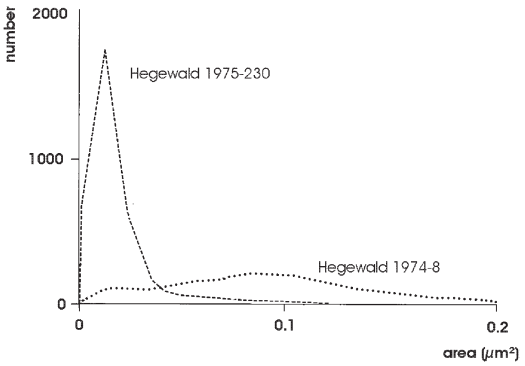

Fig. 20. Distribution of mesh sizes of two strains, Hegewald 1974–8 *Desmodesmus communis* and Hegewald 1975–230 *Desmodesmus pseudocommunis* f. *verrucosus*.

with author name, but exclude its type and use instead as type a strain of a different taxon "[specimen from strain] Hungary, Lake Belsö–tó, Hegewald 1971/ 256 (Research Center Jülich, Germany) (typ. cons.)". This strain was already the type of *Scenedesmus communis* HEGEWALD (1977) and it cannot be used for two different taxa. The strain was lost years ago. However, fixed samples of the strain were distributed to different herbaria. This strain was isolated in 1971, hence about 150 years after the description of *Achnanthes quadricauda*.

The first illustration of the *A. quadricauda* was about 1820 by TURPIN (1816–1829). This taxon is similar to *D. armatus* var. *longispina* (CHODAT) E.HEGEWALD et HINDÁK, while *A. quadricauda* of TURPIN (1828) resembles *D. opoliensis* (P. RICHT.) E.HEGEWALD as discussed by CHODAT (1913, 1926), see also HEGEWALD (1977). In order not to not fall back to the confusion of the past, we recommend using the name *Desmodesmus communis* (E.HEGEWALD) E.HEGEWALD for a well–defined taxon instead of using of the name "*Achnanthes/ Scenedesmus quadricauda*". Sporadically in literature the combination *"Desmodesmus quadricauda* (TURPIN) E.HEGEWALD" was also found, but it is an invalid combination. E. HEGEWALD never used such a combination and would not do so.

A synopsis for the group studied here is given in Fig. 1. The *D. communis* was well described by HEGEWALD (1977). However, our studies here, based on EM and DNA, showed the existence of several closely related taxa. The *D. communis* is in nature a common taxa (Table S1). Under light microscope, under electron microscope and/or according to ITS–2 base sequence it was distinguishable from other taxa of the group. *Desmodesmus communis* had a wide range in cell size and all other taxa studied here were within this cell size range, except the *D. protuberans* which had the outer cells longer than inner of the coenobia (for our comparison only inner cells of the coenobia were measured) and additionally it had more elongated cells than *D. communis*. For *D. protuberans* a forma *minor* was also described by LEY (1947). Its cell size range was 22–25 µm, hence in the range of *D. protuberans*. The *D. protuberans* var. *communioides* differed from *D. protuberans* var. *protuberans* in two bases only, but it is somewhat smaller in cell size and the outer cells of the coenobia were not or only slightly longer than the inner cells. Morphologically it was hardly or not at all possible to distinguish the taxon from *D. communis*. In ITS2 it differed from *D. communis* and was clearly close to *D. protuberans* (Fig. S1), hence we treated it as a variety of *D. protuberans* and not of *D. communis*. The first author, although he studied the genus for decades, had determined the strain UTEX 76 as *D. communis* (HEGEWALD 1989). The strain UTEX 76 is identical with strain SAG276/4b (HEGEWALD 1982), hence both strains were not *D. communis* but *D. protuberans* var. *communioides*. The taxa *D. communis* and *D. protuberans* var. *communioides* needed ITS2 determination for reliable identification. Because the first author has been retired for several years, we had no chance to culture, measure and sequence all doubtful strains. Hence the taxonomy of *D. protuberans* and *D. communis* could not yet be finally resolved. The strains of *D. communis* were identical in ITS2 (exept strain Hegewald 1977–170, isolated from Lake Titicaca, Peru) while *D. protuberans* and its variety had several strains with base exchanges (Fig. 17), e.g. UTEX 76 (GenBank AM410660) and SAG 276/4b (unpublished data of KITSCHKE) had one base exchange (position 221), and strains EH 52, EH 84, ET 85 of VANORMELINGEN in position 24.

