

of two triads with a mean value of the triangle's branches of 46.00  $\mu\text{m}$  and 47.33  $\mu\text{m}$  respectively. The mean of the two values is 46.66  $\mu\text{m}$  and clearly shows a "Wide" type dispersion of the pores. The same algorithm can be used for the inner side of the valve displayed in the Fig. 1B and one gets a DI value of 38  $\mu\text{m}$  which confirms the "Wide" type dispersion computed for the external surface of the valve.

**Identification of StPC on the inner side of the valve.** This is an important aspect of the protocol for the description of these structures as discussed by Hanai (1970). StPC are visible on the inner side on valves where the non-calcified inner lamella is removed (Figs 1B, 3D–E). In well-calcified and well-preserved valves the apertures of tubuli are visible on the inner wall of the carapace (Figs 2A–D, 3D–E, 15A–B).

**The statistics used.** Quantitative data were expressed as arithmetic means with 95% confidence limits. This latter gives an indication of how much uncertainty there is in our estimate of the true mean.

The G-test for association between two variables using a contingency table (Sokal & Rohlf 1995) was applied to the spatial distribution of round and oblong StPC observed on two valves of *Gomphocythere besni*. For the computation of G-test we used the Williams' correction (Fowler *et al.* 1998). Values above the critical value 3.84 of the chi-square distribution at  $P = 0.05$  are considered as significant difference between the distribution of the two variables (Table D in Rohlf & Sokal 1995).

The Mann-Whitney U-test (Sokal & Rohlf 1995) was used to compare the differences existing between the medians of the diameter size of round StPC of *Gomphodella aura* and *G. quasihirsuta*. Using this non-parametric statistic we also analysed the difference between the spatial areas of the round and oblong StPC observed on *Gomphodella quasihirsuta*. The U-statistics for our data were compared with the critical values of Table U in Rohlf & Sokal (1995).

The Kendall rank correlation coefficient (known also as Kendall's tau coefficient) was applied for the examination of the possible existence of an association between the number of tubuli and the size of the StPC area. The Kendall rank correlation coefficient is a simple statistic belonging to the group of non-parametric tests for association between two quantities measured on an ordinal scale (Sokal & Rohlf 1995). The value of the coefficient tau gives "the degree of association or correlation between the two sets of ranks. The sampling distribution of tau under the null hypothesis is known and therefore tau...is subject to tests of significance (Siegel 1956, p. 214). Data were computed with the software package Biom-3.30 (Rohlf & Slice 1999); for significance values of tau we used the statistical table S in Rohlf & Sokal (1995). We applied this non-parametric test for association to data belonging to *Cytheridella ilosvayi* (sensu lato), *Gomphocythere besni*, *Gomphocythere* sp. (aff. *G. angulata* Lowndes), *Gomphodella maia* and *Gomphodella quasihirsuta*.

## Results

### Morphology of StPC for selected taxa of the subfamily Timiriaseviinae Mandelstam, 1960

#### Representatives of the tribe Cytheridellini Danielopol & Martens, 1989

##### *Gomphocythere* Sars, 1924

***Gomphocythere besni* Klkyliođlu, Yavuzatmaca, Cabral & Colin, 2015.** The A2 pores are visible and could be mapped (Fig. 6V-2). There are five sub-marginal A2 pores in the anterior quarter of the valve, one placed more posteriorly on the anterior half (pore 13), three pores in the central third of the valve (numbered as pores 6, 7, 8) and four pores in the posterior quarter (the pores 9–12). The peculiar structure of the A2 pore and seta as compared to the A1 entity are presented in the Figs 6A–F. The diameter of the A2 pore is 2.2  $\mu\text{m}$  leaving space for a seta with a diameter of 0.94  $\mu\text{m}$  and a length of 55  $\mu\text{m}$ . A well developed rim surrounds the pore. The space left between the A2 seta and the outer canal represents 43 % of the pore's radius. The A1 pore has no rim and displays a diameter of 1.9  $\mu\text{m}$ , from which emerges a seta with a diameter of 1.6  $\mu\text{m}$  and a length of 29  $\mu\text{m}$ . The space between A1 pore's lumen and the seta represents only 15 % of the pore's radius. The A2 seta is about 40% thinner and about 90% longer than the seta of A1.

The B pores are distributed on the surface area of the tectum of the valves (Figs 10–13, 15D). They do not penetrate the depressions (e.g. foveolae) or incisures (like sulci) of the valve. The sieve-plates of *G. besni* can be classified in two basic shapes, round and oblong. These pores are of reduced size, as compared to those of the

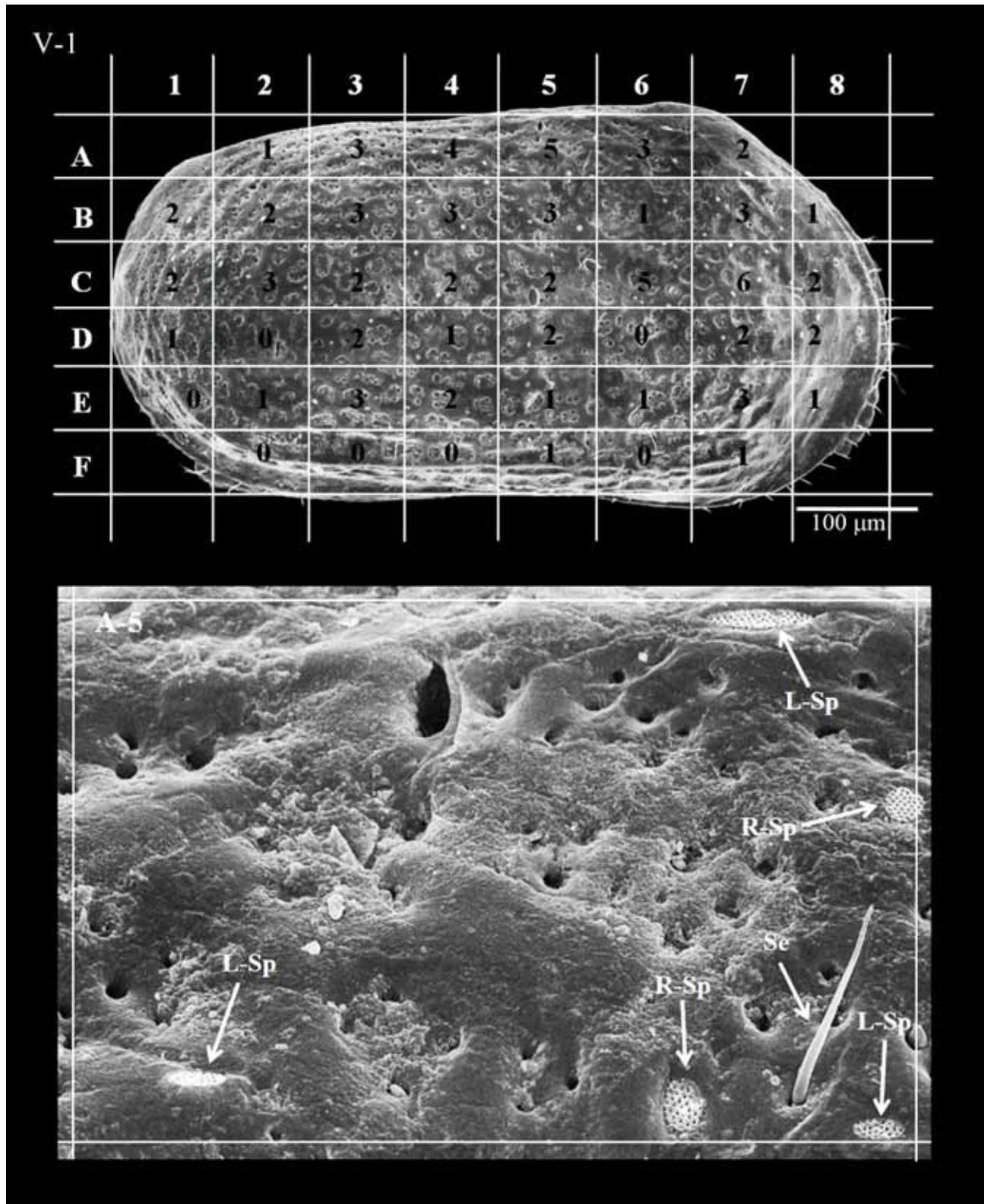
Cytherideidae we studied (cf. next section). The diameter is 3.8  $\mu\text{m}$  and the mean surface 11.75  $\mu\text{m}^2$  (Table 1). The mean number of tubuli is 28. The oblong StPC display a mean area of 9.75  $\mu\text{m}^2$  and do not differ much in the density of tubuli as compared to the round ones, namely 23 (CL95% 17–29).

**TABLE 1.** Characterisation of StPC, *Gomphocythere besni* Klkyliglu, Yavuzatmaca, Cabral & Colin, Adiyaman, Turkey; RVf, specimen V-1, Length 0.649 mm.

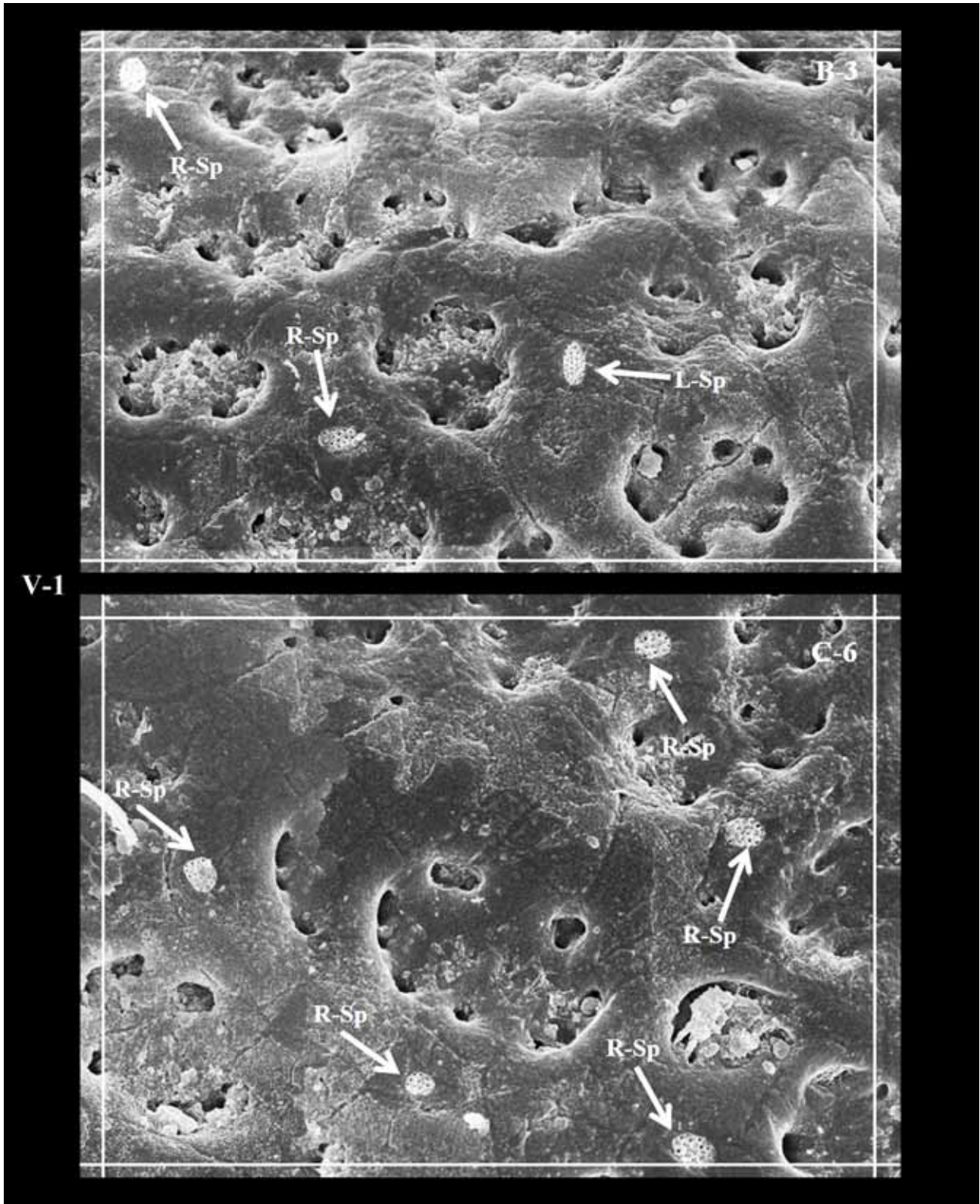
Shape-type	Observation n°	Length ( $\mu\text{m}$ )	Area ( $\mu\text{m}^2$ )	Number Tubuli
Round StPC		Diameter		
-“-	1	4.9	18.85	47
-“-	2	3.67	8.34	23
-“-	3	3.9	8.34	21
-“-	4	4.68	17.19	46
-“-	5	3.8	11.34	27
-“-	6	3.2	8.04	20
-“-	7	3.2	8.04	16
-“-	8	4	12.56	33
-“-	9	4	12.56	27
-“-	10	3.5	9.61	18
-“-	11	5	19.62	49
-“-	12	3.6	10.17	32
-“-	13	3	7.65	14
-“-	14	3.7	10.75	18
-“-	15	3.4	9.07	29
	Mean (n 15)	3.80	11.75	28
	CL95%	3.46–4.16	9.54–13.88	22–34
Oblong StPC		Ellipse axis $\frac{1}{2} l e_1 \times l e_2$		
-“-	1	2.48x1.19	9.26	23
-“-	2	2.76x1.38	11.96	30
-“-	3	1.84x0.92	5.31	14
-“-	4	1.38x0.55	2.38	10
-“-	5	2.76x1.1	9.53	29
-“-	6	3.95x0.9	11.16	33
-“-	7	2.76x1.38	11.96	22
-“-	8	3.21x1.1	11.08	18
-“-	9	2.76x0.92	7.97	27
	Mean (n 9)		9.75	23
	CL95%		6.59–12.92	17–29

The number of the StPC observed on the two valves mapped is variable in total number as well as the numbers of the two shapes (Table 2). The total number for the 44 cells in the two valves is 83 and 117, respectively. We observed a spatial difference in the number of pores between the 20 peripheral cells and the central (inner spaced) cells, namely the oblong pores are more numerous at the periphery while the round ones display a higher relative frequency within the central area of the valve (Table 2). Figures 10 and 12, upper panels, display the spatial variability of the number of StPC between the 44 cells (each cell approximates an area of 4200  $\mu\text{m}^2$ ). Within selected homologous cells, namely the A-5, B-3 and C-6 (Figs 10–13), one can see the variability of the position and of the number of the round and oblong StPC. For a more precise evaluation of the mean density of StPC related to the standardised surface area of the valve we calculated the number of StPC entities within those cells which

cover 100 % of the valve's surface for both V-1 and V-2 valves. Table 3 shows for *G. besni* the mean number and the total variability expressed as a range, namely 2.4 respectively 3 StPC per cell with a range of 6, respectively 8 entities. If we take an approximate value of 3 entities for an area of 4200  $\mu\text{m}^2$  and we extrapolate to a standardized area of 5000  $\mu\text{m}^2$  we get 4 StPC.

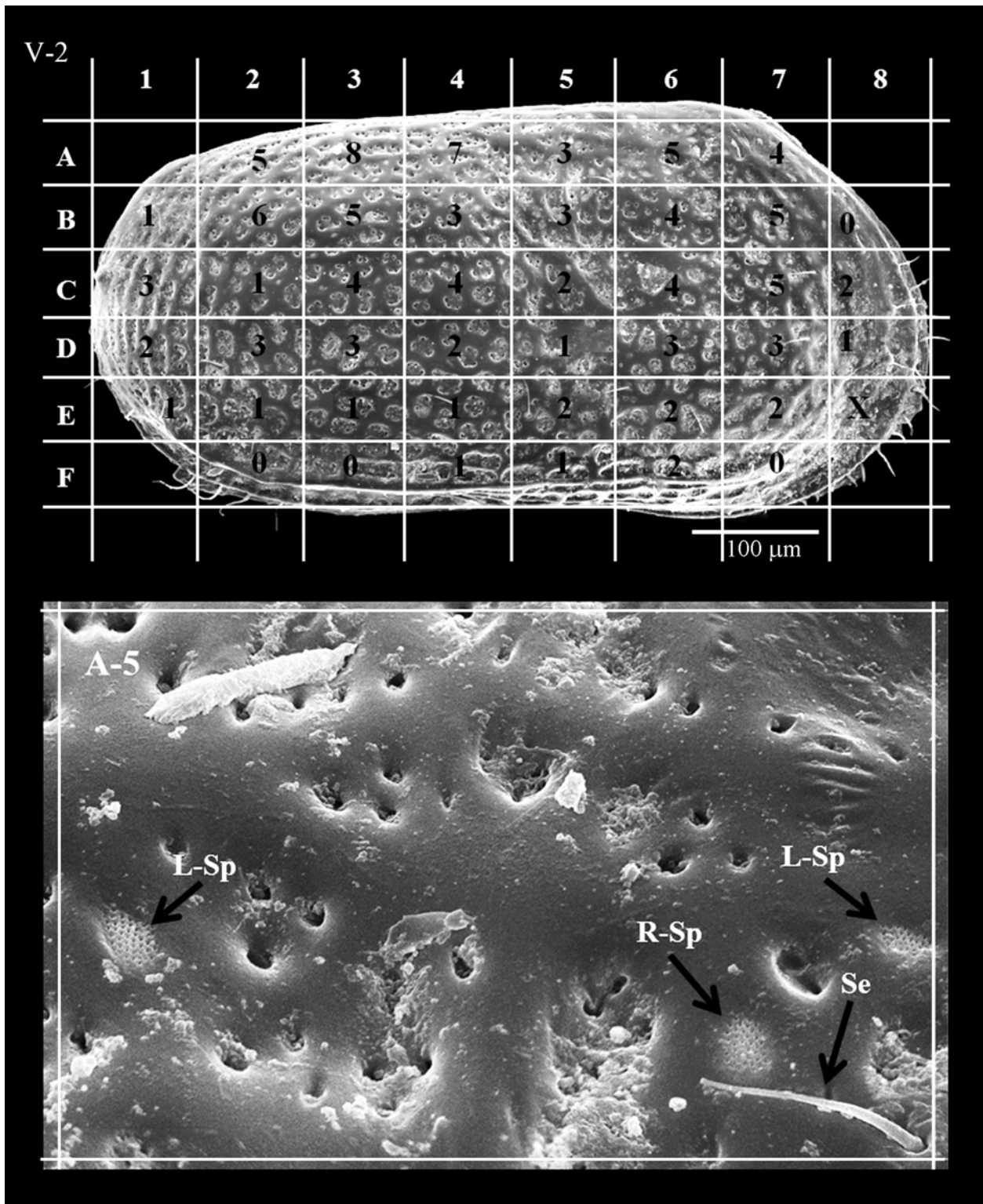


**FIGURE 10.** *Gomphocythere besni* Klkyliglu, Yavuzatmaca, Cabral & Colin., Adiyaman, Turkey, RVEf, specimen V-1; Upper panel—density of StPC/per cell (total number cells with StPC, 44, surface of one cell, about 4200  $\mu\text{m}^2$ ); Lower panel—Cell A-5, details of the spatial distribution of StPC (R-Sp—Round StPC; L-Sp—Oblong StPC; Se—Seta emerging from an A1 pore).

