

Comparative Study on the Resting Eggs of Several Anostracans (Crustacea).

Key for the Determination of the Species based upon the Egg Structure and Diameter

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The egg size and the external egg morphology in fourteen species of anostracans were described. In the Branchinectidae species studied two basic patterns in the external layer were distinguished. In Thamnocephalidae: *Dendrocephalus cervicornis* and *D. brasiliensis* differ in the shape of cells, size, length and thickness of the ridges. In Chirocephalidae: *Phallocryptus salinicola* differs from other genera. The combined analysis of the diameter and the morphology of the outer covering constitutes a very useful methodology for the determination of genera and species. Using the mentioned characteristics it has been possible to elaborate a key for the identification of these species.

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Introduction

The resting eggs of the anostracans are surrounded by several layers (Baird, 1849; Mawson & Younge, 1938; Hall, 1952, and Linder, 1960), of which the outer one is formed by the secretion of the uterine glands that are in the female brood pouches. This layer is separated from the cuticular membrane that surrounds the embryo by means of a layer of alveolar nature (Gilchrist, 1978), Fig. 23.

The outer layer that surrounds the egg is generally thick and ornamented in a characteristic way. The ornamentation differs at a generic level (Baird, op cit.; Hall, op cit.; Hsu, 1953, and Linder, op cit.). Mura et al. (1978), studying the resting eggs of four species of the genus *Chirocephalus* (Chirocephalidae) with the scanning electron microscopy, found interspecific ornamental variations in the outer layer morphology and in the egg diameter.

In this contribution, the size and morphology of the outer layer of the resting eggs were studied comparatively using the scanning electron microscopy in fourteen species of anostracans belonging to the following genera: *Branchinecta* Verrill, 1869, *Dendrocephalus* Daday, 1908, and *Phallocryptus* Birabén, 1951.

Materials and Methods

To carry the present study, the resting eggs of the species cited below, together with the places they were found, were examined: *Branchinecta gigas* Lynch, 1937, from Grant County, Washington, U.S.A.; *Branchinecta paludosa* (O.F.M.) from Greenland; *Branchinecta gaini* Daday, 1902, from Petermann Island (west of the Antarctic Peninsula); *Branchinecta ferox* (M. Edw.) from Kecskemét, Hungary; *Branchinecta rocaensis* Cohen, 1982, from a pool at the sides of the National Road number 251 (from Conesa to Río Colorado, Río Negro province, Argentina); *Branchinecta santacruzensis* (1), from a muddy pond arriving at Santa Cruz from Coyle, Santa Cruz province, Argentina; *Branchinecta palustris* Birabén, 1946, from the La Escondida pond, Río Negro province, Argentina; *Branchinecta papillosa* Birabén, 1946, from Colonia Sarmiento, in fresh water pools close to Senguer river, Chubut province, Argentina; *Branchinecta tarensis* Birabén, 1946, found in fresh water pools in the area of San Martín Lake, some kilometers before arriving at Tar lake, Santa Cruz province, Argentina; *Branchinecta leonensis* (2) from a large pond in the vicinity of Leon hill, Santa Cruz province, Argentina; *Branchinecta achalensis* César, 1985, from Pampa de Achala, found in pools with stony bottom, Córdoba province, Argentina; *Dendrocephalus brasiliensis* Pesta, 1921, from a pond in the way to Totoralejos, Córdoba province, Argentina; *Dendrocephalus cervicornis* (Weltner) from Totoralejos and *Phallocryptus salinicola* Birabén, 1951, from Lucio V. Mansilla, Córdoba province, Argentina.

The materials corresponding to *B. gaini*, *B. ferox* and *B. paludosa* were lent by the Natural History Museum of Paris and the rest were deposited in the collection of the Division of Invertebrate Zoology of the Natural Science Museum of La Plata, Buenos Aires province, Argentina.

To observe the resting eggs we proceeded like this:

1. They were removed from the brood pouches of several females separated from species (preserved in alcohol 70%), and soaked in alcohol 70%, then 50 eggs from each species were taken (except *B. paludosa* from which 24 were measured and *B. gaini* from which only one could be measured, as the others were collapsed in different degree). For all we measured two perpendicular diameters which resulted equally. The measurements are in millimeters and were obtained by using an eye-piece micrometer and a binocular stereoscopic microscope.
2. The biometric data obtained in the present study were treated with the following statistics: $\sum X/n$ (average of the diameters), $s^2 = \sum X^2/n - 1$ (varianza, $s = \sqrt{s^2}$ (standard deviation). $S_m = s/\sqrt{n}$ (typical error of the mean) and $L_1, L_2 = X \pm t_{0.05} \times s/\sqrt{n}$.
3. The same groups of eggs measured were dried in a stove at 36-40° C during some minutes. Afterwards they were cleaned as well as possible from foreign particles.
4. When they were clean, they were mounted on a two-faced adhesive tape, shaded to the carbon and then to the gold-palladium in the metallizador. Afterwards they were observed and photographed by means of the scanning electron microscope.