The cell size depended on temperature (KOMÁREK & RUŽIČKA 1969) and other culture condi-

tions as was shown in Table 4. Medias having low salt concentration produced smaller cells. Therefore in medium CHU X the smallest cells were always produced, in the medium of Pringsheim with additional CO_2 the largest coenobia were produced. Intermediate were cultures with medium Pringsheim, but without additional CO_2. Hence for the group (serie *Desmodesmus*) studied herein, the cell size is not always useful for distinguishing the studied taxa.

Desmodesmus curvatocornis was not a true planktonic species, in culture the strain Hegewald 1977–144 was "foaming in pack" and sedimentated easily. Although it is not different from *D. communis* in ITS2 it is morphologically strikingly different from that species and a relationship between these species was never suspected. However, it was overlooked that the outer cell wall layer was visible between the cell poles even under the light microscope, which clearly indicates its relationship to *D. communis*. The spines of the taxon are short and often strongly curved. Extraordinary for the subsection are the single tubes scattered on the surface (Figs 5c, e). Eventually these are responsible for the above mentioned cell packs.

The *D. rectangularis* differed under the light microscope from *D. communis* var. *communis* in cell shape and spine length. The cell tips were not acute as in the typical variety but were obtuse to truncate. Additionally short spines were often produced in a polar region on one of the cell poles of the outer cells and of the neighboring cell of the coenobia (e.g. ACOI 1438 sub nom. „Scenedesmus smithii Chodat", see http://acoi.ci.uc.pt/spec_detail.php?searchSpecie2=ACOI-1438&cult_id=1498 and Fig. 6). The *Scenedesmus smithii* Chodat had some morphological similarity, but the taxon had a much smaller cell size than *D. rectangularis* and it seems to be another taxon. All seven strains of *D. rectangularis* had only two differences in ITS2 compared to *D. communis*: a semi–CBC in helix I and one exchange in the end loop of helix III (Fig. 16).

The five strains of *D. pseudocommunis* and its variety and forma, had compared to *D. communis* one semi–CBC and 5 exchanges in loops (Fig. 18).

The five sequenced strains of *D. pseudoprotuberans* (including its variety and its forma) had eight differences to *D. communis*: four in loops, one additional base in a loop and three semi–CBC´s (Fig. 19). The morphology of species resemble *D. protuberans* by longer outer than inner cells but it is smaller in size.

In Fig. 21 the development of the different taxa was shown. Most taxa apparently were developed in one step only, but in the *D. pseudocommunis*–branch the subtaxa f. *verrucosus* and var. *texanus* (not mentioned in Fig. 21 because not ITS2 data were available) were included. These taxa differ not in ITS2 (as far as analyzed), but in cell wall ultrastucture only. However, the "*D. protuberans* branch" is subdivided and included *D. protuberans* and its var. *communioides*, *D. pseudoprotuberans* and *D. schmidtii*. All these taxa were similar in cell wall ultrastructure to *D. communis* (although reduced structures in *D. schmidtii*) but differed in ITS2.

Although the differences of the taxa in ITS2 are low in number, these differences were consistent in all strains of the taxa. We put our main weight on the ITS2 data and on the cell wall ultrastructure.