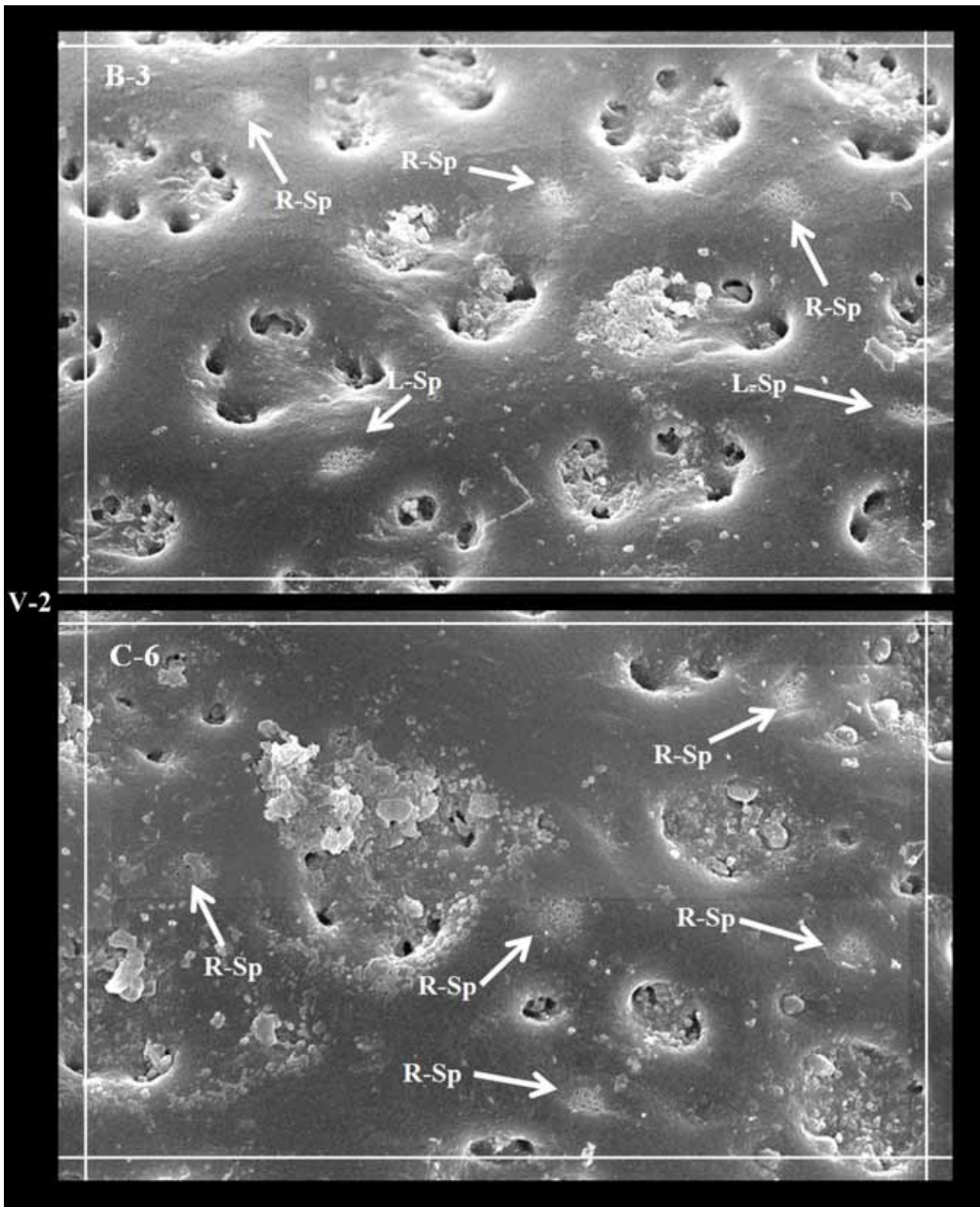


**FIGURE 11.** *Gomphocythere besni* Külköylüoğlu, Yavuzatmaca, Cabral & Colin, Adiyaman, Turkey, RVEf, specimen V-1, details of the spatial distribution of StPC; Upper panel—Cell B-3; Lower panel—Cell C-6 (symbols as for Fig. 10).

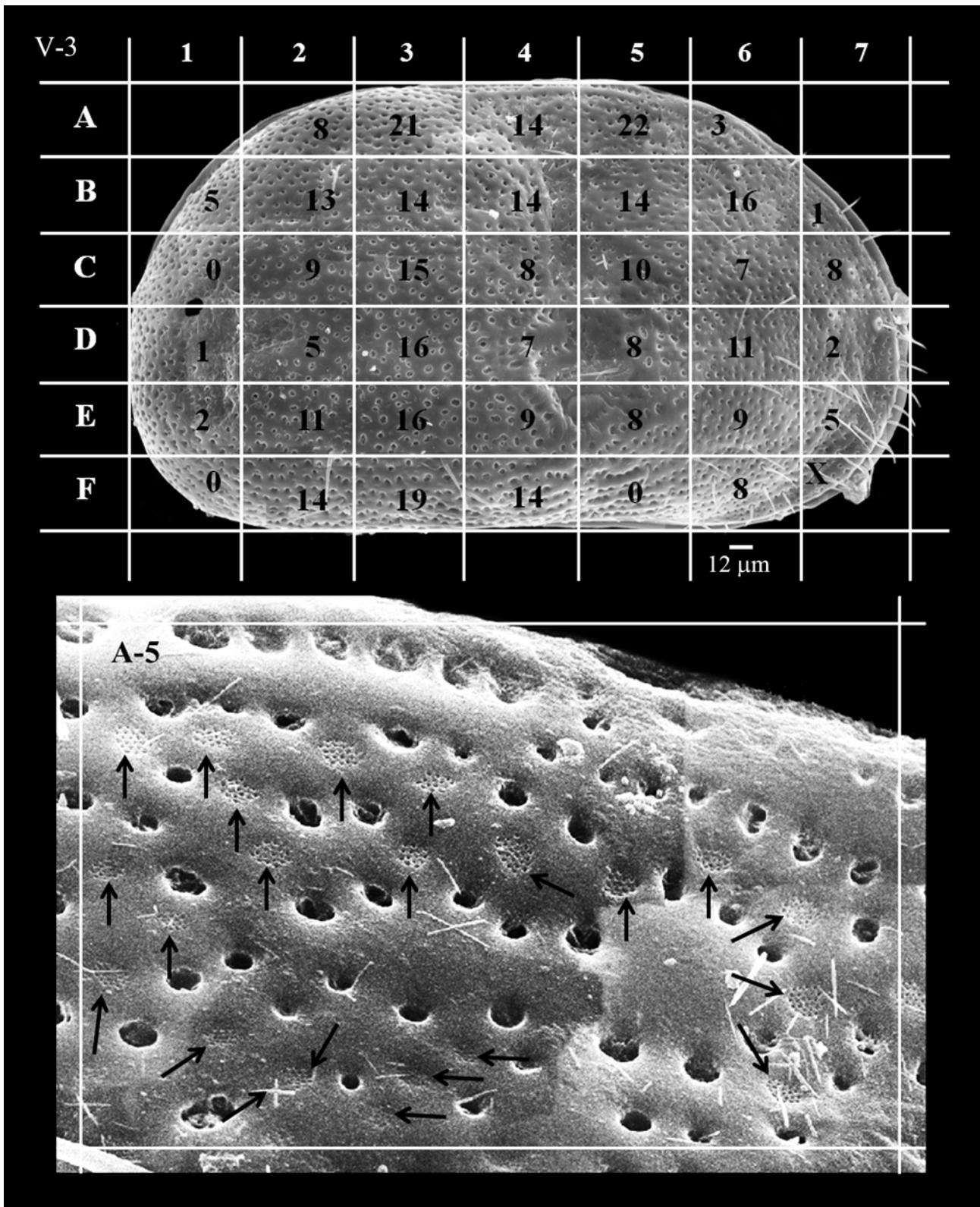




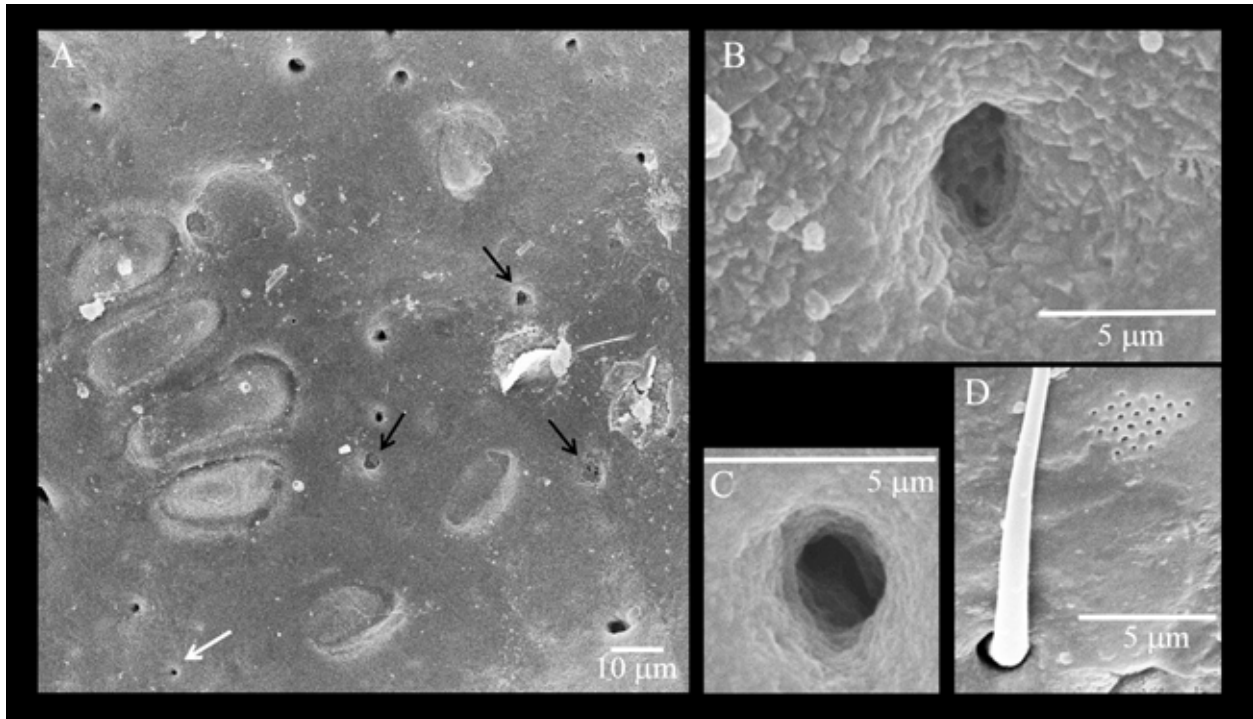
**FIGURE 12.** *Gomphocythere besni* Külköylüoğlu, Yavuzatmaca, Cabral & Colin, Adıyaman, Turkey, RVEf, specimen V-2; Upper panel—density of StPC/per cell (total number of cells with StPC, 43, surface of one cell, about 4200  $\mu$ m<sup>2</sup>; X—cell not examined); Lower panel—Cell A-5, details of the spatial distribution of StPC (symbols as for Fig. 10).



**FIGURE 13.** *Gomphocythere besni* Külköylüoğlu, Yavuzatmaca, Cabral & Colin, Adiyaman, Turkey, RVEf, specimen V-2, details of the spatial distribution of StPC; Upper panel—Cell-B3; Lower panel—Cell C-6 (symbols as for Fig. 10).



**FIGURE 14.** *Gomphodella maia* De Deckker, Turner Springs, Australia, RVEf, specimen V-3; Upper panel—number of StPC/ per cell; total number cells examined, 39 (X—cell not examined); surface of one cell, about 2200 µm<sup>2</sup>; Lower panel—Cell A-5, spatial distribution of StPC (arrows indicate location of StPC).



**FIGURE 15.** *Gomphocythere besni* Külköylüoğlu, Yavuzatmaca, Cabral & Colin, Adıyaman, Turkey, details of the StPC; A–C, details of LVIf; A—central area with apertures of StPC (black arrows) and of a pore A (white arrow); B—enlarged view of StPC from A; C—aperture of pore A1 from A; D—RVEf, pore B and pore A1 with seta.

**TABLE 2.** Frequency distribution of StPC on two RVEf specimens, V-1 (Fig. 10) and V-2 (Fig. 12) of *G. besni* Külköylüoğlu, Yavuzatmaca, Cabral & Colin, Adıyaman, Turkey; N—number of StPC; Peripheral space = cumulated area of 20 cells, Central space = cumulated area of 24 cells (Figs 10 and 12).

Shape of StPC	N—Peripheral space	N—Central space	Totals N
Valve V-1			
Round-shape	13	37	50
Oblong-shape	18	15	33
Totals N	31	52	83
Valve V-2			
Round-shape	13	50	63
Oblong-shape	33	21	54
Totals N	46	71	117

**TABLE 3.** Number of StPC in Full-surface cells (Fs–cell) of the valves belonging to *Gomphocythere besni* Külköylüoğlu, Yavuzatmaca, Cabral & Colin and *Gomphodella maia* De Deckker; N—number of entities (original data, in the upper panels of Figs 10, 12, 14). Fs–cell = 100% coverage of valve surface.

Species	Valve	Fs–cells N	Cell Area ( $\mu\text{m}^2$ )	StPC Total N in Fs–cells	StPC Mean/cell	N—StPC Min.-Max.
<i>G. besni</i>	RVf-1	25	4212	62	2.4	1-6
<i>G. besni</i>	RVf-2	30	4195	90	3	1-8
<i>G. maia</i>	RVf	25	2200	310	12.4	5-22



**TABLE 4.** Total Area of Tubuli for Standardised StPC computed for *Gomphocythere besni* Kulköylüoğlu, Yavuzatmaca, Cabral & Colin, *Gomphodella maia* De Deckker, *G. aura* Karanovic, *G. quasihirsuta* Karanovic, compared to *Limnocythere sanctipatricii* Brady & Robertson, *Cyprideis torosa* (Jones), *Cyprideis americana* Sharpe. \*—unique value. (For additional information on computation, see “section 3.3”.—Quantitative analysis of the StPC.)

Taxa	Valve Length (mm)	N—Tubuli Counted	Tubuli Mean-Area ( $\mu\text{m}^2$ )	StPC N-Tubuli Mean & *	Total Area Tubuli ( $\mu\text{m}^2$ )
<i>G. besni</i>	RVf (0.649)	18	0.022	28	0.616
<i>G. maia</i>	RVf (0.402)	15	0.017	15	0.255
<i>G. aura</i>	LVf (0.508)	17	0.022	26	0.572
<i>G. quasihirsuta</i>	RVf (0.570)	15	0.036	20	0.720
<i>L. sanctipatricii</i>	RVf (0.9)	10	0.013	45	0.585
<i>C. torosa</i> (MEL-7)	RVm (1.06)	45	0.087	100*	8.7
<i>C. torosa</i> (MEL-7)	-“-	40	0.083	106*	8.798
<i>C. torosa</i> (CAR-P1)	RVf (0.85)	45	0.149	101*	15.049
<i>C. torosa</i> (CAR-P1)	-“-	40	0.144	127*	18.288
<i>C. americana</i>	RVf (0.9)	45	0.302	234*	70.668

Figure 15A displays on the inner side of the valve the aperture of pores type A (white arrow) and type B (black arrow). The size of the aperture of type B pore (Fig. 15B) compared to inner side of a type A pore (Fig. 15C) shows that there are differences, namely the former is larger, having a width of 3.4  $\mu\text{m}$  while the latter is smaller with a size of 2.2  $\mu\text{m}$ . The external side of the valve (Fig. 15D) displays similar differences between the size of an A pore (2.2  $\mu\text{m}$ ) and a sieve-pore (4.3  $\mu\text{m}$ ).

The area of total tubuli was calculated for the round sieve-plates which display a mean number of 28 tubuli (Table 4). Taking a mean area value per tubuli of 0.022  $\mu\text{m}^2$  we arrive to a total virtual tubular area of 0.616  $\mu\text{m}^2$ .

We noted also that in the case of the round StPC investigated for this species there is a trend of increasing number of tubuli within a StPC with the increase of the diameter of the total surface of the sieve-plate. This relationship is statistically expressed through the significant value of the Kendall’s tau coefficient (Table 5).

The Size Index for the round sieve-plates (Table 1) is 0.0058, therefore of Small-type.

The Distance Index values for the spatial distribution in the A-3—A-5, B-3—B-4 and C-6 cells of the V-1 valve and of the A-5, B-3 and C-6 cells of V-2 valve are higher than 10  $\mu\text{m}$ , range 21.6–45.2 (N 11). This points to a widely spaced dispersion-type for the StPC.