Results

Branchinectidae

Branchinecta Verrill

Branchinecta gigas Lynch, 1937 (Fig. 1 and 2)

The outer layer has a complex reticular structure without a clear cell delimitation. It is furrowed by wavy ridges, each one forms one denticle or more, so that the surface consists of hills and valleys. The denticles reach a height of 5.35 micron (10-2). The egg diameter is 0.562 mm ($s^2 = 0.002852$; $l_1 = 0.5468$).

Branchinecta ferox (Milne-Edwards, 1840) (Fig. 3 and 4)

The outer layer is formed by four identical cells joined together like an orange segment and separated by sutures that delimited them clearly. Each cell is ellipsoid and externally very convex. The surface is rough and subdivisions inside the cells cannot be seen. In the intersection of three cells the outer covering becomes concave,

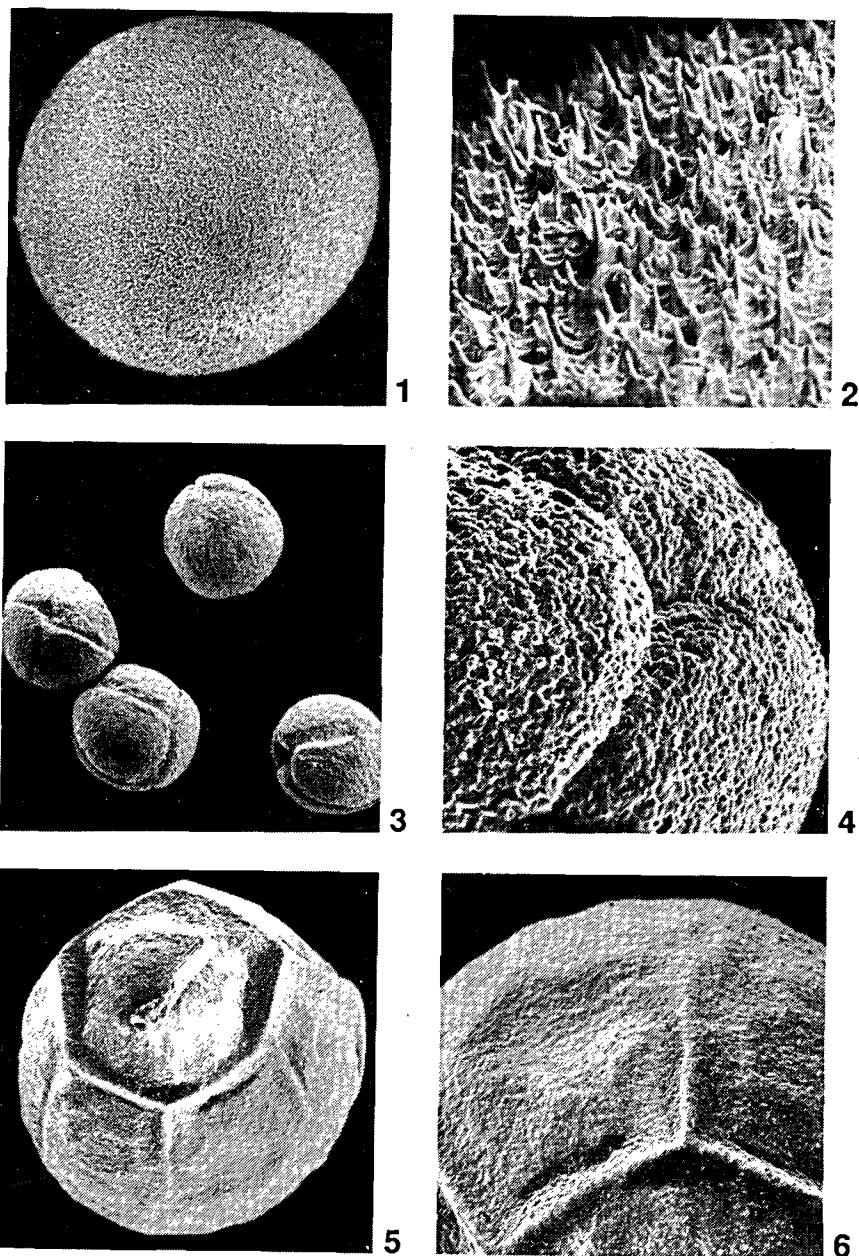


Fig. 1-6. Resting eggs of *Branchinecta*. 1: *B. gigas*, 180 X. 2: *B. gigas*, 2,000 X. 3: *B. ferox*, 300 X. 4: *B. ferox*, 1,500 X. 5: *B. gaini*, 300 X. 6: *B. gaini*, 500 X.

forming in this way the sutures. The egg diameter is 0.2416 mm ($s^2 = 0.002375$; $l_1 = 0.02553$ and $l_2 = 0.2278$).