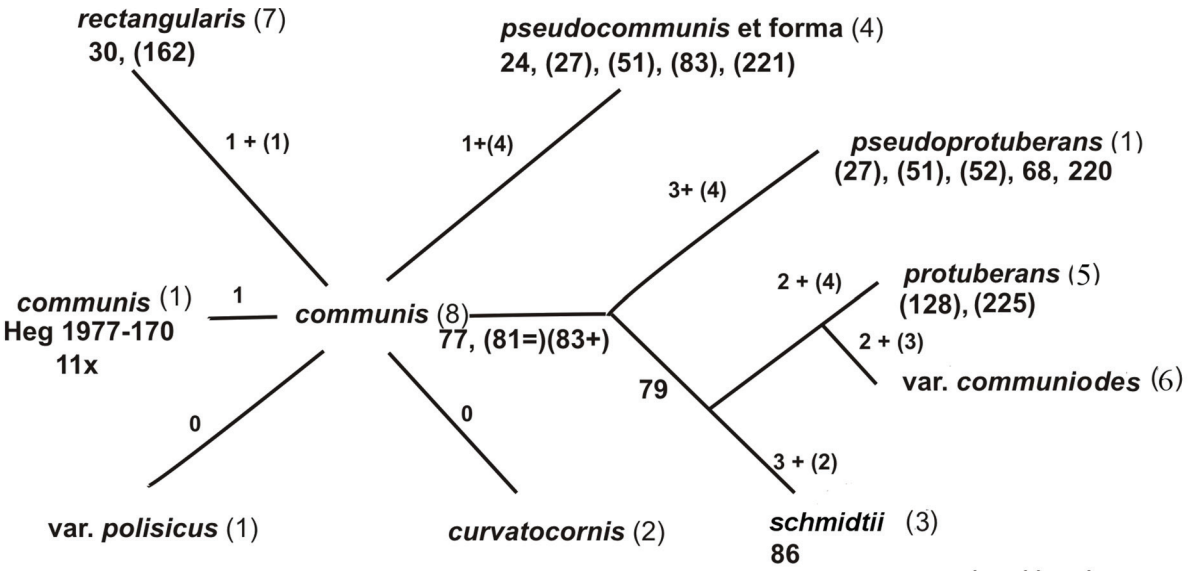

Fig. 21. Differences between *D. communis* and related taxa according to ITS–2 base composition. Number in brackets after taxon name: number of sequenced strains; number below taxon name: position of bases exchanged (see Figs 17–20). Number without brackets: exchange in helix; with brackets: exchange in loop; number followed by "=": base exchange resulted in a new base pair; number followed by "x": base exchange resulted in breaking of base pair; 83+: additional base after position 83; number above final branches: number of base exchanges; number below branches: base position exchanged in all taxa of the following cluster.

Table 3. Cell size of cultures in different media or methods: (a) medium Pringsheim, bubbled with 1% CO_2; (b) Medium Pringsheim, shaken cultures; (c) medium CHU X, shaken cultures; (L) length; (W) width.

	culture method	L × W average	L / W	L × W min–max
Desmodesmus communis				
Bai 1971–26	a	12.0×4.3	2.9	10.8–13.2×3.6–5.4
	b	10.3×3.4	3.1	9.0–11.4×3.0–4.2
	c	9.5×3.2	3.0	8.4–11.4×2.7–3.9
Hegewald 1971–256	a	11.6×4.4	2.7	10.2–13.8×3.3–5.4
	b	10.4×3.7	2.9	9.0–13.2×2.5–5.4
	c	9.3×3.1	3.0	8.4– 9.6×3.0–3.3
Hegewald 1973–66	a	14.7×5.2	2.8	12.0–18.6×3.9–6.6
	b	14.2×4.0	3.6	12.6–18.0×3.0–6.3
	c	12.4×4.7	2.6	10.8–13.8×3.9–5.4
Desmodesmus pseudoprotuberans **E.HEGEWALD**				
Hegewald 1973–293	a	16.4×6.0	2.8	15.0–18.6×4.8–7.2
	b	17.5×5.0	3.5	15.0–19.2×4.2–6.6
	c	16.0×5.3	3.0	12.0–18.0×3.9–6.0
Hegewald 1973–295	a	16.9×6.8	2.5	15.0–18.0×4.8–7.8
	b	18.3×5.6	3.4	15.0–22.8×3.6–7.8
	c	14.0×4.7	3.0	12.0–18.6×3.6–6.6
Hegewald 1973–303	a	17.2×6.9	2.5	14.4–18.6×6.0–7.8
	b	17.8×5.9	3.1	15.0–21.0×5.4–6.6
	c	14.5×5.0	2.3	12.6–16.8×4.2–6.0
Desmodesmus protuberans				
Hegewald 1971–23	a	20.9×5.3	3.9	18.0–25.2×4.2–6.6
	b	21.8×5.2	4.3	18.0–24.0×3.6–6.3
	c	20.3×5.5	3.7	18.0–24.0×4.5–6.0