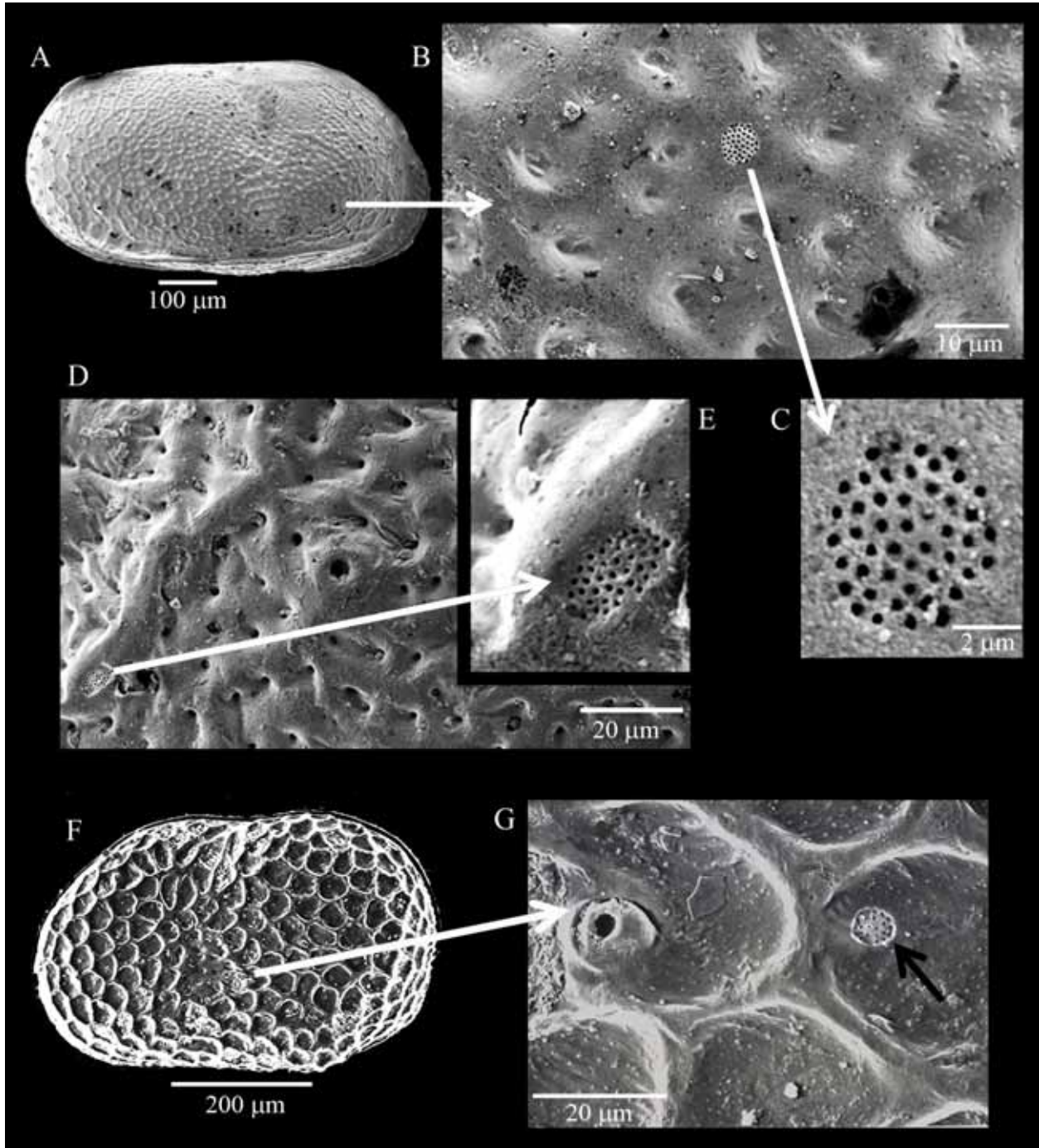
***Gomphocythere* sp. (aff. *G. angulata* Lowndes, 1932).** The valves we investigated display on their external side numerous fossae with random plications and muri (Fig. 16A). The A2 pores are only partly visible (Fig. 16A) because of the strong ornamentation. The type B pores are located on the plications, most of them are round (Figs 16B–C). On the muri one notices oblong-shaped sieve-plates (Figs 16D–E). StPC do not occur on the soli of the fossae.

**TABLE 5.** Kendall Rank Correlation for number of tubuli with the size of StPC area for five Timiriaseviinae taxa *G.g.*—*G. quasihirsuta*; R—Round; O—Oblong.

Taxon	Original data	N—Sample size	Kendall’s Tau Correlation coefficient	P—Significance
<i>Gomphocythere besni</i>	Table 1	24	0.575	P < 0.01
<i>Gomphocythere</i> sp.	Table 6	21	0.464	P < 0.01
<i>Cytheridella ilosvayi</i>	Table 7	15	0.624	P < 0.01
<i>Gomphodella maia</i>	Table 9	21	0.593	P < 0.01
<i>G. quasihirsuta</i>	Table 11	32	0.564	P < 0.01
<i>G.g.</i> —R-morphotype	-“-	16	0.667	P < 0.01
<i>G.g.</i> —O-morphotype	-“-	16	0.496	P < 0.01

The round sieve-plates (Table 6) display an average diameter of  $4.67\ \mu\text{m}$  and a mean surface of  $17.43\ \mu\text{m}^2$ ; the mean number of tubuli is 33 (CL95% 29–37). The size of oblong StPC is comparable to those of the round ones (Fig. 16E, Table 6).

As in the case of *G. besni* we noted a positive trend of the number of tubuli increasing with the size of the diameter and/or of the surface of the StPC. Using the value of the Kendall's tau coefficient we note that this relationship is statistically significant (Table 5).



**FIGURE 16.** Sieve-type pores of *Gomphocythere* taxa; A–E, *Gomphocythere* sp. (aff. *G. angulata* Lowndes), Lake Bogoria, core Bogoria 1, Kenya, RVEm; A—general view; B–E—details of the position and shape of a round and oblong StPC; F–G, *Gomphocythere* sp. (aff. *G. alata* Rome), Lake Tanganyika, S-W at Cameron Bay, Burundi, LVEf; F—general view; G—details of StPC (black arrow) and of pore A2.

The value of the SI index characterising the size of the round sieve-plates is 0.0064 (Table 6). It was calculated from 14 StPC of the RVm with a length of 700  $\mu\text{m}$  and the mean diameter of 4.46  $\mu\text{m}$ . The spatial distribution of the StPC is of W-type with values for the DI ranging from 28  $\mu\text{m}$  to 45.3  $\mu\text{m}$  (N 7).

***Gomphocythere* sp. (aff. *G. alata* Rome, 1962).** The species is remarkable for its reticulate ornamentation of the valve (Figs 16F–G). The muri are steep and thin, surrounding large fossae. Both the A2 pore and the sieve-plate (B pore) are located on the solum of the fossa. The diameter of the A2 pore for the valve we illustrate here (Fig. 16G) is 2.64  $\mu\text{m}$  while that of the B pore is 6.41  $\mu\text{m}$  (with a surface of 32.27  $\mu\text{m}^2$ ). There are 25 tubuli. The SI value for the studied valve (LVf) is 0.0112 (6.41/571), therefore of Large-type.

A second left valve we examined had round sieve-plates with a diameter of 6  $\mu\text{m}$  (i.e. a surface of 28.27  $\mu\text{m}^2$ ). There are 45 tubuli. The SI value is 0.0131 (6/456), which confirms the Large-type peculiarity of the pore size for this taxon.

**TABLE 6.** Characterisation of StPC, *Gomphocythere* sp. (aff. *G. angulata* Lowndes), Lake Bogoria, Kenya; Observation n°: 1–4, LVf, Length 0.909 mm; 5 and 21, LVf, Length 0.792 mm; 6, LVm, Length 0.685 mm; 7–20, RVm, Length 0.700 mm.

Shape-type	Observation n°	Length ( $\mu\text{m}$ )	Area ( $\mu\text{m}^2$ )	Number Tubuli
Round StPC		Diameter		
-“-	1	5.61	24.72	38
-“-	2	4.85	18.47	31
-“-	3	5.23	21.48	31
-“-	4	5.91	27.43	35
-“-	5	5.39	22.82	48
-“-	6	4	12.57	28
-“-	7	4.1	13.2	26
-“-	8	3.6	10.18	22
-“-	9	4.2	13.85	18
-“-	10	5.18	21.07	46
-“-	11	4.6	16.61	45
-“-	12	5.4	22.9	40
-“-	13	4.4	15.21	29
-“-	14	4.37	15	31
-“-	15	5.06	20.11	43
-“-	16	4.17	13.65	27
-“-	17	4.29	14.45	26
-“-	18	4.14	13.46	33
-“-	19	4.8	18.09	33
-“-	20	4.13	13.39	34
	Mean (n 20)	4.67	17.43	33
	CL95%	4.37–4.97	15.22–19.64	29–37
Oblong StPC		Ellipse axis $\frac{1}{2}$ le1 x le2		
-“-	21	3.33x1.66	17.42	40

### *Cytheridella* Daday, 1905

***Cytheridella ilosvayi* (sensu lato) Daday, 1905.** The pattern of the A2 pores we described for *G. besni* is visible also in the case of the valves of *C. ilosvayi* (sensu lato) from Jamaica (Fig. 7A). The positions of the A2 pores are very similar to those of *G. besni*.

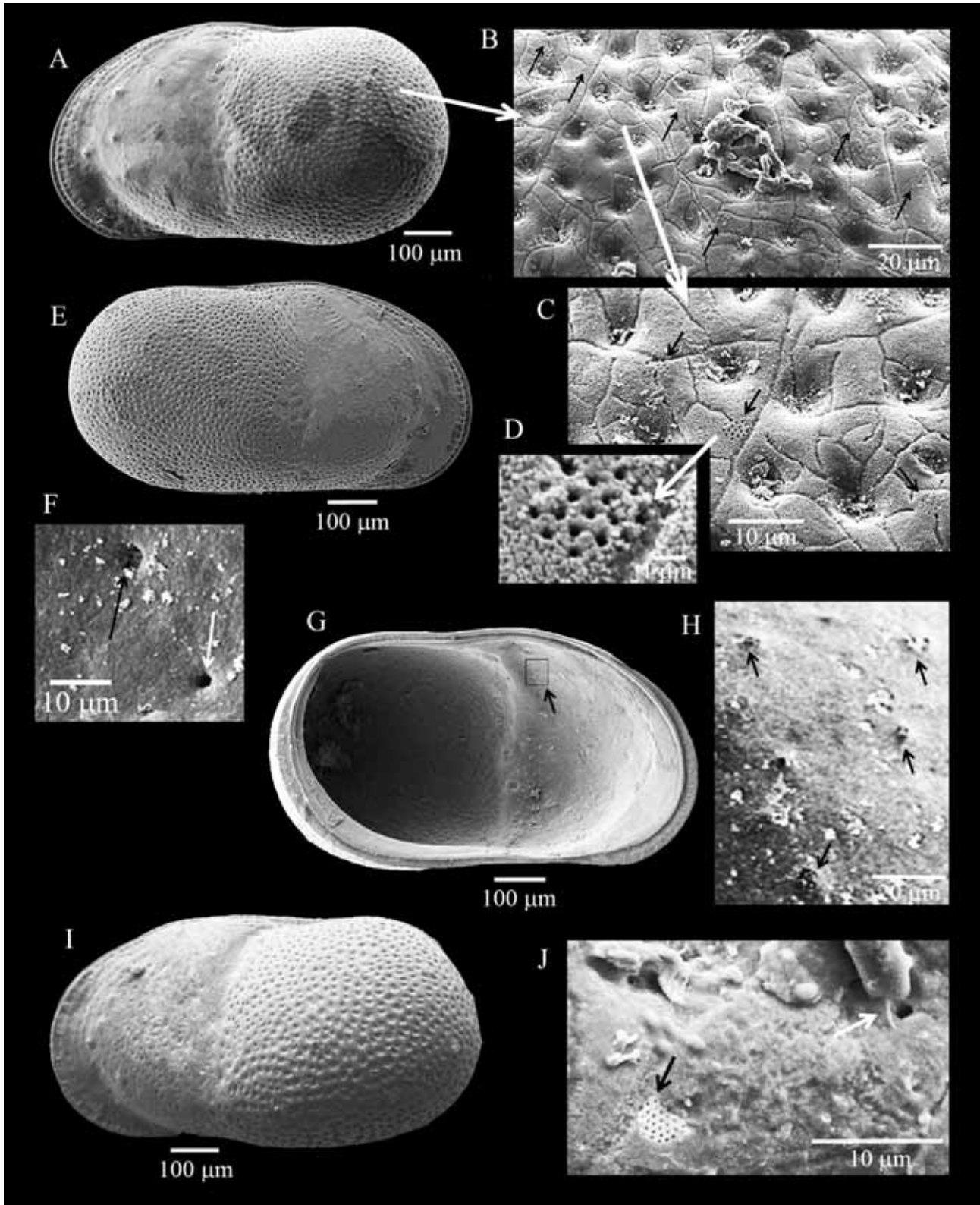
The B pores are remarkable because at least for the Jamaica valves they are very small and difficult to locate (Figs 17A–D, Table 7). We found most of them in the posterior half of the valves. Most of them are round (Table 7), the diameter for those belonging to adult female valves have on average 2.5  $\mu\text{m}$  with a mean surface area of 6  $\mu\text{m}^2$ . There are on average 12 tubuli per StPC (Table 7).

The two sieve-plates in material from Tuspan, Guatemala, display StPC with over 20 tubuli per plate (Table 7). The diameter of the A1 pore (white arrow on Fig. 17J) represents half of the diameter of the B pore (cf. for latter, same figure, the black arrow). The round sieve-plate of the *C. ilosvayi* (sensu lato) from Lake Valencia, Venezuela, originally identified as *C. boldi* (Fig. 4F), displays values slightly larger than those of the valves from Lake Tusman, Guatemala (Table 7), namely the diameter of the StPC is 4.43  $\mu\text{m}$  (with an area of 15.41  $\mu\text{m}^2$ ) and 31 tubuli. The SI index is 0.005 (4.43/885) a value characteristic for the Small-type StPC.

**TABLE 7.** Characterisation of StPC, *Cytheridella ilosvayi* Daday (sensu lato), Observation n°: 1-6, Wallywash Great Pond, Jamaica, LVf, Length 0.828 mm; 7-20 and 23, Eirunepé-Amazonia, Brazil, LVj, Length 0.535 mm; 21-22, Laguna Tuspan, Guatemala, LVf, Length 0.892 mm; 24\*, *Cytheridella boldi* Purper, Lake Valencia, Venezuela, RVf, Length 0.885 mm.

Shape-type	Observation n°	Length ( $\mu\text{m}$ )	Area ( $\mu\text{m}^2$ )	Number Tubuli
Round StPC		Diameter		
-“-	1	3.1	7.54	16
-“-	2	2.59	5.27	11
-“-	3	2.71	5.77	12
-“-	4	2.16	5.83	12
-“-	5	2.66	5.56	10
-“-	6	2.16	5.83	10
	Mean (n 6)	2.56	5.96	12
	CL95%	2.19–2.94	5.12–6.81	9–14
-“-	7	2.37	4.41	10
-“-	8	2.18	3.73	8
-“-	9	3	7.07	15
-“-	10	2.25	3.97	10
-“-	11	3.12	7.64	14
-“-	12	2.75	5.94	11
-“-	13	3.31	8.60	12
-“-	14	3.37	8.91	19
-“-	15	2.94	6.79	15
-“-	16	3.56	9.95	12
-“-	17	2.51	4.90	9
-“-	18	3.62	10.32	14
-“-	19	2.87	6.47	10
-“-	20	2.69	5.68	12
	Mean (n 14)	2.9	6.74	12
	CL95%	2.63–3.17	5.51–7.98	10–14
-“-	21	3.11	7.60	24
-“-	22	3.54	9.84	30
Oblong StPC		Ellipse axis $\frac{1}{2} l e_1 \times l e_2$		
-“-	23	3.44x1	10.80	21
Round StPC	24*	4.43	15.41	31

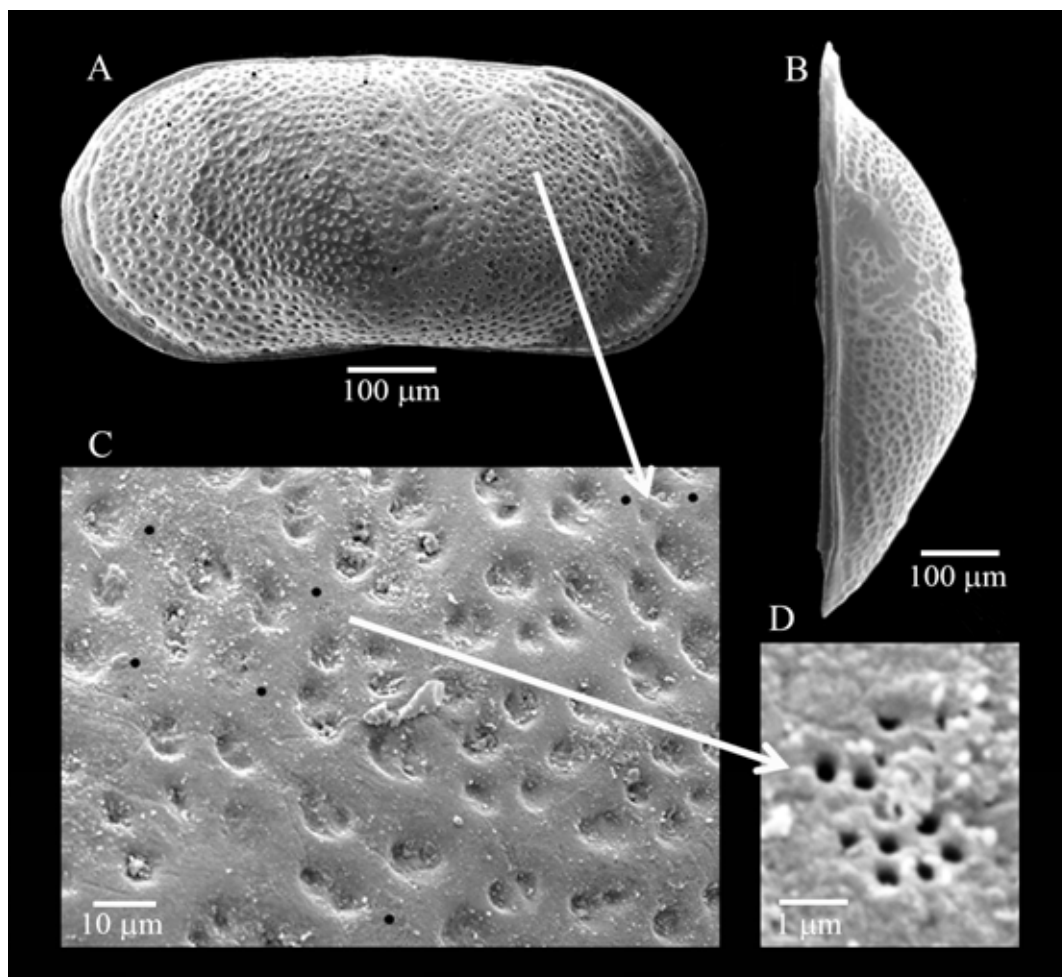




**FIGURE 17.** *Cytheridella ilosvayi* Daday (sensu lato), general view and details of LVf and RVf; A–H, Wallywash Great Pond, WGP2, depth 674–675, Jamaica; I–J, Laguna Tuspan, Petén, Guatemala; A—LVEf, general view; B–D—details from A (black arrows indicate the position of StPC); E—RVEf, general view; G—LVif, general view; F, H—details of pores from G (cf. square area); black arrows indicate apertures of StPC, white arrow shows aperture of pore A; I—LVEf, general view; J—details of pore A1 (white arrow) and pore B (black arrow).