Branchinecta gaini Daday, 1902 (Fig. 5 and 6)

The outer covering presents a subhexagonal or subpentagonal polygonal reticulum, free from pores on the surface. The ridges that form the sides of the polygons get to such a development that give the outline a well-defined aspect. Each cell is delimited by its sides of straight edge. The ridge length is 77 microns; its height and thickness 13 microns. The egg diameter is 0.280 mm.

Branchinecta paludosa (O.F.N.) (Fig. 7 and 8)

The outer layer is delicate and not much rigid, with subrectangular, subquadrangular and subpentagonal polygonal cells. The cell surface has a complex structure; the inner space, delimited by the ridges, is formed by tiny pieces like canes that are placed in different directions. The ridges delimiting the cells are formed by the union of those structures in one direction. The ridges length is from 50 to 87 microns, the thickness 3 microns and the approximate size of the pieces 7 microns. Egg diameter: 0.3966 mm ($s^2 = 0.000442$; $l_1 = 0.4051$ and $l_2 = 0.3880$).

Branchinecta tarensis Birabén, 1946 (Fig. 9 and 10)

The reticulum forming the outer layer is formed by polygonal cells of different size that have their sides complete in almost all the cases and are approximately subpentagonal. A denticle generally rises from each cell vertex but there can be more than one or no one, according to the development and thickness of the delimiting ridges. The denticles have a mean height of 8 microns (11-6). The approximate relationship between the number of cells and the egg diameter is of 26:1 and the ridge thickness is 3 microns (4-1). Egg diameter: 0.351 mm ($s^2 = 0.00067$; $l_1 = 0.3583$ and $l_2 = 0.3436$).

Branchinecta papillosa Birabén, 1946 (Fig. 11 and 12)

The outer covering has a very delicate reticle, with a large multiplication of the denticles, which gives it a thorny aspect. There are polygonal cells of different sizes. The denticle height is 6.75 microns (10-5); the relationship between the number of cells and the egg diameter is of 25:1. The egg diameter is 0.2916 mm ($s^2 = 0.001455$; $l_1 = 0.3024$ and $l_2 = 0.2808$).

Branchinecta palustris Birabén, 1946 (Fig. 13 and 14)

The outer covering is formed by a polygonal reticle throughout its extent. The ridges are well-defined and rise from the surface with a zigzagging route. The cells can be subquadrangular, subrectangular, subpentagonal, etc. The ridge maximum height is represented by the development of the denticle body and is 6 microns (7-5).

The ridge thickness is 22:1. The egg diameter is 0.2816 mm ($s^2 = 0.000209$; $l_1 = 0.2816$ and $l_2 = 0.2815$).

Branchinecta santacruzensis César, 1987 (Fig. 15, 16 and 23)

The outer covering is formed by a reticle of irregular polygonal cells. The ridges separating the cells rise in a mono or bicuspidated denticle; the cells measure approximately 150 microns and the relationship between the number of cells and the egg diameter is 20:1. The ridge height and thickness is variable. The mean height is 5