SUMMARY

The serie *Desmodesmus* ("*D. communis* group") includes several taxa and some of these were difficult to distinguish. *Desmodesmus communis* had a wide range of characteristics and for its differentiation to *D. communis* var. *polisicus* and *D curvatocornis* morphological and cell wall ultrastructural characteristics were necessary. Although *D. protuberans* var. *protuberans* was morphologically clearly distinct, its var. *communioides* was similar to *D. communis* and ITS2 data were necessary for distinguishing these taxa. Cell wall ultrastructures or ITS2 alignment based on secondary structure information served for the identification of *D. pseudocommunis, D. smithii, D. rectangularis* and *D pseudoprotuberans*.

While the for *D. communis* as typically suspected, quadricaudate spination were found in *D. communis*, its var. *polisicus* and in *D. protuberans, D. pseudocommunis* and *D pseudoprotuberans*. The *D. schmidtii* also produced additionally bicaudate and spineless (!) coenobia. *Desmodesmus rectangularis* and *D. curvatocornis* had often in addition short spines on outer and or inner cells, while *D. pseudocommunis* var. *texanus* sometimes had short spines scattered over the cell wall surface or arranged in short rows.

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Supplementary material

the following supplementary material is available for this article:

Table S1. List of strains, locality of origin and GenBank number.

Table S2. Size measurements of cultured strains.

Table S3. Pairwise comparison of the strains of the serie *Desmodesmus*.

Table S4. Key for LM characteristics for Subsection *Desmodesmus.*

Table S5. Key for EM characteristics.

Table S6. Key for ITS–2 characteristics. Numbering of bases see Fig. S1.

Fig. S1. Differences in ITS–2 base composition between *D. communis* strain Hegewald 1974–35 and all strains of *D. rectangularis.*

Fig. S2. Differences in ITS–2 base composition between *D. communis* strain Hegewald 1974–35 and all strains of *D. protuberans* et var.: (1–5) *D. protuberans* var. *protuberans*, (1) Hegewald 2000–1, (2) Hegewald 1971–23, (3) Hegewald 1996–10, (4) AICB 141, (5) RMUO8; (6–13) *D. protuberans* var. *communioides*, (6) CCALA 464, (7) Hegewald 1997–2, (8) UTEX 76, (9) EH 50, (10) ET93, (11) EH 52, (12) EH 84, (13) ET 85. Base exchanges in one strain only were neglected.

Fig. S3. Differences in ITS–2 base composition between *D. communis* strain Hegewald 1974–35 and all strains of *D. pseudocommunis* and its f. *verrucosus.*

Fig. S4. Differences in ITS–2 base composition between *D. communis* strain Hegewald 1974–35 and all strains of *D. pseudoprotuberans.*

Fig. S5. Differences in ITS–2 base composition between *D. communis* strain Hegewald 1974–35 and two strains of *D. schmidtii.*

Fig. S6. Differences in ITS–2 base composition between *D. communis* strain Hegewald 1974–35 and all other taxa of the series *Desmodesmus*.

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