On the inner side of a valve of *C. ilosvayi* (sensu lato) one sees the apertures of the B pores (Figs 17F, H, black arrows) as compared to an A pore (Fig. 17F, white arrow). Their dimensions are similar to those of the outer face of the valve.

As with *G. besni* and *Gomphocythere* sp. (aff. *G. angulata*), we note in Table 5 for *C. ilosvayi* (sensu lato) a significant positive trend of the number of tubuli increasing with the increase of the diameter and/or of the surface area of the StPC.



**FIGURE 18.** *Cytheridella gantensis* Monostori, Gánt, Transdanubia, Hungary, RVEm; A—lateral view; B—dorsal view; C—detail of the anterior area of the valve in A, with position of pores B (black points indicate the location of minute StPC); D—detail of a StPC; arrows indicate the origin of location of the StPC on the valve from A.

Juvenile valves (A-2) from Eirunepé, Amazonia (Table 7), display B pores with similar characteristics to those mentioned above for the adult valves of Jamaica. Therefore we expect the adult valves belonging to the Brazilian population to display StPC of size with a higher number of tubuli similar to the adult valve of Tuspan.

The value of the SI is 0.0031 calculated as  $2.56/828$  (Table 7) hence of Small-type StPC. The density of StPC per valve using the information for the valves from Wallywash is low. For the surface area displayed in Fig. 17B of  $7906 \mu\text{m}^2$  we found 6 StPC. Extrapolated to a standardised area of  $5000 \mu\text{m}^2$  it represents a value equivalent to 4 entities.

The DI index for the valves of Wallywash, Jamaica and Eirunepé, Brazil point to a Wide-spaced dispersion with values between  $10.2\text{--}39 \mu\text{m}$ .

***Cytheridella gantensis* Monostori, 1975.** This species displays valves of large size (Table 8) with slight sexual dimorphism for the length ( $0.750 \text{ mm}$  for the female,  $0.725$  for the male) and with weak sexual dimorphism for the posterior part of the carapace. The adult male presents in lateral view a symmetric development of the anterior and posterior halves (Fig. 18A). In dorsal view the male has a larger development in the anterior half as compared to

the posterior one (Fig. 18B). The surfaces of the valves are covered with fossae. The medio-dorsal sulcus is poorly developed.

**TABLE 8.** Characterisation of StPC, *Cytheridella gantensis* Monostori, Gánt, Hungary; Observation n°: 1, LVf, Length 0.750 mm; 2, LVm, Length 0.725 mm; 3, RVm, Length 0.730 mm.

Shape-type	Observation n°	Length (µm)	Area (µm <sup>2</sup> )	Number Tubuli
Round StPC		Diameter		
-“-	1	2.29	4.12	12
-“-	2	1.88	2.78	12
-“-	3	2.53	5.02	13

**TABLE 9.** Characterisation of StPC, *Gomphodella maia* De Deckker, Turner Springs, W. Australia; Observation n°: 1–21, RVf, Length 0.402 mm.

Shape-type	Observation n°	Length (µm)	Area (µm <sup>2</sup> )	Number Tubuli
Round StPC		Diameter		
-“-	1	1.73	2.35	14
-“-	2	1.84	2.66	17
-“-	3	1.65	2.14	14
-“-	4	2.21	3.84	20
-“-	5	1.80	2.54	15
-“-	6	1.69	2.24	15
-“-	7	1.84	2.66	14
-“-	8	1.65	2.14	11
-“-	9	1.69	2.24	13
-“-	10	1.58	1.96	13
-“-	11	1.36	1.45	10
-“-	12	1.39	1.52	12
-“-	13	1.65	2.14	27
-“-	14	1.28	1.29	11
-“-	15	1.76	2.43	20
-“-	16	1.62	2.06	13
-“-	17	1.76	2.43	15
	Mean (n 17)	1.68	2.24	15
	CL95%	1.57–1.79	1.95–2.54	13–17
Oblong StPC		Ellipse axis ½ le1 x le2		
-“-	18	0.99x0.51	1.59	10
-“-	19	0.99x0.66	2.05	16
-“-	20	1.17x0.73	2.71	20
-“-	21	1.17x0.48	1.76	10
	Mean (n 4)		2.02	14
	CL95%		1.24–2.81	6–22

We identified on the RVm we illustrate (Fig. 18C) a rather high number of StPC of very small size. Unfortunately many of them are covered with fine sediment. Most of the StPC display a round shape. We could select three StPC (Table 8) for which we have information of their characteristics: all of them are round of minute size, namely their diameter varies between 1.88 µm and 2.53 µm and their areas range between 2.58 µm<sup>2</sup> and 5.02

$\mu\text{m}^2$ . The number of tubuli is low (12–13/StPC). The oblong StPC had also 13 tubuli. The SI is 0.003 (Table 8, LVf: 2.29/750). Two triads of StPC allowed us to compute the distance index. The values are 23.7  $\mu\text{m}$  and 24.3  $\mu\text{m}$ , therefore DI points to the Wide-spaced type.

***Cytheridella chariessa* Rome, 1977.** Two SEM images from Koen Martens belong to a LVf (length 0.889 mm) and to a StPC. This latter has a round shape with a diameter of 4.58  $\mu\text{m}$  (respectively an area of 16.47  $\mu\text{m}^2$ ). The sieve-plate contains 39 tubuli, a value which characterizes the Low-number class. The SI for the StPC is 0.005 (4.58/889), hence it belongs to the Small-type.

### ***Gomphodella* De Deckker, 1981**

***Gomphodella maia* De Deckker, 1981.** This species is remarkable for the high number of small sieve-plates (pore B). Figure 14 upper panel (specimen V-3) shows an adult female RV which displays a total number of 367 StPC, dispersed within 39 cells. A cell-unit has an area of about 2200  $\mu\text{m}^2$  and the mean number of StPC calculated from 25 cell-units which cover 100 % of the surface of valve is 12.4 (Table 3). Extrapolated to an area of 5000  $\mu\text{m}^2$  the number of StPC represents 28 entities.

Most of the StPC display a round shape (Fig. 14 lower panel and Table 9) with a mean diameter of 1.68  $\mu\text{m}$  and a mean area of 2.24  $\mu\text{m}^2$ . The oblong pores display a similar area, and the mean number of tubuli for both round and oblong StPC is also similar 15/14 (Table 9). The number of tubuli significantly increases with the size of the diameter and/or the total area of StPC (Table 5).

The size of the aperture of the StPC on the inner side of the valve is in the range of those of the outer side for the same valve. Compare in Fig. 3A the outside shape with similar StPC visible on inner side (Figs 3D–E) of the valve.

The diameter of the A1 pores is slightly larger than the seta emerging through them. The diameter of the pore A1 (Fig. 3B) is 1.6  $\mu\text{m}$  while those of the seta 1.4  $\mu\text{m}$ . The pore A2 displays a larger diameter as compared to that of its emerging seta. In Fig. 3C the pore A2 displays a diameter of 2.4  $\mu\text{m}$  while that of the seta 1.2  $\mu\text{m}$ . This latter has a diameter similar to those of *Cyprideis torosa* (Fig. 3F).

The evaluated area of total tubuli for one StPC was calculated for the round sieve-plates with a mean number of 15 tubuli (Table 4). Taking the mean area value per tubuli of 0.017  $\mu\text{m}^2$  we arrive to a total virtual tubular area of 0.255  $\mu\text{m}^2$ .

The SI for the LV of Table 7 is 0.0042 (1.68/400), hence of Small-type. The range value of the DI is between 4.8 and 8.7 (N-6) pointing to a Narrow-spaced type.

***Gomphodella aura* Karanovic, 2009.** This species, like *G. maia*, displays all the three types of pores on the valves. The diameter of the A1 pore is slightly smaller than that of the A2. This latter pore has a rim and through this peculiarity can be easily distinguished from the A1 pore (Fig. 7B). Most of the A2 pore locations on the *G. aura* valve correspond to those we documented for *Cytheridella ilosvayi* (Fig. 7A) and noticed also on the *Kovalevskiella* sp. valves (Fig. 7C). The diameter of the A1 pore on the Fig. 8B is 1.73  $\mu\text{m}$  which is slightly smaller than the diameter of the A2 pore (this latter about 2  $\mu\text{m}$ ).

The StPC, or pore B, is usually larger than the A-type pores (Figs 8A–F). Their diameter, area and number of tubuli are displayed in Table 10. Most of the StPC are round with 20–40 tubuli. The density of the StPC is high (Fig. 8B). For an area of 521.3  $\mu\text{m}^2$  we counted 14 StPC which, extrapolated to a surface equivalent to those of *G. maia* (about 2200  $\mu\text{m}^2$ ), equates to 59 entities and for a standardised surface of 5000  $\mu\text{m}^2$  is estimated to 134 units.

The mean area of the B pores is 3.72  $\mu\text{m}^2$  (Table 10) and of tubuli measured (Table 4) is 0.022  $\mu\text{m}^2$ . The area of tubuli aperture calculated for a mean pore B represents a total virtual area of 0.572  $\mu\text{m}^2$ , which is larger than those evaluated for *G. maia*.

Type A and B pores can be recognised on the inside of the valves (Figs 8C–E). The diameter of the A1 pores (Fig. 8D) is more-or-less similar to those of the A2 pores (Fig. 8E). Note that this latter pore in our figure differs from the former one by its three visible tubuli apertures. The B pore on the inside of the valve has the general structure already discussed in the previous section, namely with a visible sieve-plate that opens in the calcified inner chamber (Fig. 8F). This latter one has a diameter of 1.2  $\mu\text{m}$ , which is larger than those of the A pores (about 0.6–0.7  $\mu\text{m}$ ) but smaller than the outer side of the B pores (Table 10).



**TABLE 10.** Characterisation of StPC, *Gomphodella aura* Karanovic, Yandeyarra Reserve, Pilbara, W. Australia; Observation n°: 1–11, LVf, Length 0.508 mm.

Shape-type	Observation n°	Length (µm)	Area (µm <sup>2</sup> )	Number Tubuli
Round StPC		Diameter		
-“-	1	2.20	3.80	23
-“-	2	2.24	3.94	40
-“-	3	1.88	2.78	22
-“-	4	2.05	3.30	25
-“-	5	2.50	4.90	31
-“-	6	2.61	5.31	27
-“-	7	2.09	3.43	23
-“-	8	2.14	3.59	24
-“-	9	1.92	2.90	20
-“-	10	2.05	3.30	25
	Mean (n 10)	2.17	3.72	26
	CL95%	2.00–2.33	3.14–4.31	22–30
Oblong StPC		Ellipse axis ½ le1 x le2		
-“-	11	1.43x0.84	3.79	32

The SI index displays a value of 0.0043 (2.17/508) and the DI 4.86 (N 10). Both indices point to the pattern of the small size and the narrowly spaced distribution of the StPC. Combined with the high density of StPC they offer a quantifiable objective description of this complex of morphologic traits.

***Gomphodella quasihirsuta* Karanovic, 2009.** The species, as compared to *G. aura*, displays more diverse shapes of the StPC. Beside the round B pores there are pores that are of the oblong type (Figs 8G–J, Table 11). The mean diameter of the round StPC is about 3 µm, or expressed as surface size they display 6.85 µm<sup>2</sup> and bear on average 20 tubuli (Table 11). The oblong B pores display a mean area significantly larger than those of the round ones and a slightly higher number of tubuli (Table 11). There is a statistically significant trend of increasing tubuli numbers with the enlargement of the StPC, this latter expressed as either diameter or as total area, and confirmed by Kendall’s coefficient rank of correlation for round-shaped and separately for the oblong StPC (Table 5). The diameters of the pores A1 and A2 are about half the size of the round StPC (Fig. 8H).

**TABLE 11.** Characterisation of StPC, *Gomphodella quasihirsuta* Karanovic, Uaroo Station, Pilbara, W. Australia; Observation n°: 1–32, LVf, Length 0.570 mm.

Shape-type	Observation n°	Length (µm)	Area (µm <sup>2</sup> )	Number Tubuli
Round StPC		Diameter		
-“-	1	2.72	5.81	16
-“-	2	2.83	6.29	17
-“-	3	2.76	5.98	18
-“-	4	2.94	6.79	21
-“-	5	3.12	7.64	22
-“-	6	2.79	6.11	23
-“-	7	2.90	6.60	20
-“-	8	2.65	5.52	17
-“-	9	2.94	6.79	19
-“-	10	3.05	7.31	24
-“-	11	3.23	8.19	23

...Continued on next page

**TABLE 11.** (Continued)

Shape-type	Observation n°	Length (µm)	Area (µm <sup>2</sup> )	Number Tubuli
-“-	12	2.98	6.97	21
-“-	13	2.57	5.19	14
-“-	14	3.23	8.19	21
-“-	15	3.09	7.05	23
-“-	16	3.38	8.97	25
	Mean (n 16)	2.95	6.86	20
	CL95%	2.83–3.07	6.30–7.43	19–22
Oblong StPC		Ellipse axis ½ le1 x le2		
-“-	17	2.02x1.29	8.19	20
-“-	18	2.28x1.18	8.45	23
-“-	19	2.35x1.29	9.52	20
-“-	20	2.02x1.39	8.82	21
-“-	21	2.09x8.95	8.95	20
-“-	22	2.28x1.47	10.53	24
-“-	23	1.98x1.29	8.04	24
-“-	24	2.02x1.29	8.19	24
-“-	25	2.57x1.29	10.41	26
-“-	26	2.83x1.47	13.07	30
-“-	27	1.58x1.17	5.80	20
-“-	28	2.46x1.29	9.97	24
-“-	29	1.84x1.29	7.46	21
-“-	30	2.43x1.1	8.40	19
-“-	31	1.76x1.1	6.08	17
-“-	32	2.35x1.47	10.85	25
	Mean (n 16)		8.92	22
	CL95%		7.95–9.89	21–24

The evaluated mean area of tubuli apertures represent 0.036 µm<sup>2</sup>, which, calculated for a mean value of the B pore, gives a total virtual area of 0.720 µm<sup>2</sup> (Table 4). This latter value is due to the large size of the whole StPC and to a larger aperture of each tubuli (Figs 8I–J, Table 11).

The density of StPC for an area of 520 µm<sup>2</sup> is 8 plates. Extrapolated to the chosen standard surface of 2200 µm<sup>2</sup> we obtain 34 entities or standardised to 5000 µm<sup>2</sup> we get an estimated value of 77 entities.

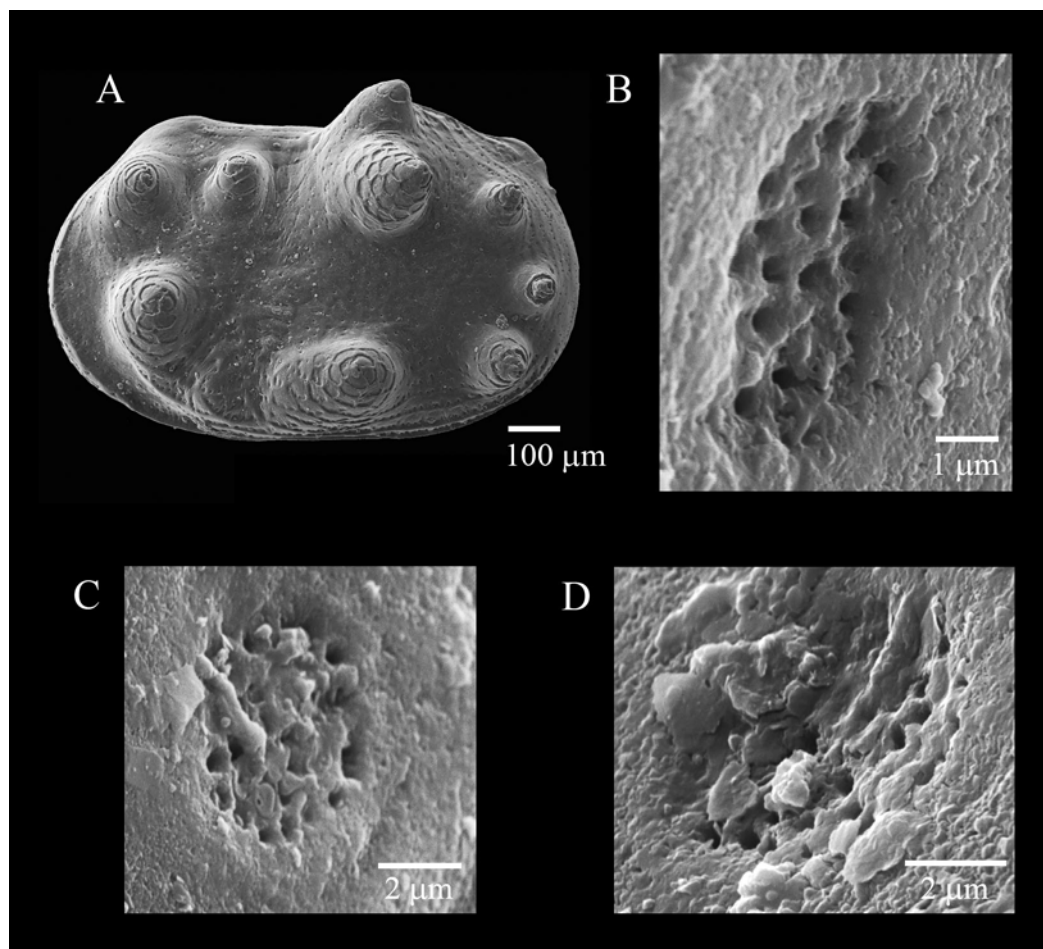
The values for the SI and DI indices are in the range calculated for *G. maia* and *G. aura*, namely SI = 0.0051, i.e. of small-type and DI = 6.22, namely narrow-spaced.