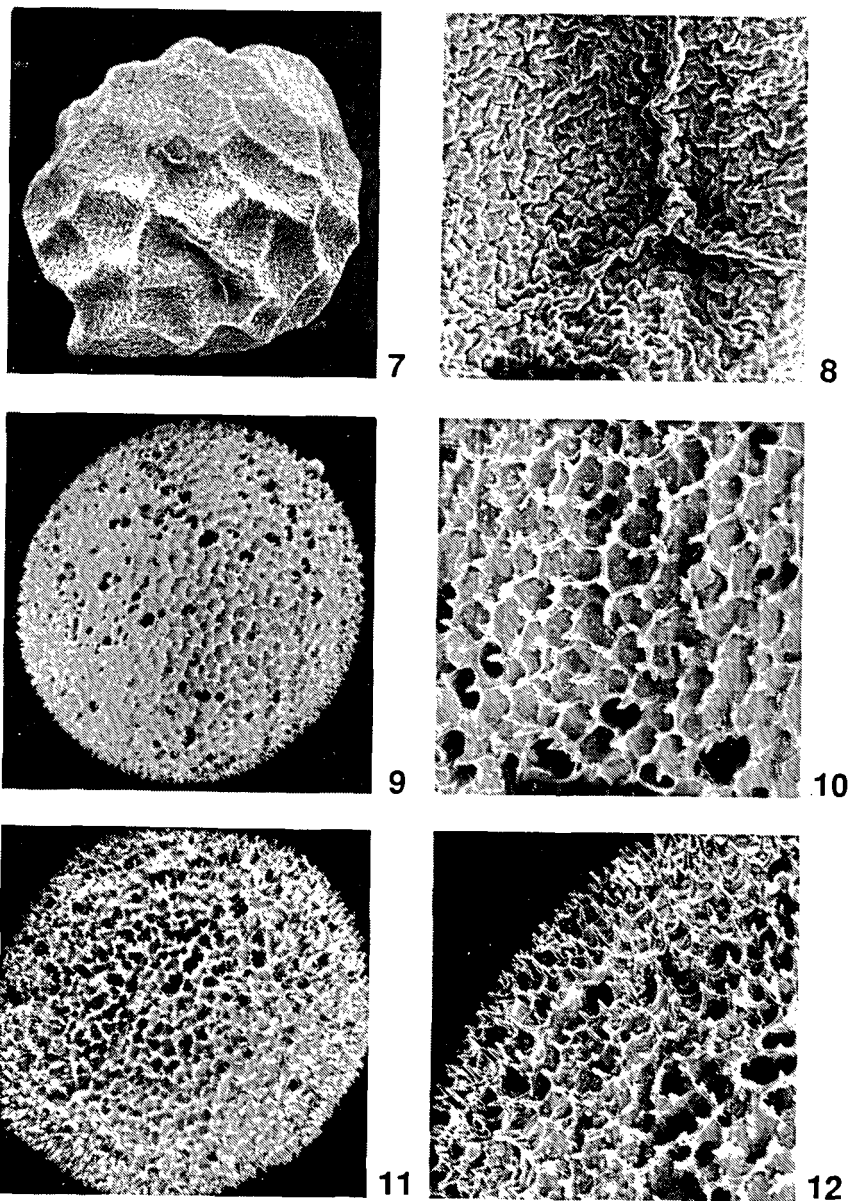


Fig. 7-12. Resting eggs of *Branchinecta*. 7: *B. paludosa*, 300 X. 8: *B. paludosa*, 3,000 X. 9: *B. tarensis*, 300 X. 10: *B. tarensis*, 700 X. 11: *B. papillosa*, 300 X. 12: *B. papillosa*, 600 X.

microns (7-3) and corresponds to the denticles height and their thickness is approximately 2.2 microns. The egg diameter is 0.3664 mm ($s^2 = 0.0006$; $l_1 = 0.3772$ and $l_2 = 0.3631$).

Branchinecta leonensis César, 1987 (Fig. 17 and 18)

The outer covering is formed by an irregular reticle of polygonal cells separated by the ridges. The point where three ridges meet determines the maximum height of the whole structure conforming a kind of a truncated pyramid. The ridges generally have interruptions in their route (Fig. 18) and this incomplete cell delimitation increases or decreases the cell size. The egg diameter is 0.3316 mm ($s^2 = 0.01764$; $l_1 = 0.3812$ and $l_2 = 0.2819$).

Branchinecta achalensis César, 1985 (Fig. 19 and 20)

The outer layer is formed by a reticle of polygonal cells which surface is rough. The cells are rather regular and hexa- or pentagonal; they do not present thorns or denticles on their surface and each cell vertex is formed by the meeting of three bars. The presence of an incomplete septum can be noted in some cells (Fig. 2); if the septum is completed, the cell will divide into two fields. The approximate relationship between the number of cells and the egg diameter is 3:1; the ridge length is 46 microns; their thickness is 4.3 microns and their height is 18 microns. The egg diameter is 0.2384 mm ($s^2 = 0.0146$; $l_1 = 0.2726$ and $l_2 = 0.2041$).

Branchinecta rocaensis Cohen, 1982 (Fig. 21 and 22)

The polygonal cell reticle forming the outer layer has regular structure. The cells are subcircular, the septum or ridges that delimited them are smooth and the cell surface rather flattened. Each vertex is formed by the meeting of three ridges and spreads over an extensive platform. The egg outline is delicate on the whole and the surface of the outer layer is rough. The relationship between the number of cells and the egg diameter is 5:1; the ridge length is 58 microns, their thickness is 6.4 and their height is 13 microns. The egg diameter is 0.3542 mm ($s^2 = 0.00142$; $l_1 = 0.3448$ and $l_2 = 0.3235$).

Thamnocephalidae

Dendrocephalus Daday, 1908

Dendrocephalus cervicornis (Weltner) (Fig. 24 and 25)

The outer layer is formed by very large subtriangular and subquadrangular cells of rough sculptured surface. The delimiting ridges are conspicuous structures measuring 63 microns (31-80) of length, 12 microns of thickness (6-16) and 17.5 microns of height, approximately. The cells have in general from 87 to 100 microns of maximum length, the egg diameter is 0.2632 ($s^2 = 0.000479$; $l_1 = 0.2639$ and $l_2 = 0.2570$).