### ***Theriosynoecum* Branson, 1936**

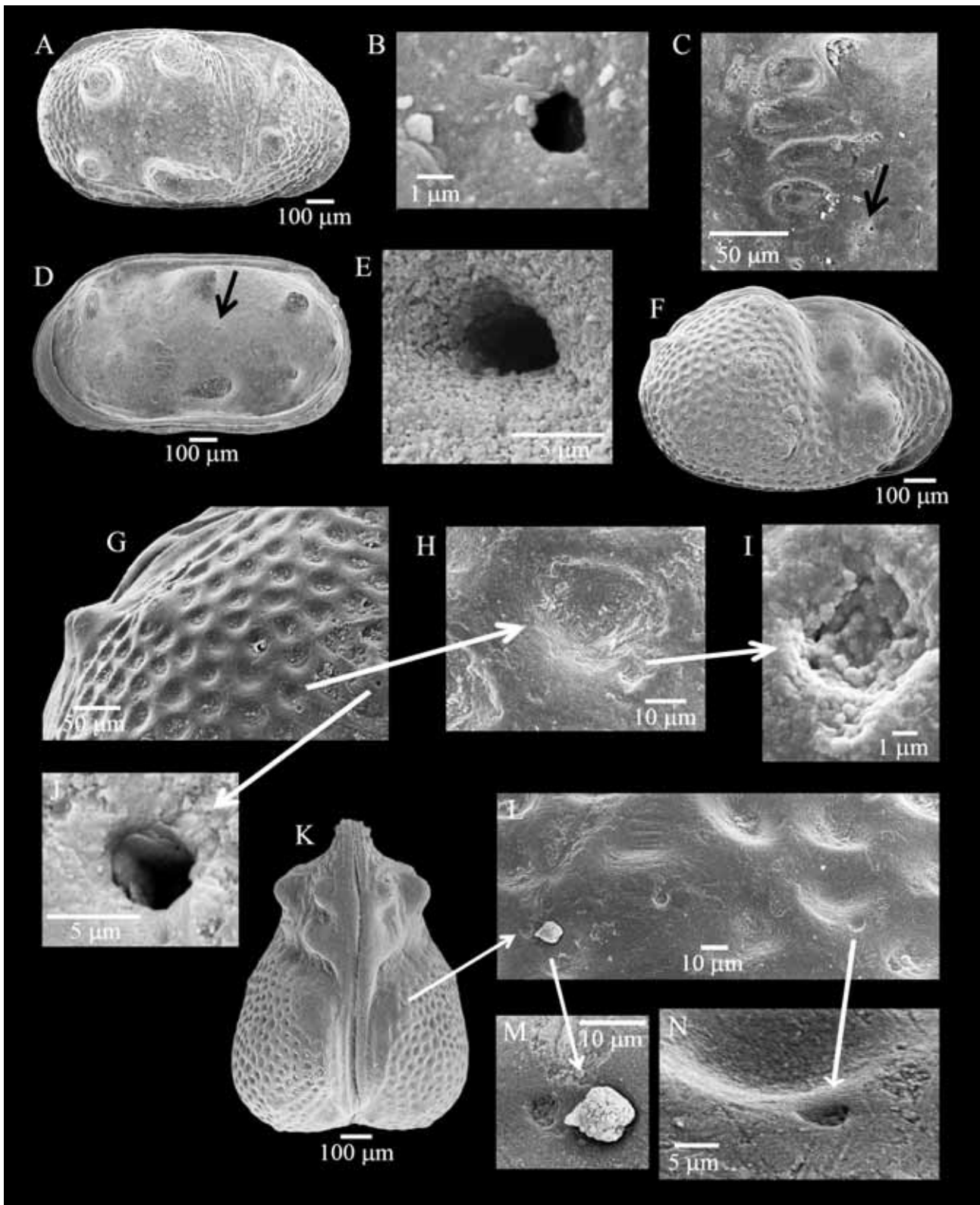
***Theriosynoecum fittoni* (Mantell, 1844).** The valve on which we identified StPC is a male adult LV (Fig. 19A). Four StPC provided useful information (Figs 19B–D, Table 12). The first one, an oblong StPC (Fig. 19B, Table 12), displays an area of 10.07 µm<sup>2</sup> comparable with those of the 4<sup>th</sup> pore (round shaped, not figured) documented for this species in Table 12. We recognised for the oblong pore 20 tubuli apertures. The most visible ones have a diameter varying from 0.24 µm to 0.32 µm. Two StPC of round shape (pores 2 and 3 in Figs 19C–D, Table 12) have larger areas, namely 21.24 µm<sup>2</sup> and 16.76 µm<sup>2</sup>, as compared to the two previously mentioned pores, respectively 4.62 µm and 5.2 µm diameters (Table 12). The estimated numbers of tubuli for the round pores is in the same range as the oblong ones.

**TABLE 12.** Characterisation of StPC, *Theriosynoecum* and *Sinuocythere* species; *Theriosynoecum fittoni* (Mantell), Observation n°: 1–4, LVm, Length 0.995 mm; *Theriosynoecum kirtlingtonense* Bate, 5, RVm, Length 1.1 mm; *Theriosynoecum* sp., 6–7, RVf, Length 0.95 mm; 8, Cf, Length 0.97 mm; “*Theriosynoecum*” *pygmaea* Stoica, 9, RVIf, Length 0.39; *Sinuocythere pedrogaensis* Cabral & Colin, 10, LVm, Length 0.574 mm; *Sinuocythere sinuosa* (Mette), 11, Cm, Length 0.547; \*—For the StPC of *Th. fittoni* the numbers of tubuli are underrepresented due to their poor preservation.

Shape-type	Observation n°	Length (µm)	Area (µm <sup>2</sup> )	Number Tubuli*
Oblong StPC		Ellipse axis ½ le1 x le2		
-“-	1	2.85x1.125	10.07	20
Round StPC		Diameter		
-“-	2	4.62	16.76	19
-“-	3	5.2	21.24	19
-“-	4	3.71	10.81	17
-“-	5	5	19.63	-
-“-	6	4.8	18.09	-
-“-	7	4.24	13.85	-
-“-	8	4.13	13.39	-
-“-	9	7.57	44.65	60
-“-	10	4.57	16.4	-
-“-	11	3.48	9.5	-



**FIGURE 19.** *Theriosynoecum fittoni* (Mantell), Weald Clay Formation, Compton Bay, Isle of Wight, U.K., LVEm; A—general view; B–D—details of Type B pores from A.



**FIGURE 20.** A–E, *Theriosynoecum kirtlingtonense* Bate, Old Cement Quarry, Kirtlington, U.K., Jurassic, Oxfordian; A—RVEf, general view; B—detail of pore Type A from A; C—detail of muscle scars from a RVIm (black arrow indicates the position of pore Type A); D—RVIm general view (black arrow indicates the position of pore Type A); E—detail of pore Type A from D; F–N, *Theriosynoecum* sp., Borehole Lathen 8, K1113.5–1117.1, K2, Germany, Jurassic, Bathonian; F–J, Cf, general view and details; F—general right view; G–J, details from F; G—valve ornamentation, postero-dorsal area; H—details of a foveole and a pore Type B; I—detail of StPC (Type B) from H; J—detail of pore’s canal Type A from G; K–N, Cf, general view and details; K—general dorsal view; L–N, details of carapace ornamentation and pores; L—foveolae and position of pores B on the carapace; M–N—details of two pores B. F–N, white arrows indicate the position of pores.



The SI index is 0.0046. This value was calculated from the ratio of the diameter of the round pore 3 to the length of the valve (4.62/995), therefore a Small-type StPC.

***Theriosynoecum kirtlingtonense* Bate, 1965.** The two valves we show here belong to adult specimens (Figs 20A–E). We assign these valves to a female and presumably a male after we compared their shape in lateral view with the information published by Bate (1965, Plate 110, Fig. 8). In this latter plate, a female is represented that has the maximal ventral curvature in the posterior and the middle third of its length. This is the case for our valve (Fig. 20A). The male valve in the Bate publication (1965, Plate 110, Fig. 2) displays a straight marginal line and this appears also in our Fig. 20D. Additionally, on our valve with the inner side up the postero-ventral curvature of the brood pouch, specific for females does not appear, hence our assumption of a male is confirmed.

In our material only on the inner face of the male we could find a pore with a diameter of 5  $\mu\text{m}$  and an area of 19.63  $\mu\text{m}^2$  (Figs 20D–E), which corresponds more-or-less to the size of the round StPC of *T. fittoni* (Table 10). On the female valve we recognise an A pore having a diameter of 2.25  $\mu\text{m}$  (Fig. 20B). The value of the SI index using the male's valve from Fig. 20D is 0.0045 (5/1100), hence a Small-type StPC.

***Theriosynoecum* sp..** We identified on a right valve and a carapace of this unnamed species several porous alveoles that we interpret as sieve-plates (Figs 20F–N). On the RVEf of 0.5 mm length there is a round StPC (Figs 20H–I) with a diameter of 4.8  $\mu\text{m}$  and an area of 18.02  $\mu\text{m}^2$ . A second pore with a similar diameter (4.24  $\mu\text{m}$ ) had apparently lost the sieve-plate (Figs 20G, J). Two other StPC were recognised on the dorso-lateral side of the carapace (Figs 20K–N). The round StPC in Fig. 20M has a diameter of 4.13  $\mu\text{m}$  for which we calculated an area of 13.39  $\mu\text{m}^2$ . The StPC in Fig. 20N has an elongated shape. The number of tubuli could not be counted with any accuracy. The SI index is 0.0051 for the pore of the RVf in Fig. 20F (i.e. 4.8/950), which is comparable with those of the *Theriosynoecum* species above (Table 12).

***Theriosynoecum fluxans* Helmdach, 1972, *T. helmdachi* Sohn, 1982.** We studied material of these two species for NPC characteristics without success for reasons of preservation related to taphonomic and/or diagenetic processes, however, “absence of evidence is not evidence of absence” and we urge colleagues to routinely check NPC both externally and internally on valves.

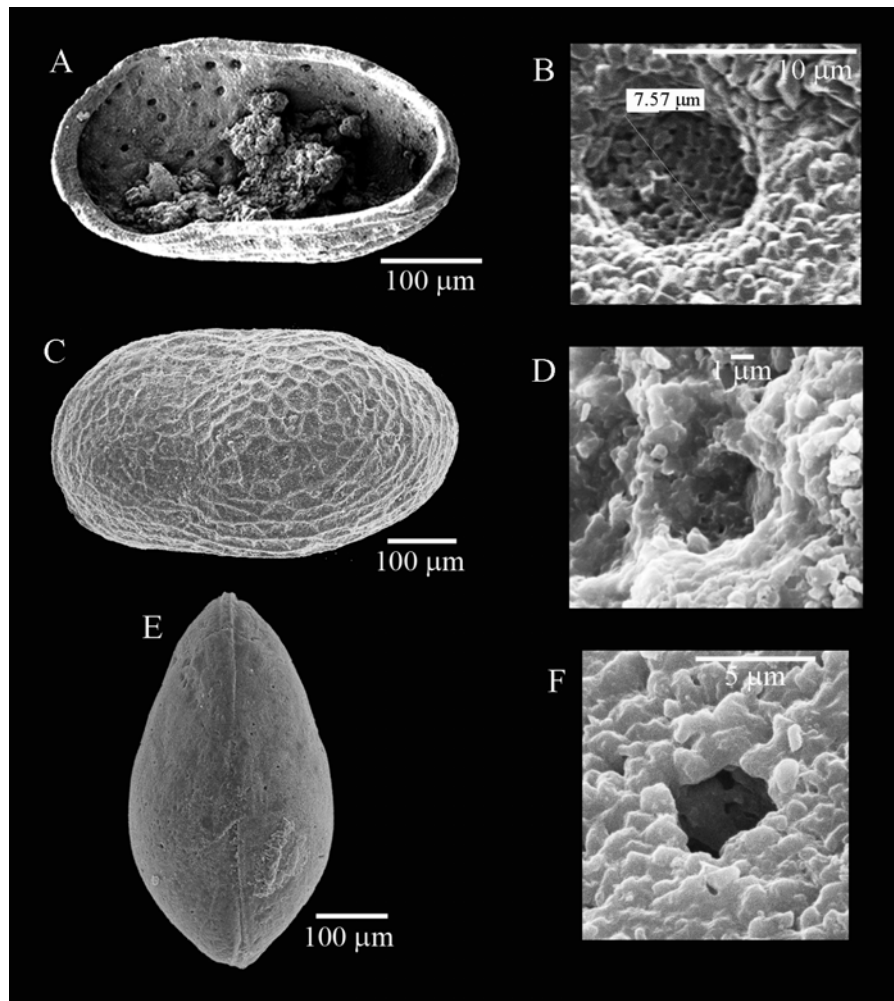
**“*Theriosynoecum*” pygmaea Stoica, 2007.** Female adult valves display a posterior inflated area (the brood pouch); surface of valves reticulated; hinge lophodont with an anterior elongated socket. The four valves (1RVf and 3LVf) examined vary in length between 0.38 to 0.45 mm. The surface of the valves is reticulate and no StPC apertures are visible. The inner sides of those valves display round holes that we interpret as the inner aperture of StPC. The RVIf studied and here figured (Fig. 21A) has a length of 0.39 mm. It documents the presence of sieve-plates having on average a diameter of 8.53  $\mu\text{m}$  (N 6), CL95% 7.54–9.52). One StPC (Fig. 21B) that displays well preserved tubuli has a diameter of 7.57  $\mu\text{m}$ , a surface of 44.65  $\mu\text{m}^2$ , and shows about 60 tubuli.

The value of the SI is 0.0218 (8.53/390) and characterizes the Large-size type. The DI index for four triads displays values ranging from 14.9  $\mu\text{m}$  to 25.1  $\mu\text{m}$  with a mean of 19.99  $\mu\text{m}$ , therefore we have a Wide-spaced type StPC. Both the SI and the DI indices are atypical when compared with the above studied *Theriosynoecum*, as well as with most of the other timiriaseviines here documented.

### ***Sinuocythere* Colin, Cabral, Dépêche & Mette, 2000**

***Sinuocythere pedrogaensis* Cabral & Colin, 2000 (in Colin *et al.* 2000).** The length of the female valve of this species is of medium size, i.e. 0.574 mm (Fig. 21C). We identified a StPC with a diameter of 4.57  $\mu\text{m}$  and an area of 16.4  $\mu\text{m}^2$  (Fig. 21D). This value is in the range of other fossil Cytheridellini species we studied (Table 12). The SI index is 0.0079 (4.57/574) therefore belonging to the Small-type StPC.

***Sinuocythere sinuosa* (Mette, 1995).** The carapace in dorsal view (Fig. 21E) points to a female with a length of 0.547 mm. The unique StPC we identified (Fig. 21F) displays a diameter of 3.48  $\mu\text{m}$  and an area of 9.5  $\mu\text{m}^2$ . The SI index measures 0.0064 (3.48/547) and points to Small-type StPC.



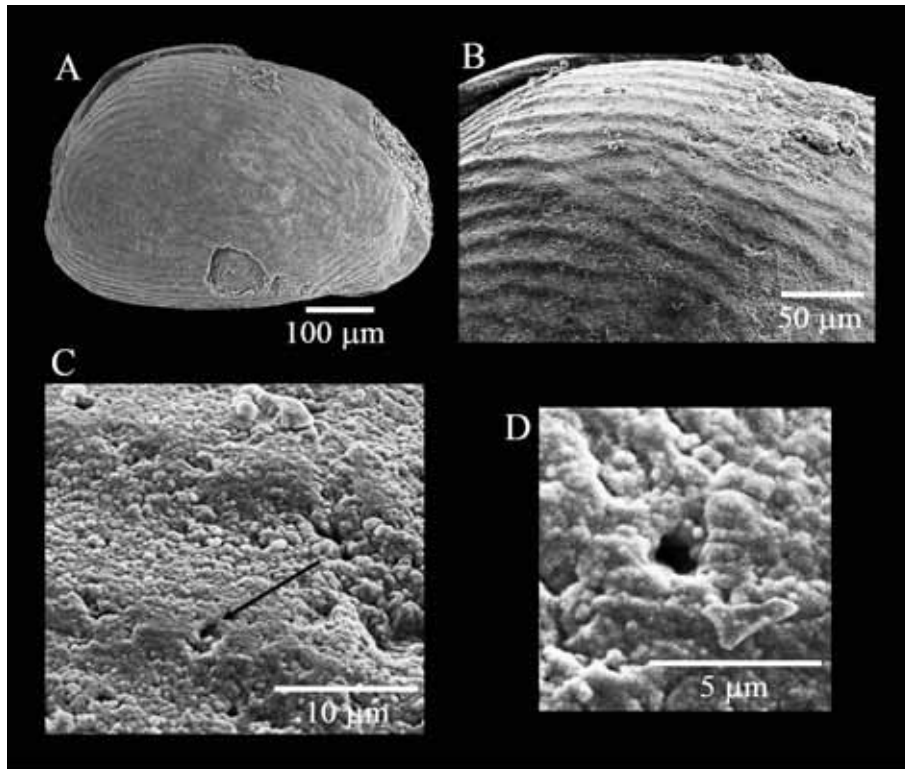
**FIGURE 21.** A–B, “*Theriosynoecum*” *pygmaea* Stoica, Nazarcea, south Dobrogea, FD6, Romania, Lower Cretaceous, ?early Berriasian, RVIf; A—general view; B—detail of pore B; C–D, *Sinuocythere pedrogaensis* Cabral & Colin, Pedrógão section, Portugal, Jurassic, Oxfordian, LVEf, Paratype, SMF Xe 23601; C—general view; D—detail of pore B; E–F, *Sinuocythere sinuosa* (Mette), Tataouine, Tunisia, Jurassic, Callovian, Cf, dorsal view; E—general view; F—detail of pore B.

## Representatives of the tribe Timiriaseviini Mandelstam, 1960

### *Timiriasevia* Mandelstam, 1947

***Timiriasevia mackerrowi* Bate, 1965.** This is a species of medium size (length of RVf—0.576 mm) and the specimen we studied is poorly preserved due to recrystallisation of the valve’s surface (Figs 22A–B). One minute aperture on the right side of the carapace (Figs 22C–D) is here interpreted as a potential normal pore of A1 type. Its diameter is 1.06 µm. No StPC could be observed.

***Timiriasevia guimarotensis* Schudack, 1998 (in Schudack *et al.* 1998) and *T. aff. uptoni* Timberlake, 1988.** As for *Theriosynoecum fluxans* and *T. helmdachi* we studied material of these two species of *Timiriasevia* for NPC characteristics without success for reasons of preservation related to taphonomic and/or diagenetic processes, however, ‘absence of evidence is not evidence of absence’ and again we urge colleagues to routinely check NPC both externally and internally on valves.

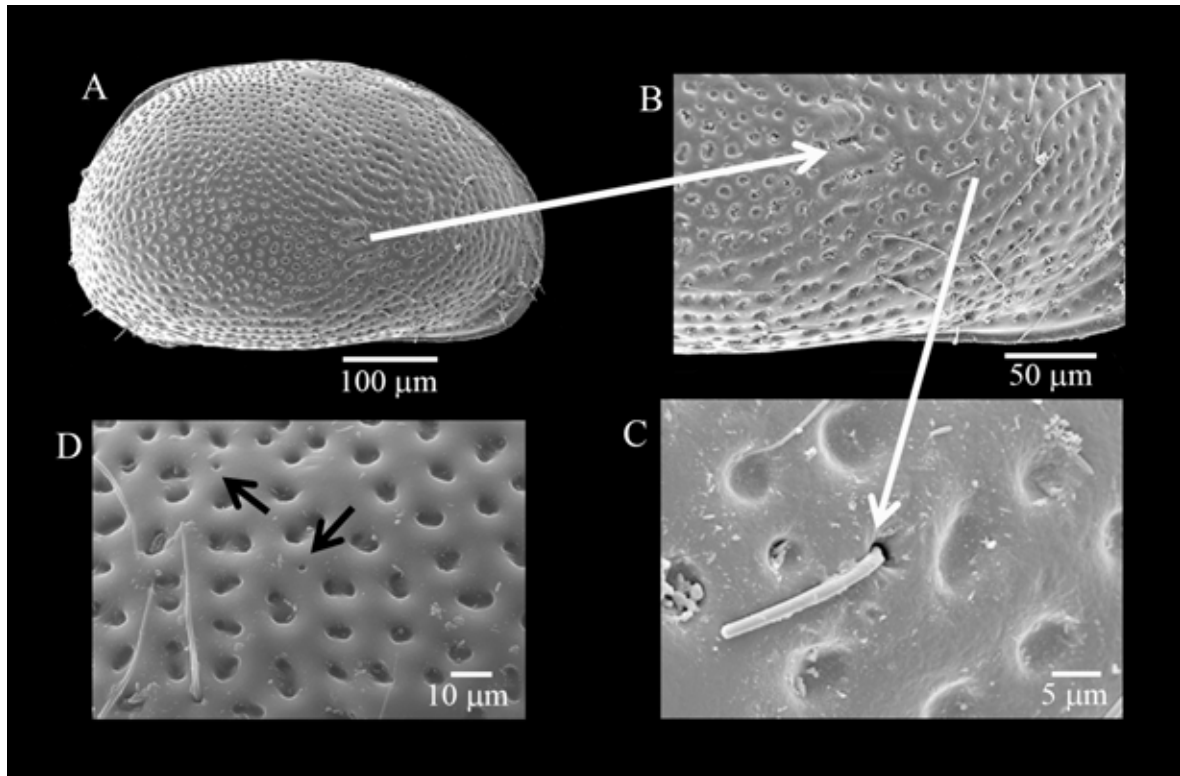


**FIGURE 22.** *Timiriasevia mackerrowi* Bate, Old Cement Quarry, Kirtlington, U.K., Jurassic, Oxfordian; A–D, Cf; A—general view, right side; B—detail of the dorso-posterior area; C—detail of the area with a presumed A1 pore (black arrow); D—enlarged detail from C, pointing to the presumed A1 pore.

### *Metacypris* Brady & Robertson, 1870

***Metacypris cordata* Brady & Robertson, 1870.** On the specimens we examined only A type pores and setae are visible. No StPC of B type could be found. The distribution/number of A type pores and setae is higher on the antero-ventral side of valves as compared with the other areas of the valves, when examined in lateral view (Figs 23A–C). Two types of A pores are visible as mentioned in previous sections and already figured (Figs 5A–B). The A1 pore has no rim and the emerged seta covers practically the whole lumen. The difference between the diameter of the pore's aperture and that of the seta in Fig. 5A is 5%. The A2 pore has a rim and the seta is slim and does not fill the whole space of the pore (Fig. 5B). The difference between the diameter of the pore's aperture and that of the seta in Fig. 5B is 35%. The aperture of the A pore on the inner side of the valve (Fig. 24A) shows that in this case the diameter is similar to those we measured on the outer side of the valve.

Figure 23D shows the external ornamentation of the valve with dense foveolae. Interspaced between them are minute pits of pore-like shape, which could be A1 pores having a diameter similar to this pore type (Fig. 23D). Examination with high magnification of these minute puncti indicated by black arrows show that they are shallow cuticular depressions with variable depths. Such small pits on the external side of the valve do not traverse the calcitic wall to the inner side of the valve.



**FIGURE 23.** *Metacypris cordata* Brady & Robertson, Caldarusani, Romania; A–C, RVEf; A—general view; B–C, details of the valve ornamentation; B—coverage of pores/setae on the antero-ventral area of the valve; C—pore A1 with an emerging seta; D—details of CEj foveolae and puncti (black arrows).

### *Kovalevskiella* Klein, 1963

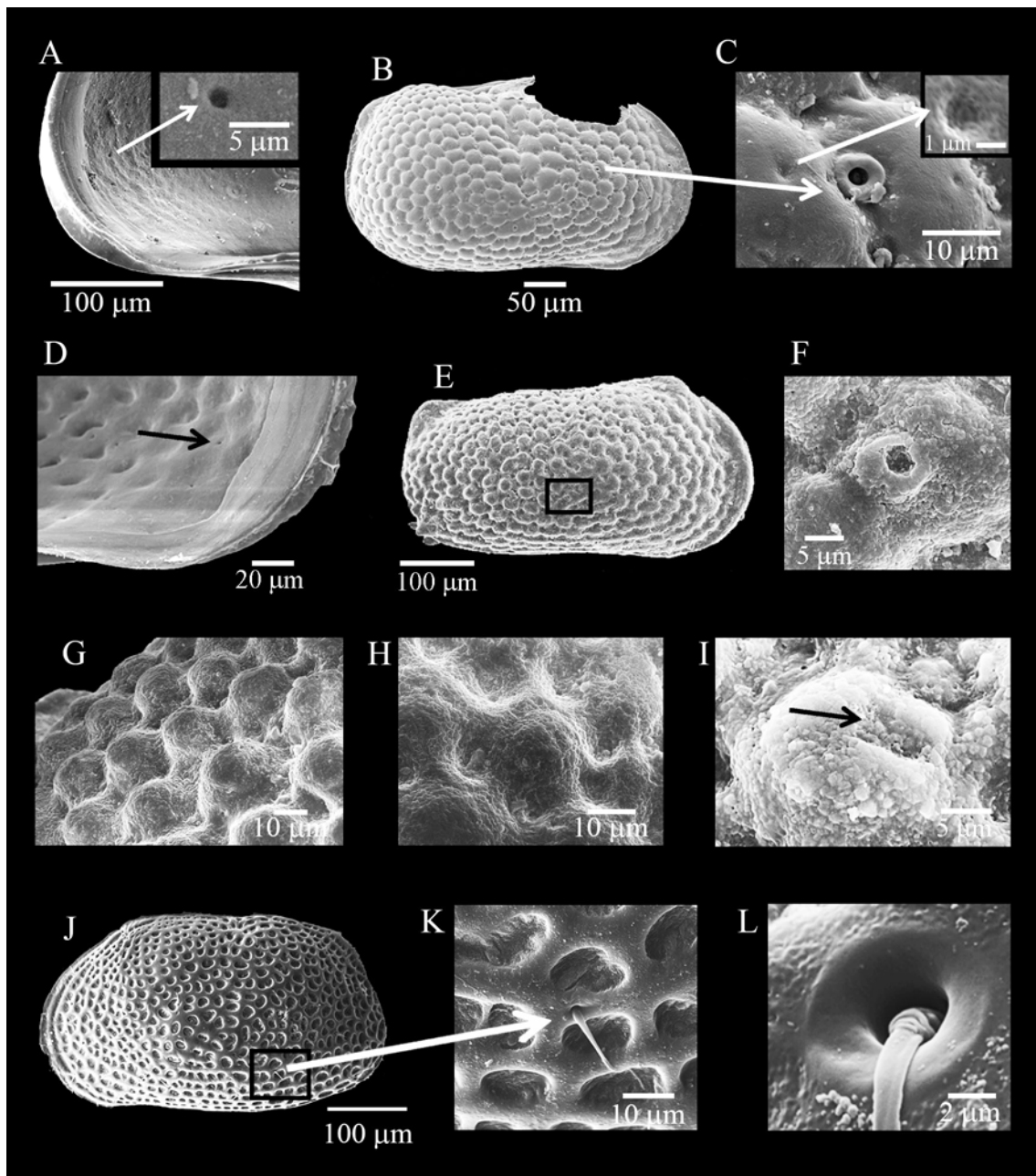
***Kovalevskiella* sp.** Examination of both sides of the valves shows that only pores and setae of A1 and A2 types exist. Their sparse distribution is visible on the external side of the valve (Fig. 24B). For examples where we measured the diameter of A1 and A2 pores and setae closely located one to the other, we noted for the former a diameter of 1.4 µm with a diameter of seta 1.3 µm at its base. For the A2 pore the diameter is 2.1 µm and the emerging seta has a small diameter, approximately half that of the pore's canal; it thus leaves a large free space between the pore's wall and the seta. The rim surrounding the A2 pore is thick approaching the size of the pore diameter (Fig. 24C). This peculiar type of rim makes it possible to map the A2 pores at lower magnification (Fig. 7C) and even to identify it on the Pliocene valves of *Kovalevskiella turianensis* Klein, 1963 (see Plate 8, Figures 14–15 in Schornikov 2017) and the same for *K. caudata* (Lutz, 1965) (Fig. 1a in Carbonel *et al.* 1987). On the surface of the valve of *Kovalevskiella* sp. interspaced with the foveolae there are minute puncti with a diameter of approximately 1.5 µm (cf. insert in Fig. 24C). On the inside of the valve (Fig. 24D) we recognise the aperture of A pores with a diameter of about 1.3 µm.

### *Rosacythere* Colin, 1980 (in Colin & Danielopol, 1980) emend. Colin & Carbonel, 1996

***Rosacythere lacobrigensis* Cabral & Colin, 1998.** This fossil dimorphic species is of small size (length of Cm—0.46 mm) and is characterised by a “raspberry-type” ornamentation (Colin 1991; Colin & Danielopol, 1980), typical of the genera *Frambocythere* and *Kovalevskiella* (Colin & Carbonel 1996), i.e. with hemispheric micropustules surrounded by foveolae arranged in “rosettes” (Figs 24E–I). In *R. lacobrigensis* the micropustules are smooth (Figs 24G–H) but sometimes due to recrystallisation of the valve's surface, they seem ornamented by very small apertures, which may be confused with StPC (Fig. 24I). In fact no StPC could be found, and only several A2 pores with thick rims exist (Fig. 24F); the six A2 pores definitely identified in the studied specimen



have similar locations to those documented for *Gomphocythere besni* (Fig. 6V-2), *Cytheridella ilosvayi* (Fig. 7A), *Gomphodella aura* (Fig. 7B) and *Kovalevskiella* sp. (Fig. 7C).



**FIGURE 24.** Timiriaseviini species, aspects of valve morphology; A—*Metacypris cordata* Brady & Robertson, Caldarusani, Romania, RVIf, anterior area with detail of the aperture of the canal belonging to a pore Type-A (see also insert for enlarged view); B–D, *Kovalevskiella* sp., Lobau, Austria; B—RVEf, general view; C—detail from B for the surface ornamentation of the valve with emphasis on foveolae, puncti (cf. insert for the shape of a punctum) and the A2 pore; D—detail of the anterior area of the LVif (arrow indicates the emergence of the canal of a pore Type A); E–I, *Rosacythere lacobrigensis* Cabral & Colin, Praia da Luz, Portugal, Cretaceous, early Aptian, Cm, lateral view; E—general view, right side; F—detail of an A2 pore from E (black square); G—detail from E showing the “raspberry-type” ornamentation; H—detail from E showing the hemispheric micropustules surrounded by foveolae disposed in “rosettes”; I—detail of E showing a false StPC due to recrystallisation; J–L, *Dolekiella europaea* Gidó, Artheau, Colin, Danielopol & Marmonier, Calmeilles, south-western France, LVEf; J—general view; K–L, postero-ventral details of J; K—representation of an intramural pore A1; L—detail of a pore A2 with seta.

*Dolekiella europaea* Gidó, Artheau, Colin, Danielopol & Marmonier, 2007. This species displays on its valves only pores of type A (Figs 24J–L), most of them without a rim or presenting a funnel instead of a rim. Therefore it is difficult to categorise them. The few A2 pores we identified (having a rim) have diameters between 2.1 µm and 2.9 µm (Fig. 24L). The rim of the A2 pore is well developed and its thickness is about 80 % of the pore's diameter. Typical A1 pores, with an aperture at the surface of the valve, have diameters which vary between 1.9 and 2.2 µm (Fig. 24K). No StPC were identified.

**Comparative aspects—Morphology of StPC belonging to representatives of the subfamily Limnocytherinae Sars, 1928 and of the family Cytherideidae Sars, 1925**

*Limnocythere* Brady, 1868

*Limnocythere sanctipatricii* Brady & Robertson, 1869 and *Limnocythere inopinata* (Baird, 1843). The species *L. sanctipatricii* displays ornamented valves; the external side of the valve is generally covered by shallow fossae of variable shape, separated by thin muri (Fig. 25A). Sieve-pores with an excentric seta, Type C of Puri & Dickau (1969), occur rarely on the bottom of the fossae (Figs 25B–D). The StPC have generally oblong shapes with areas larger than those of the Cytheridellini (Table 13). The identification of such StPC is difficult because of the undefined peripheral margin and the unordered spread of tubuli within the plate perimeter (Figs 25B–D). The diameters of tubuli are small, generally less than 0.2 µm. Their apertures are visible especially when the epicuticle of the valve is still present (Fig. 25F). The number of tubuli is variable, e.g. the Lake Wigry valve had a mean value of 45 tubuli, while for a Mondsee valve two StPC were examined with higher numbers of 59 and 79 tubuli respectively. Because of the rather wide dispersion of tubuli within the StPC space, the area of such pores is larger than those of the Cytheridellini studied (Table 13). A thin seta located at the margin of the StPC displays a flexible base and a slim shaft of about 1.2 µm basal diameter (Figs 25B–D).

**TABLE 13.** Characterisation of StPC, *Limnocythere sanctipatricii* Brady & Robertson; Lake Wigry, northern Poland, Observation n°: 1-4, RVf, Length 0.900 mm.

Shape-type	Observation n°	Length (µm)	Area (µm <sup>2</sup> )	Number Tubuli
Oblong StPC		Ellipse axis ½ le1 x le2		
-“-	1	5.47x2.14	36.76	48
-“-	2	5.74x3.15	56.77	66
-“-	3	4x1.42	17.59	33
-“-	4	4x1.3	16.34	34
		Mean (n 4)	31.74	45
		CL95%	1.48–61.99	21–70

The inner side of the valve allows observation of the aperture of the tubuli forming the sieve-plate and at the margin of its area the well calcified canal belonging to the sensillum (Figs 25E–F).

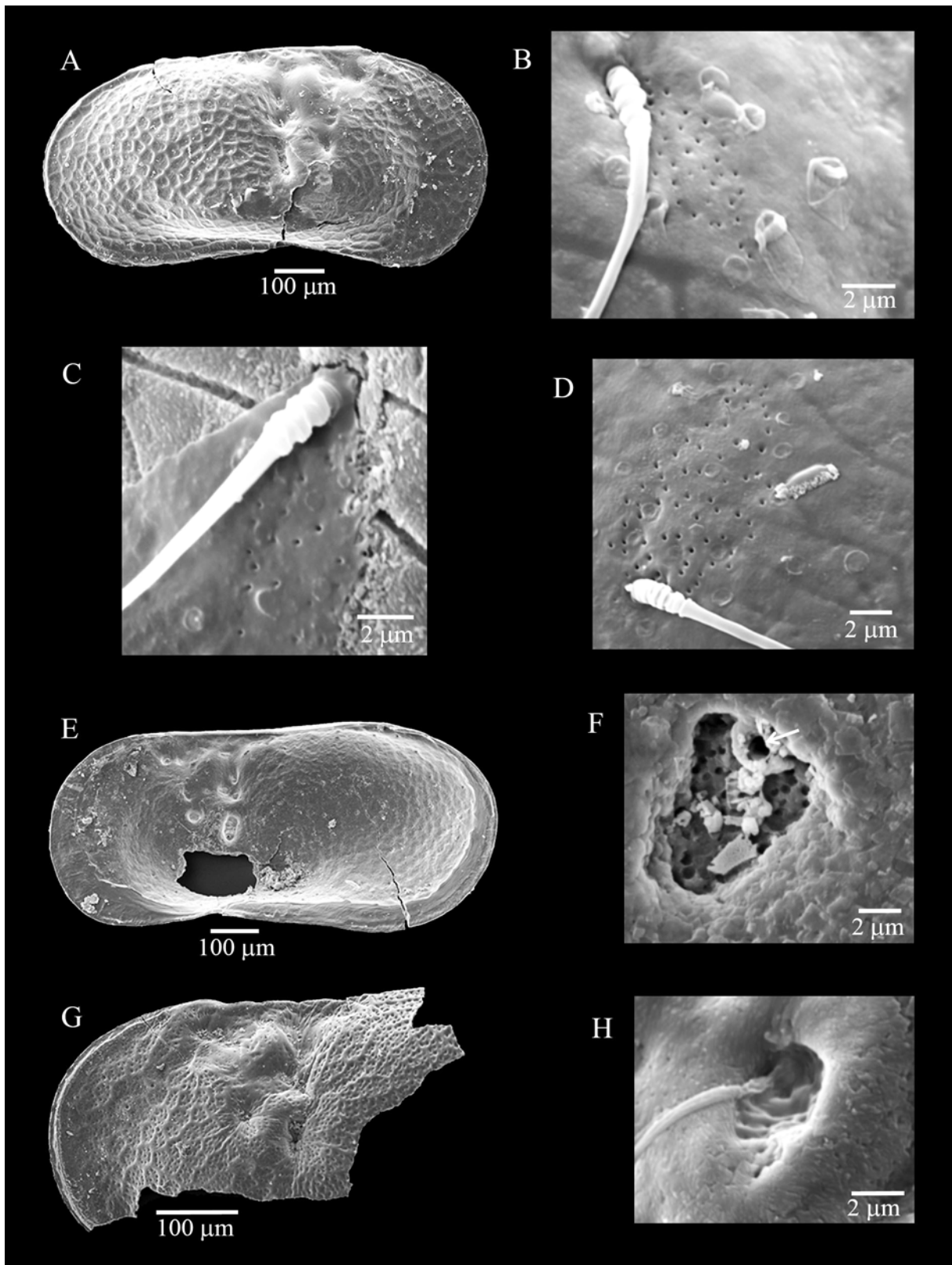
The mean area of tubuli apertures for the female valve from Lake Wigry is 0.013 µm<sup>2</sup>, which when used with the mean number of tubuli per pore leads to a total virtual tubuli area of 0.585 µm<sup>2</sup> per pore (Table 4).

*Limnocythere inopinata* displays StPC similar to those described here for *L. sanctipatricii* (Figs 25G–H).