Dendrocephalus brasiliensis Pesta, 1921 (Fig. 26 and 27)

The outer covering is formed by very large subquadrangular cells delimited by high ridges of great thickness. Each cell forms a side of the egg and this layout makes the egg general outline a bit less spherical. The outer covering surface is rough and fairly

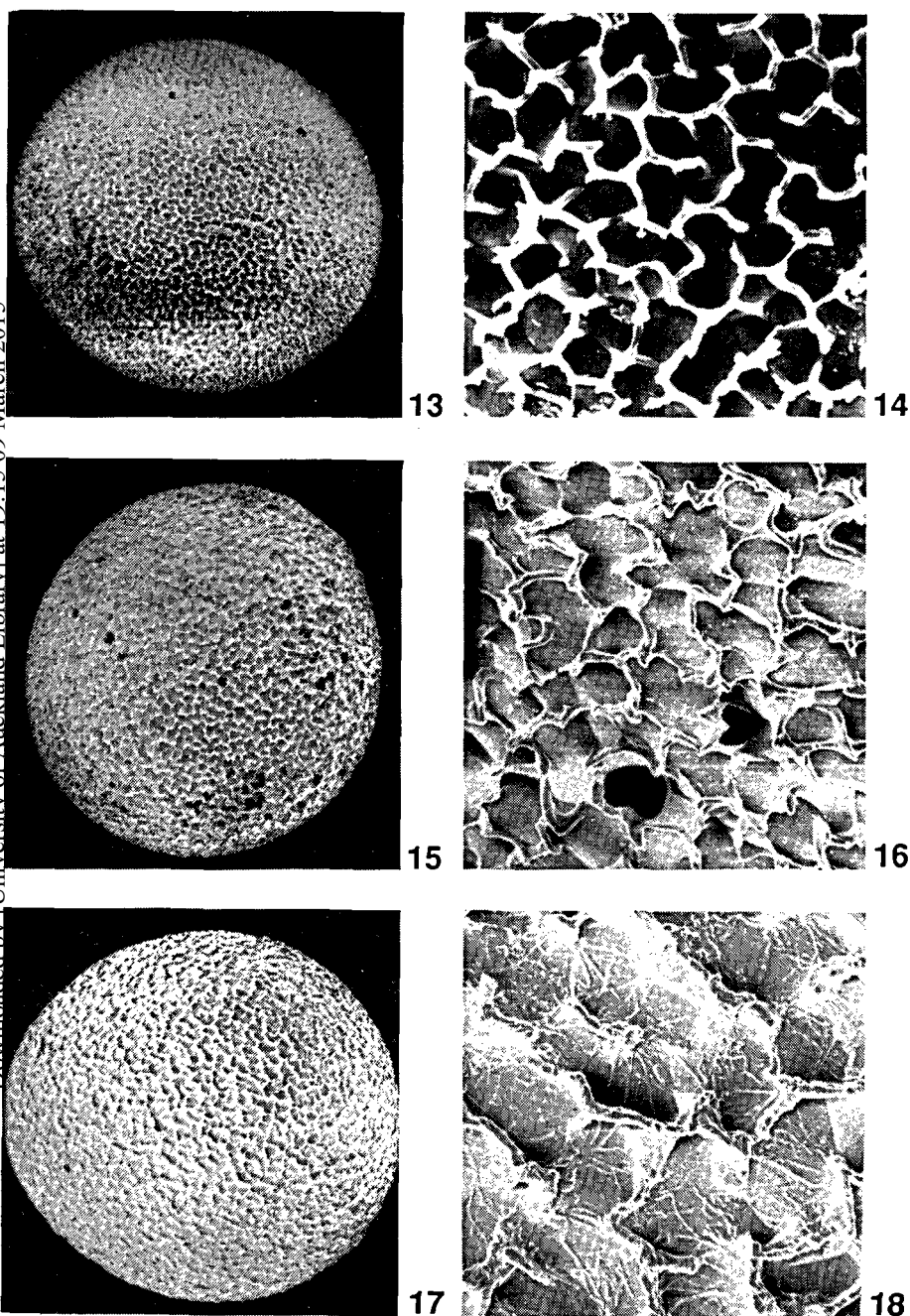
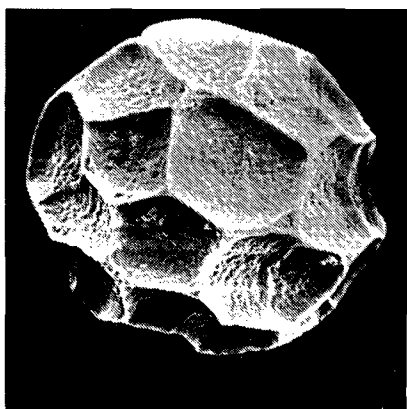
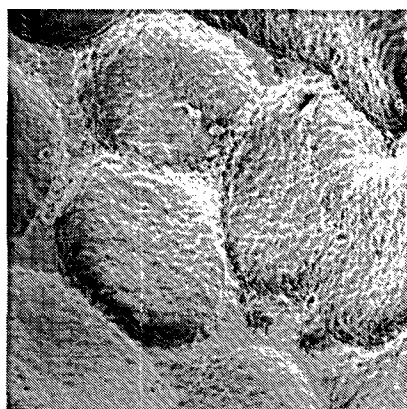