*Cyprideis* Jones, 1857

*Cyprideis torosa* (Jones, 1850). The valves of *C. torosa* from sites CAR-P1 and MEL-6 and MEL-7 display lengths between 0.85 mm and 1.1 mm (Table 14). The valves are weakly ornamented (Fig. 9C). On the valves are StPC of type C with an excentric setal pore from which emerges a seta (Fig. 9D). All the three shapes of StPC (i.e. round, oblong and irregular types) are present; details of the round StPC are shown in Fig. 26A and oblong in Figs

26B–D. Their size (expressed in area units) varies between about 100 and 200  $\mu\text{m}^2$  (Table 12). Two RV, male and female, for which we calculated the SI index have values of 0.0144 (12.3/850) and 0.0115 (12.7/1100) respectively, which are characteristic for StPC of the Large-size type.



**FIGURE 25.** *Limnocythere* valves with details of Pore C; A–F, *Limnocythere sanctipatricii* (Brady & Robertson), Lake Wigry, northern Poland; A–D, RVEf; A—general view; B–D—details of pores C (seta and sieve-plate), external view; E–F, RVIm; E—general view; F—detail of a pore C from the posterior area of the valve illustrated in E; G–H, *Limnocythere inopinata* Baird, Lake Wigry, northern Poland, LVEf, anterior area; G—general view; H—detail of pore C (seta and sieve-plate).

**TABLE 14.** Characterisation of StPC, *Cyprideis* taxa; Observation n° 1–13: *C. torosa* (Jones), Portugal: 1–10; Observation n° 1–3 and 9: Sado estuary, site CAR-P1; 1, LVm, Length 0.98 mm; 2 and 9: RVf, Length 0.85 mm; 3, RVm, Length 0.96 mm; Observation n° 4 and 10: Melides lagoon, site MEL-6, RVm, Length 1.14 mm, Observation n° 5–6: LVf, Length 1.07 mm; Observation n° 7–8: Melides lagoon, site MEL-7, RVm, Length 1.06 mm; *C. ituiaie* Gross, Ramos & Piller, Observation n° 11: Sucuriçu, Brazil, LVf, Length 0.66 mm; *C. munoztorresi* Gross, Ramos & Piller, Observation n° 12: Sucuriçu, Brazil, LVm, Length 0.78 mm; *C. americana* Sharpe, Observation n° 13: Parrotee Pond, Jamaica, LVf, Length 0.66 mm.

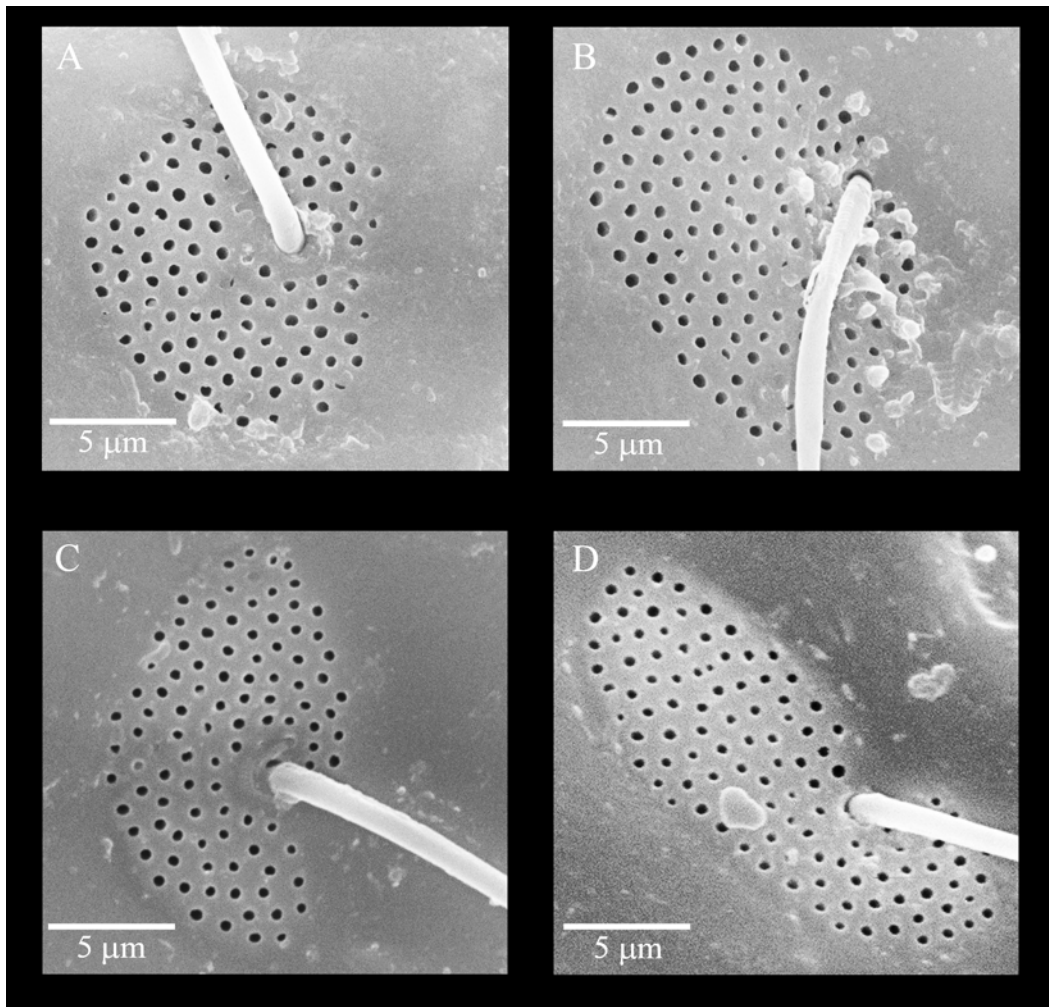
Shape-type	Observation n°	Length (µm)	Area (µm <sup>2</sup> )	Number Tubuli
Oblong StPC		Ellipse axis $\frac{1}{2} le_1 \times le_2$		
-“-	1	7.43x4.725	110.29	105
-“-	2	8.3x5.5	143.3	127
-“-	3	7.77x5.06	123.51	120
-“-	4	9.5x5.5	164.14	148
-“-	5	10.45x4.35	142.8	137
-“-	6	11.45x5.8	208.5	138
-“-	7	7.63x4.65	111.44	100
-“-	8	10x3.65	96.29	106
Round StPC		Diameter		
-“-	9	12.3	120.76	101
-“-	10	12.7	126.7	119
-“-	11	10.8	91.56	81
-“-	12	13	132.7	150
Irregular StPC	13		189.49	234

The number of tubuli within one StPC varies between 100 and about 150 canals (Table 12). This density of tubules is characteristic for the Large-type of tubuli numbers. The diameters of tubuli differ between the valves sampled at the sites CAR and MEL. We compared the mean areas of tubuli apertures at the outer side of the valve in samples from CAR-P1 and MEL-7 (Table 4). The size of mean areas for the former (cf. pores in Figs 26A–B) is more-or-less double those belonging to pores from the valves of the MEL-7 site (Figs 26C–D). The mean area of tubuli apertures multiplied with the mean number of tubuli per pore leads to a total virtual tubuli area which varies between 8.7 µm<sup>2</sup> and about 18.3 µm<sup>2</sup> (Table 4). The CAR-P1 site with high salinity conditions displays double the value observed for the MEL-7 valve (Table 4).

***Cyprideis americana* Sharpe, 1908.** The species is of large size, i.e. our female measures 0.9 mm length and displays irregular StPC placed in shallow depressions of the valve’s surface (Figs 9A–B). The StPC is of C type with a seta emerging from the setal canal located at the junction of two oblong segments of the sieve-plate (see arrow on Fig. 9B). The irregular shape of the StPC is due to the coalescence of oblong StPC segments; this is visible on the inner side of the valve where the canals of at least two StPC open in one hollow cavity.

The number of tubuli within the three branches of the StPC is high. In the present example we counted 234 tubuli. The total area of the StPC in the pore in Fig. 9B is 189.49 µm<sup>2</sup>. As compared to other *Cyprideis* species we investigated the total area of the StPC is in the range of some of the sieve-plates of *C. torosa*, but the number of tubuli for such Irregular-type StPC is extremely high (Table 14). The mean area of tubules obtained from the measurement of 45 tubules is 0.302 µm<sup>2</sup> (Table 4). The total virtual area of tubuli derived from the multiplication of the mean tubuli area with the 234 tubuli gives a total tubuli area of 70.668 µm<sup>2</sup> for this pore; it represents the highest value we measured in this study (Table 4).

***Cyprideis ituiaie* Gross, Ramos & Piller, 2014.** The species has medium size valves with StPC of type C; the specimen we studied measures 0.66 mm length (Fig. 27A). The StPC of round shape have large diameters more than 10 µm, e.g. in Fig. 27B the StPC displays a diameter of 10.8 µm and an area of 91.56 µm<sup>2</sup>. There is a large number of tubuli, i.e. more than 60 (Table 14) of small diameter (the mean for 8 tubules 0.28 µm). The setal pore has a diameter of 0.9 µm and is excentrically placed (Fig. 27B). The value of the SI is 0.0163 (10.8/660), hence a Large-type StPC.

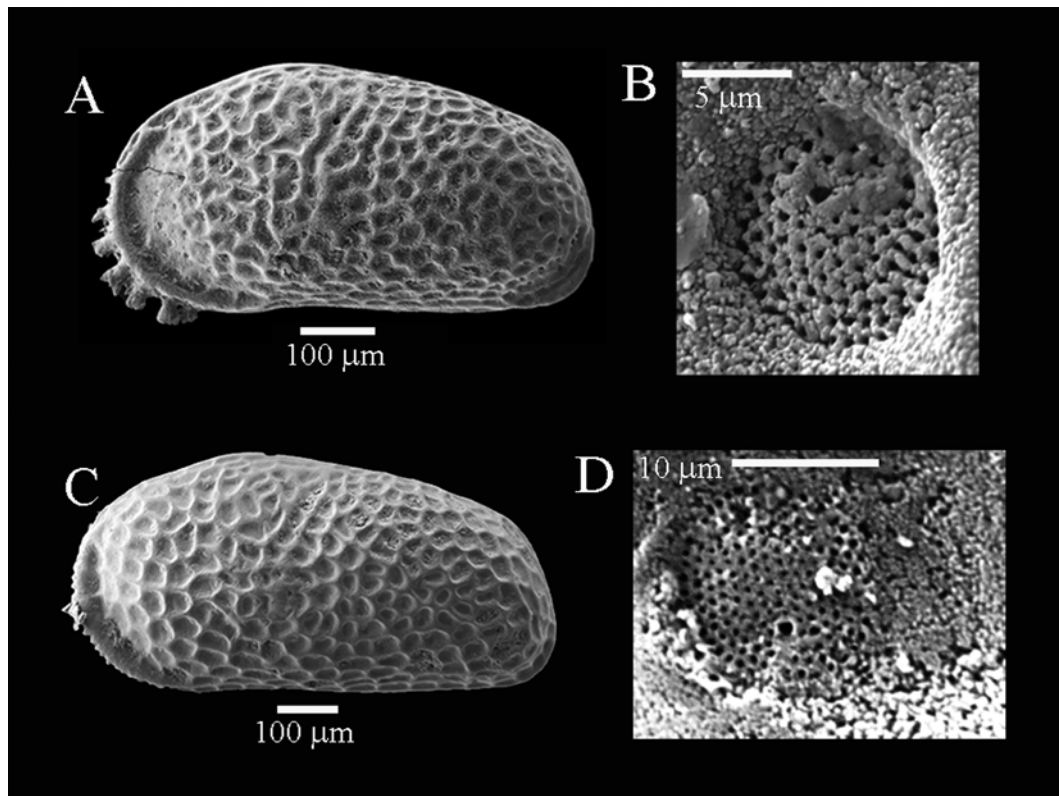


**FIGURE 26.** *Cyprideis torosa* (Jones), details of StPC from two sites in Portugal with contrasting salinity concentration; A–B, Sado estuary, Carrasqueira (sample CAR-P1, Spring), salinity *c.* 30 ‰; C–D, Melides lagoon (sample MEL-7, Winter), salinity 8.5 ‰.

***Cyprideis munoztorresi* Gross, Ramos & Piller, 2014.** This species, like *C. ituiaie*, has large valves and StPC of type C (length 0.78 mm in Fig. 27C and StPC in Fig. 27D). The diameter of the round StPC is of Large type with a SI value of 0.0166 (13/780) in the case of the valve studied (Table 14). The StPC area for the pore of Fig. 27D is 91.56  $\mu\text{m}^2$ . We counted 150 tubuli (0.33  $\mu\text{m}$  mean diameter). The setal pore has a diameter of 0.8  $\mu\text{m}$  and is located near the margin of the sieve-plate.

### **The usage of Sieve-type Pore Canals (StPC) as diagnostic traits for taxa of the family Limnocytheridae Sars, 1928**

Table 15 summarises the morphological characteristics of StPC for the various taxa studied. StPC have to be considered as morphological characters displaying intrinsic and extrinsic traits. We show below that these traits have qualitative states that can be used for taxonomic diagnosis.



**FIGURE 27.** *Cyprideis* species with details of pore C, Sucuriju, western Amazonia, Brazil; A–B, *Cyprideis ituiaie* Gross, Ramos & Piller, LVEf; A—general view; B—detail of pore C from A; C–D, *Cyprideis munoztorresi* Gross, Ramos & Piller, LVEf; C—general view; D—detail of pore C from C.

**TABLE 15.** Sieve type Plates Canals—Synoptic view of morphological traits with their qualitative states.

StPC Characters	Qualitative states
<b>Intrinsic traits</b>	
General Shape	Round, Oblong or Irregular
Relative size of round StPC (diameter/length of valve) (Size Index SI)	Small/Large (0.001/0.01 µm)
Approximate number of tubuli/StPC	Low/Large (<60/>61)
Approximate cumulated area of tubuli/StPC (TAT-S-StPC)	Small/Large (<1/>1 µm <sup>2</sup> )
<b>Extrinsic traits</b>	
Density as relative number of StPC/unit valve area (5000 µm <sup>2</sup> )	Low/High (<10/>10)
Dispersal as relative distance between StPC (Distance Index DI)	Narrow/Wide (<10/>10 µm)
Position of StPC at the surface of ornamented valves	On tectum of corrugate or muri/in trough or sollum

### **Diagnostic characteristics of the subfamily Limnocytherinae Sars, 1928 versus those of the subfamily Timiriaseviinae Mandelstam, 1960**

The StPC facilitates the separation of Limnocytherinae and Timiriaseviinae. The former group displays generally normal pores of type C (i.e. StPC with a seta within or at the periphery). There is one exception, species of the genus *Pampacythere* where beside the type C with a seta Whatley & Cholich (1974) also identified type B pores. This suggests the possibility of uniting taxonomically the Limnocytherinae with the Timiriaseviinae. Arguments for closer morphologic relationships between these two groups were made by Danielopol (1969) using the distal minute setae of the 4<sup>th</sup> endopodial segment of the 5<sup>th</sup> to 7<sup>th</sup> limbs, which are visible in the living representatives of both lineages.



The Limnocytherinae display a diversity of StPC, from poorly structured plates, expressed on the surface on the valve's tectum, as in *Limnocythere sanctipatricii* and *L. inopinata* (Figs 25B–D, F, H), in *L. thomasi* (Martens 1990, Figs 16F, 19C) and *Leucocythere mirabilis* (Danielopol *et al.* 1989, Fig. 19C), to well structured StPC situated slightly deeper into the tectum of the valve as in *Ovambocythere milani* (Martens 1989, Fig. 3J) and *Limnocythere cf. gibbosa* (Martens 1990, Fig. 22E). The StPC of *Leucocytherella sinensis* have a peculiar position, namely the C pore lays in a narrow alveolar depression; it displays tightly packed tubuli (Fürstenberg *et al.* 2015). This is unusual for Limnocytherinae C pores which are commonly disposed on flat surfaces of the valve.

The subfamily Timiriaseviinae displays either pores of type B (sieve-plates without a seta) and/or pores of type A1 and A2. The taxa we studied and that we originally assigned to the tribe Cytheridellini have generally small (S) sieve-type plates as defined with the SI index. This latter parameter for characterization of StPC shows for most of the representatives we investigated values in parts per thousand (or “mili” units), and the number of tubuli gives values that do not exceed 60, hence they belong to the Low-number class. We found two exceptions to this pattern, namely *Gomphocythere* sp. (aff. *G. alata*) and “*Theriosynoecum pygmaea*”, which have valves with large sieve-plates. Therefore, the taxonomic position of these so-called Timiriaseviinae taxa at both generic and suprageneric levels requires review.

The position of StPC on the surface of valves can also be used as a taxonomic criterion. Most of the sieve-plates of the Timiriaseviinae investigated are located on the tectum of the valve. *Gomphocythere* sp. (aff. *G. alata*) from Tanganyika (Figs 16F–G) represents an exception. The valves display a reticulate ornamentation and the StPC are located on the solum of fossae, while in the case of *G. besni* and *G. aff. angulata* the StPC are on the plications or on the muri. Therefore, this is an additional argument to assign *Gomphocythere* sp. (aff. *G. alata*) to a new supraspecific taxon.

### **Diagnostic characteristics of the tribes Timiriaseviini Mandelstam, 1960, Cytheridellini Danielopol & Martens, 1989 and Gomphodellini Danielopol, Cabral & Lord nov. tribe**

The tribe Timiriaseviini is remarkable for the lack of normal pores of type B, but displays pores of type A2, some of them having characteristic locations. We assign to this tribe the taxa we have studied that lack StPC, namely the genera *Timiriasevia* Mandelstam, *Metacypris* Brady & Robertson, *Kovalevskiella* Klein, *Rosacythere* Colin and *Dolekiella* Gidó, Artheau, Colin, Danielopol & Marmonier. To this tribe are generally assigned also the genera *Elpidium* F. Müller, *Vecticypris* Keen, *Abrotocythere* Zhao, *Frambocythere* Colin, *Progomphocythere* McKenzie, Engelbretsen, Archer & Price, *Intrepidocythere* Pinto, Rocha & Martens, *Thaicythere* Savatentalintou, Borgonie & Martens. With the exception of *Elpidium* for which Danielopol *et al.* (2014) showed the presence of exclusively A pores, the other genera mentioned lack information concerning normal pores.

Timiriaseviinae of the tribe Cytheridellini do not display StPC of Irregular type, as in the case of *Cyprideis americana* (Fig. 9B), or as those of various *Cytherissa* species (cf. *Cytherissa plana tuberculata*, in Danielopol *et al.* 1990, Fig. 12J).

Here we assign to the tribe Cytheridellini the following genera: *Cytheridella* Daday, *Gomphocythere* Sars, *Theriosynoecum* Branson and *Sinuocythere* Colin, Cabral, Dépêche & Mette. These genera have StPC with a small sieve-plate and low number of tubuli, conforming to the type Small-type StPC and Low-number of tubuli. Taxa of the former two genera display additionally a Wide-spaced dispersion pattern.

Of interest is the taxonomic allocation of the genus *Theriosynoecum* within the tribe Cytheridellini due to the discovery of the StPC and their characteristics (i.e. small size of StPC and low number of tubuli within a StPC). These data revise the taxonomic position commonly used, i.e. the genus belonging to the tribe Timiriaseviini (e.g. Sames 2011).

Representatives of the genus *Gomphodella* have on the valves a high number of narrowly spaced StPC, i.e. the dispersion of the StPC is the Narrow-type when expressed by the DI index. Taking into account also the absence of a seta on the 2<sup>nd</sup> segment of the antennule then a separation of this Timiriaseviinae group in a new tribe is justified and we name it here tribe Gomphodellini Danielopol, Cabral & Lord nov. tribe. Additionally to the morphological arguments, there is also the peculiar biogeographic distribution of this ostracod group, namely its restriction to Australia, while the other two tribes, Timiriaseviini and Cytheridellini, have wider geographic distributions, over large areas that cover the most important biogeographic regions (information in Karanovic & Humphreys 2014).

The systematic position of the new tribe Gomphodellini Danielopol, Cabral & Lord nov. tribe within the family Limnocytheridae is given below with a diagnosis, based on the StPC (see Table 16):

**TABLE 16.** Synoptic view of the improved diagnostic system, proposed for the taxonomy of the Family Limnocytheridae, with main emphasis on the Subfamily Timiriaseviinae.

Taxa	Diagnostic trait StPC	Diagnostic trait Antennular p2 seta
F. Limnocytheridae	SF. Limnocytherinae Type C, seldom B	Distal position
	SF. Timiriaseviinae Type B or absent	Sub-distal position or absent
SF. Timiriaseviinae	Tr. Timiriaseviini Absent	Sub-distal position
	Tr. Cytheridellini Type B; small round (lower number oblong shape); low numbers of tubuli and low area; low density of StPC widely spaced	Sub-distal position
	Tr. Gomphodellini Type B; small round, few oblong-shaped; low numbers of tubuli and low area; high density of StPC narrowly spaced	Absent

## Family Limnocytheridae Sars, 1928

### Subfamily Timiriaseviinae Mandelstam, 1960

#### Tribe Gomphodellini Danielopol, Cabral & Lord nov. tribe

Type genus *Gomphodella* De Deckker, 1981

Type species *G. maia* De Deckker, 1981

**Diagnosis:** Carapace of small to medium size (i.e. less than 0.6 mm length); lophodont hinge; valves with small StPC bearing generally 10-30 tubuli per plate; density of StPC on the valve, high, i.e. estimated to more than 10 entities per a standardized area of 5000  $\mu\text{m}^2$ ; the spatial dispersion of StPC is of Narrow-spaced type (of less than 10  $\mu\text{m}$  mean distance in triad items); 2<sup>nd</sup> segment of the antennule without posterior seta.

Table 16 gives a synoptic view of the improved diagnostic system proposed for the taxonomy of the Family Limnocytheridae, with emphasis on the Timiriaseviinae taxa. The system is robust as it is based on new carapace characters, the StPC, combined with evidence derived from the limb morphology, the antennular seta.

### Additional morphological and putative functional aspects explaining disparity of Sieve-type Pore Canals

The position of the StPC when integrated within the general surface ornamentation of the carapace was successfully used as a taxonomic trait within several taxonomic and phylogenetic studies by Japanese ostracodologists (Hanai 1970; 1982; 1988; Ikeya & Tsukagoshi 1988; Tsukagoshi 1990; Tsukagoshi & Ikeya 1987; 1991; Ishi *et al.* 2005; Ozawa *et al.* 2014). Here we show that after mapping the location of StPC of *Gomphocythere besni* valves the variation of position between two individual valves was important and therefore it appears unrealistic to be used for taxonomic purposes. However, we noted that the StPC densities (as number of entities) within local (standardised) areas of the valve are informative as diagnostic characters when defining Timiriaseviinae taxa (see Discussion below).

The normal pores of A2 type display a relatively stable position between four Recent (living) genera (Figs 6A, 7A–C); one fossil recrystallised genus also presents similar position of the preserved A2 pores. Because the A2 setae are more slender and longer than those of the A1 pore, and also because there is a free space between the seta and the outer rim, one can speculate that the A2 pores have a double function, mechanosensory and chemosensory. The latter function could be more-or-less complementary to the StPC of type B.

Another aspect we want to emphasise is the importance to examine the inner side of the valves for StPC. In many cases the reduced apertures of the tubuli on the valve's tectum are obscured or eroded making accurate observation impossible. If the inner side of the valve is in good condition it is likely to preserve important information about the morphology of the StPC. For example, *Limnocythere sanctipatricii* viewed from inside (Fig. 25F) shows not only the sieve-plate but also the canal of the seta. In such a case one can identify the type of the normal pore, potentially valuable for taxonomic purposes. Figures 3D–E and 15A–C show the possibility to identify normal pores of types A and B internally. The value of this approach becomes apparent with the data for “*Theriosynoecum*” *pygmaea* presented above and which suggest to us the necessary taxonomic revision of this species.

Following the work of Rosensfeld & Vesper (1977) on the relationship between the shape of StPC of *Cyprideis torosa* and the salinity of the water in various habitats (information *inter alia* in Frenzel *et al.* 2017, Boomer *et al.* 2017) it is necessary to disentangle the ecophenotypic signal from the genetic one. Therefore, if one accepts the hypothesis that the tubuli of the StPC play a role in osmotic exchange between the haemolymph of the ostracod and the ionic concentration of the water within which it lives (Aladin & Potts 1996), then it is likely that in the case of Timiriaseviinae there are differences between species in the tubuli-numbers and/or tubuli-size (the latter expressed either as diameter or total area of tubuli) that reflect habitat environmental conditions. Table 17 gives the chemical conditions in which *G. aura* and *Gomphodella quasihirsuta* were found. The latter species tolerates higher ionic concentrations compared to the former one. Tables 10 and 11 provide comparative information on the size of the round and oblong StPC of these two species. There is a slight difference in the mean size of the diameter and the surface area of the round-shape StPC of *G. quasihirsuta* as compared to *G. aura*. However, comparing differences between the Size Index for the diameter of the round StPC of the two species using the Mann-Whitney U statistic test for medians (see Methods) one gets a significant difference at  $P = 0.001$  as  $U = 148$  (i.e. above the critical value  $U = 137$ , Table U in Rohlf & Sokal 1995).

**TABLE 17.** Water chemistry in boreholes from Pilbara, WA where *Gomphodella aura* Karanovic and *Gomphodella quasihirsuta* Karanovic occur.

Chemistry Parameters	<i>Gomphodella aura</i> Yandeyarra Reserve Borehole YAN13 (09.06.2005)	<i>Gomphodella quasihirsuta</i> Uaroo Station Borehole UAR002 (31.06.2005)
TDS (mg/L)	0.45	1.1
Alkalinity (mg/L)	275	470
Hardness (mg/L)	216	488
Na <sup>+</sup> (mg/L)	83.4	284
K <sup>+</sup> (mg/L)	2.2	11.7
Cl <sup>-</sup> (mg/L)	94	374
Ca <sup>++</sup> (mg/L)	43.3	90.4
Mg <sup>++</sup> (mg/L)	26.2	63.8
EC (μS/cm)	848	2267

For *G. quasihirsuta* there is a difference between the averages of the surface areas of the two classes of pores, the oblong StPC being larger than the round ones. There is no overlap between the variability of the two types of pores, expressed as 95% of the confidence limits around the average. The Mann-Whitney U-test, computed for the surface areas of round and oblong StPC, each with 16 observations (Table 11), indicates the same conclusion. The computation of our data offers a U value of 214, superior to the critical value at  $P = 0.001$  (Table U, Rohlf & Sokal 1995). Additionally, in the case of *G. quasihirsuta*, where we had enough information to test separately the relationship between number of tubuli and the size of the StPC area for both round and oblong shape StPC using the Kendall rank correlation coefficient, there is a significant association between these two variables (Table 5).

Looking again at the data in Tables 10 and 11, the mean number of tubuli per StPC of *G. quasihirsuta* is more-or-less equivalent to those of *G. aura*, even if the size of the StPC is larger. However, when we measure the area of tubuli and express the values as their total mean surface we note that *G. quasihirsuta*, which lives in water with

higher ionic concentrations, displays a higher value for the surface aperture of the mean tubuli numbers of a StPC, as compared to those of *G. aura* (Table 4).

The comparative description of the sieve-plates of various species of *Cyprideis* presented above (Figs 9, 26–27, Table 14) points to two aspects: firstly, most *Cyprideis* species we examined display larger StPC, with higher numbers of tubuli, as compared to species of *Cytheridella*, *Gomphocythere*, *Gomphodella* and *Theriosynoecum*; secondly, *Cyprideis americana*, which lives in water with a very high ionic concentration (Meyer *et al.* 2017), displays an extremely large “tubuli area” as compared to all the other taxa we studied here (Table 4).

The presumed relationship between salinity or ionic concentration of the water and the size of the tubuli canals is strengthened by the record of *C. torosa* from the two sites in Portugal with contrasted salinities (Carrasqueira 30.9–41.7 ‰ in spring, Melides 8.5 and 15.1 ‰ in winter). The diameter or the total surface area of tubuli within a pore shows a larger size in a valve from the higher salinity site compared to those from where salinity is low (Fig. 26, Table 4).

Rosenfeld & Vesper (1977) reported that a higher frequency of elongate StPC on *Cyprideis torosa* is the result of a higher saline concentration in the habitats where ostracods live as compared with the valves of *C. torosa* coming from more-or-less freshwater habitats. Rosenfeld & Vesper (*op. cit.*) observed that the peripheral area of the valves displays a higher number of oblong StPC as compared to the central area. Hence their computation was mainly related to the central area. However, no exact quantitative information was given by these authors. Here Table 2 offers for the first time clear quantitative information on the distribution of the two types of pores occurring on the central and peripheral areas of valves of *G. besni*. The peripheral area displays a significantly higher number of oblong StPC than the central area. For both valves analysed, the V-1 and V-2, the G-values 6.35 and 10.09, computed with the G-test for association (see Methods) are above the critical value 3.84 of the chi-square distribution at  $P = 0.05$ . This means that in the case of *Gomphocythere besni*, which was sampled from a freshwater habitat, the quantitative difference between the round and oblong StPC on the same valve could be a result of developmental constraints during the calcification process of the carapace, an idea noted, in a different context, by De Deckker (2002). However, the possibility cannot be excluded that in some taxa, like the brackish water *Loxocochocha elliptica* Brady, the position of such pores is genetically controlled (Rosenfeld 1982).

Our evidence points to a complex situation for the shape, the size and the structure of the StPC. The ionic concentration or salinity of the aquatic habitat where ostracods develop their populations is only one factor for their disparity. There is also an indication, as mentioned above for *G. besni*, that shapes of the StPC could be developmentally and/or genetically controlled. It should be noted that the positive relationship of an increase in the number of tubuli with the size of the StPC documented for several Timiriaseviinae taxa (Table 5) seems to be related also to an organismic process that acts independently to the salinity or ionic concentration of the host water. This trend of increase in size of the StPC and/or the number of tubuli is not unlimited and viewed at a macroscale, the size of these entities appears characteristic of a given taxon and can be used as a taxonomic trait at a supraspecific level as documented in the previous section.

## Discussion

The following discussion concerns ideas that developed during the progress of this project. We propose several research topics that we believe are achievable using commonly available ostracod material and current research techniques:

*The systematics of the Limnocytheridae, with special emphasis on the Timiriaseviinae, should be further refined*—as compared to the schemes already proposed by Colin & Danielopol (1978), Martens (1995), Gidó *et al.* (2007), Savatentalinton *et al.* (2008), Karanovic (2009), Karanovic & Humphreys (2014) and herein. For example, various *Cytheridella* species, beginning with the most ancient record, of the Upper Jurassic *Cytheridella todiltoensis* (Kietzke, 1992) of North America and continued with *Cytheridella* species of the Upper Cretaceous from India and Africa (Bhatia *et al.* 1996; Colin *et al.* 1997), with younger records from the Lower Eocene of Eurasia (Tambareau *et al.* 1991; Monostori 1993; Bhandari 1998) and the Oligocene in Europe (Carbonnel & Ritzkowski 1969), and in South America (Bergue *et al.* 2015). Purper (1977; 1979), Sheppard & Bate (1980) followed by Gross *et al.* (2013) documented several species of *Cytheridella* from Miocene and Plio-Pleistocene lacustrine sediments from northern Brazil and Colombia. Finally, work on Recent *Cytheridella* species from the

Neotropics (Wrożyna *et al.* 2016) should be inserted in a coherent system using the framework of a phylogenetic taxonomical scheme.

*The cartography of pores*—This is one of the innovative aspects of our project that should be continued for Timiriaseviinae, as compared to the Limnocytherinae, using a multi-directional examination of the valves within a hyperspace approach. We understand by this view the spatial representation of the external face of the ostracod valve mapped from different directions, in order to reconstruct the lateral, dorsal, anterior, posterior and ventral sides and to collate them into one stereoscopic image. This latter image should be further related to a similar image of the inner side of the valve. Our pilot approach, which tried to demonstrate the usefulness of this kind of description for the normal pore types, should be extended for all the sides of the valves in such a way to be simultaneously visible. Moreover, our structural intuition of this approach (cf. for this latter concept see Kemp 2016) should be improved. In this way we will honour the memory of our idol in ostracodology, the late Peter Sylvester-Bradley and his *Stereo-Atlas* project.

*Special investigations on the taphonomic aspects of the StPC of cytherocopines*—We demonstrated that for fossil *Timiriasevia* the pores on the outside of the valves were not visible, apparently occluded by a carbonate film deposited during diagenesis or by recrystallisation of the fossilised material. The same was observed with fossil *Theriosynoecum* and *Simuocythere*. Several valves of different species of these genera were analysed and only rarely showed very few pores. On the other hand, recrystallisation can suggest the presence of superficial pores which may be confused with StPC, as shown in *Rosacythere lacobrigensis*. It is clear that recrystallisation and other processes (compaction, dissolution/corrosion, breakage) occurring during diagenesis may alter significantly the ostracod valves surface. Future work on the way diagenesis acts on ostracod carapaces will be very useful to correctly identify all normal pores in the fossil Timiriaseviinae. Additionally, we hope to contribute to an explanation for the intriguing blind tubuli of the Palaeozoic pachydomellids (Podocopa) belonging to the genus *Tubulibairdia*, described by Lundin (1988). Data on diagenesis of StPC of cytherocopines may give ideas on the causes for absence of pores at the surface of the *Tubulibairdia* valves.

*A spin-off of the project*—One could conceive an environmental protection programme for the lacustrine habitats where *Gomphocythere besni* occurs in Turkey (cf. for geographic location and ecological context, Külköylüoğlu *et al.* 2015). Such a programme was proposed for the protection of the site where the endemic *Dolekiella europaea* was found in south-eastern France (Danielopol *et al.* 2009). Such a programme in Turkey could ensure the availability of *Gomphocythere* material as a model taxon for future scientific studies.

## Conclusions

1. Sieve-type pore canals (StPC) occur in many marine Cytherocopina ostracods, in both living and fossil taxa. The diversity of shape and structure of StPC opens new avenues for research related to systematics, phylogeny and (palaeo)ecology of Ostracoda. StPC are seldom documented for non-marine cytherocopines, represented by the Limnocytheridae, Timiriaseviinae.
2. StPC are recognisable on the external side of the valve by defined areas of small apertures of thin tubes (so-called tubuli) which traverse the calcite valve; they open on the inner side of the valve within a bell shaped area. In living ostracods the tubuli are closed by the epicuticle of the valve. By these characteristics StPC differ from the so-called cluster-pores of large area and large tubes, the latter open directly on the inner surface of the valve.
3. StPC are characterised by intrinsic properties: their forms, including shape and size, and by their structures, namely the number and area covered by the tubuli; and also by extrinsic properties: their position, density and dispersal on the valves. The size of StPC increases with the number of tubuli. A number of indices are proposed for analysis of the structure and distribution of StPC to aid comparative analyses. Table 15 gives a synoptic review.
4. Representatives of the family Limnocytheridae exhibit four types of normal pore canals which are, according to Puri & Dickau (1969): (A1) simple pore canals without a surrounding rim on the external side of the valve, (A2) simple pore canals with a rim, (B) StPC without an additional sensilla-pore, and (C) StPC with a sensilla pore.
5. We demonstrate how to achieve new standards for description of StPC and their usage for taxonomic purposes;

*inter alia* a method for mapping the spatial distribution of the StPC on the valves and for the quantification of the size and number of tubules belonging to these structures.

6. We refine the description of StPC for representative Recent and fossil Timiriaseviinae taxa, compared to those of Limnocytherinae and the family Cytherideidae, summarised in Table 16, noting the need for well-preserved material and the importance of examining pore canals from the interior as well as the exterior of the valves.
7. The importance of normal pore canals for diagnosis of supraspecific taxa within the Timiriaseviinae is reflected in the proposal herein of the tribe Gomphodellini Danielopol, Cabral & Lord nov. tribe, differing from the established Timiriaseviini and Cytheridellini (cf. Table 16) and in the new assignment of the genera *Theriosynoecum* and *Sinuocythere* to the tribe Cytheridellini instead of the Timiriaseviini. The taxonomic revision (generic position) of two Timiriaseviinae species is also suggested.
8. Documentation of the relationship between the approximate size and number of the tubules belonging to the StPC and the salinity or ionic concentration of the aquatic environment where the ostracods live reveals an intimate relationship requiring biochemical and physiological investigation of a range of living ostracod taxa.

### Final. The legacy of Jean-Paul Colin

Our colleague and friend Jean-Paul Colin studied the Timiriaseviinae ostracods for 40 years. In the list of his publications (Carbonel *et al.* 2013) at least 17 contributions deal explicitly with Timiriaseviinae taxa. Colin was always interested to document their morphology in as much detail as possible with the idea that this group will represent a good example for the way non-marine cytherids diversified during more than 150 million years. He was convinced that only through cooperation between palaeontologists and neontologists can our knowledge of the evolutionary pathways of Timiriaseviinae be satisfactorily explored and understood.

We hope that this contribution will stimulate new studies of the normal pores of the Ostracoda. It is clear that what we offer here is the tip of an “iceberg” of unknown knowledge related to the valve morphology of the Timiriaseviinae to which our colleague and friend Jean-Paul Colin would certainly have made further contributions.

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