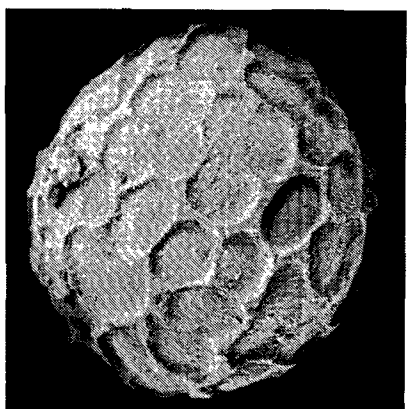
Fig. 13-18. Resting eggs of *Branchinecta*. 13: *B. santacrucensis*, 300 X. 14: *B. santacrucensis*, 1,500 X. 15: *B. leonensis*, 300 X. 16: *B. leonensis*, 3,000 X. 17: *B. palustris*, 350 X. 18: *B. palustris*, 2,000 X.



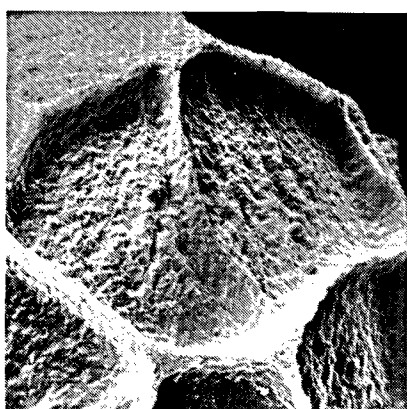
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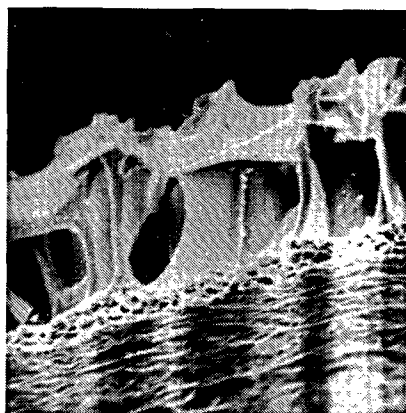
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Fig. 19-23. Resting eggs of *Branchinecta*. 19: *B. achalensis*, 400 X. 20: *B. achalensis*, 700 X. 21: *B. rocaensis*, 300 X. 22: *B. rocaensis*, 800 X. 23: *B. santacrucensis*, 3,000 X. Cross-section through resting egg.

similar to the *D. cervicornis* egg. The ridge length is 100 microns and the thickness 9. The egg diameter is 0.2304 mm ($s^2 = 0.005516$; $l_1 = 0.4404$ and $l_2 = 0.2032$).

Chirocephalidae

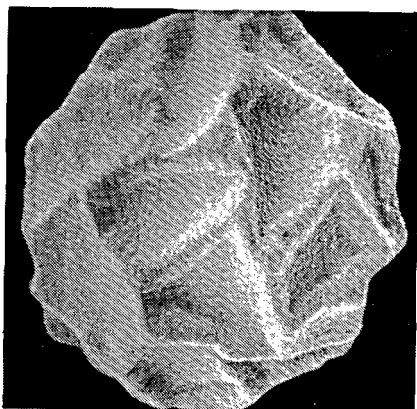
Phallocryptus Birabén, 1951

Phallocryptus salinicola Birabén, 1951

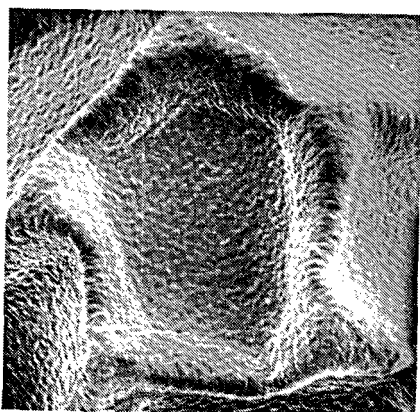
The outer layer is formed by polygonal cells with the form of a rosette. Each cell is separated from the next one by ridges of subcircular route that delimit their edges with maximum convexity. In the central area of the cell we can appreciate the maximum concavity in a regular gentle slope. The cells form groups of three or four of them, forming a group separated from the other groups of cells by means of thicker ridges. The surface of the outer covering looks rough and no pores can be seen on it. The approximate size of the cells is 10 microns and the thickness of the delimiting ridges is 5.75 microns. The egg diameter is 0.2632 mm ($s^2 = 0.1717$; $l_1 = 0.3116$ and $l_2 = 0.2148$).

Key for the determination of several species of Anostracans based upon the resting egg stereoultrastructure

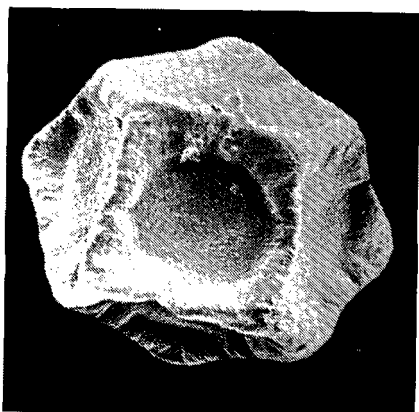
- 1— Outer layer formed by a reticle of regular polygonal cells with well-defined limits. Without denticular or pyramidal structures 2
- 1'— Outer layer formed by a reticle of regular polygonal cells, generally with well-defined limits. With denticular or pyramidal structures 4
- 2— Four subequal cells assembled in a meridional direction like an orange segment, separated from one another by means of sutures that delimit them clearly. Elliptical and externally convex cell. Rough surface of the outer covering without subdivisions. Egg diameter: 0.2416 mm*B. ferox* (M-Edwards). (Fig. 3 and 4)
- 3— Polygonal cells that can be subtriangular, subquadrangular, subpentagonal, subhexagonal or like a rosette.
- 3₁— Generally subpentagonal or subhexagonal cells; surface of the outer layer with tiny outlined structures of 7 microns of length. Ridges delimiting the cells of 68 microns of length. Egg diameter 0.3966 mm*B. paludosa* (O.F.M.) (Fig. 7 and 8)
- 3₂— Subpentagonal or subhexagonal cells. Surface of the outer covering of rough aspect. Without outlined structures.
 - a— Ridges delimiting the cells of 83 microns of length, 13 of height and 13 of thickness. Egg diameter: 0.280 mm*B. gaini* Daday 1910. (Fig. 5 and 6)
 - b— Ridges delimiting the cells of 58 microns of length, 6.4 of thickness and 13 of height. Surface of the cells somewhat flattened and rough, with subcircular outline, they are quite regular. Egg diameter: 0.3542 mm*B. rocaensis* Cohen 1982. (Fig. 21 and 22)



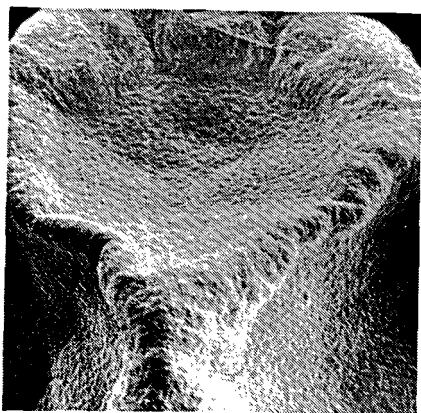
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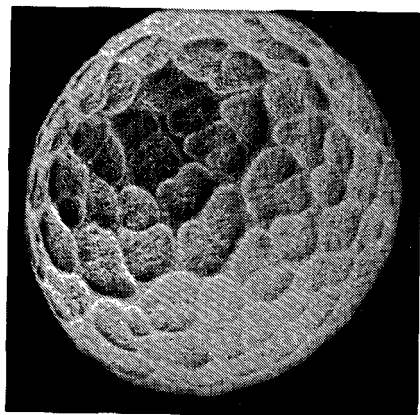
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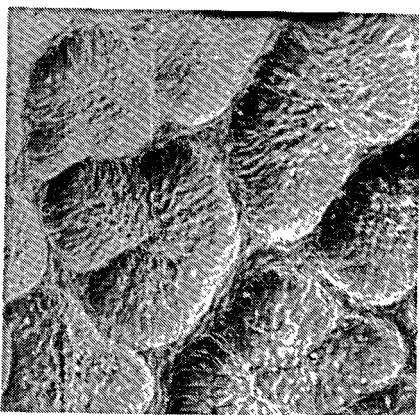
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Fig. 24-29. Resting eggs of *Dendrocephalus*. 24: *D. cervicornis*, 450 X. 25: *D. cervicornis*, 800 X. 26: *D. brasiliensis*, 450 X. 27: *D. brasiliensis*, 800 X. 28: *P. salinicola*, 380 X. 29: *P. salinicola*, 1,000 X.

- c—Ridged delimiting the cells of 46 microns of length, 4.3 of thickness and 18 of height. Rough surface of the cell tending to be concave from its edge. Egg diameter: 0.2384 mm *B. achalensis* César 1985. (Fig. 19 and 20).
- 3₃— Polygonal cells with the form of a rosette. The maximum concavity can be observed towards the center of the cell. Cells forming groups of two, three or four of them surrounded by the ridges that get thicker and their thickness is 5.75 microns. Rough surface of the outer covering. Egg diameter: 0.2632 mm *P. salinicola* Birabén 1951. (Fig. 28 and 29).
- 3₄— Subtriangular or subquadrangular cells. Ridges delimiting them of 63 microns of length, 12 of thickness and 17.5 of height. Rough sculptured surface of the outer covering. Egg diameter: 0.2632 mm *D. cervicornis* (Weltner). (Fig. 24 and 25).
- 3₅— Subquadrangular cells, each one forming one side of the egg; they are delimited by ridges of 100 microns of length and 9 of thickness. Rough surface of the outer layer. Egg diameter: 0.2304 mm *D. brasiliensis* Pesta 1921.
- 4— Outer layer with pyramidal structures. Cells generally delimited in an incomplete way. The meeting of three ridges determines the formation of a pyramidal structure of 4.2 microns of height. Ridges of 1.33 microns of thickness. Egg diameter: 0.3316 mm *B. leonensis* César.
- 4₁— Outer covering with denticular structures which denticles are of different height. Egg diameter, different.
- a— 5 microns (3-7). 0.3664 mm *B. santacrucensis* César. (Fig. 15 and 16)
- b— 8 microns (6-11). 0.351 mm *B. tarensis* Birabén 1946. (Fig. 9 and 10)
- c— 6 microns (5-7). 0.2816 mm *B. palustris* Birabén 1946. (Fig. 13 and 14)
- d— 6.75 microns (5-10). 0.2916 mm *B. papillosa* Birabén 1946. (Fig. 11 and 12)
- e— 5.35 microns (2-10). 0.562 mm *B. gigas* Lynch 1937. (Fig. 1 and 2)

Discussion

In the Branchinectidae family, the eleven species studied showed a great variability in some cases and minor in others. When comparing the three studied forms in the North Hemisphere: *B. gigas* (Fig. 1 and 2), *B. ferox* (Fig. 3 and 4) and *B. paludosa* (Fig. 7 and 8) with the ones of the South Hemisphere: *B. gaini* (Fig. 5 and 6), *B. tarensis* (Fig. 9 and 10), *B. papillosa* (Fig. 11 and 12), *B. palustris* (Fig. 13 and 14), *B. santacrucensis* (Fig. 15, 16 and 23), *B. leonensis* (Fig. 17 and 18), *B. achalensis* (Fig. 19 and 20) and *B. rocaensis* (Fig. 21 and 22), important morphological differences were found with respect to the sculpture of the outer layer.

In the South Hemisphere forms, two main models can be distinguished on one hand, *B. achalensis*, *B. rocaensis* and *B. gaini* can be put together, as they present egg diameters clearly different: 0.2384, 0.3542 and 0.280 mm, respectively. With regard to the morphology or the outer covering, the simpler or less sculptured model is represented by *B. gaini* with a polygonal reticulum of large pentagonal or hexagonal cells which are scarce. In the other two species, the model is complicated because of the multiplication of the cells, although they follow a similar morphologic pattern.

The second model is represented by *B. tarensis*, *B. papillosa*, *B. palustris*, *B. santacrucensis* and *B. leonensis*, all of them from the Patagonian Domain (Ringuelet, 1961). The egg diameter is very similar in *B. palustris* and *B. papillosa* (0.2912 and 0.2816 mm respectively). However, a comparative detailed study of the microphotographs reveals that the relationship between the diameter and the number of cells is slightly less in *B. palustris*, 22:1 as regards *B. papillosa*, 25:1, being the denticles in the latter somewhat higher, an average of 6.75 microns, just like the number of them.

Continuing with this group, *B. santacrucensis*, *B. tarensis* and *B. leonensis* present decreasing egg diameters: 0.3702, 0.351 and 0.3316 mm, respectively. The sculpture of the outer covering follows the same pattern in the three species, but the microphotographs, when highly blown up (600 X or more), show variations as regards the development of the ridges and denticles. In this way, *B. tarensis* presents ridges of 3 microns of thickness and the cells are generally well-delimited, the relationship between the egg diameter and the number of cells being 26:1. The denticles also reach an important development throughout the surface of the outer covering and their height is 8 microns. In the case of *B. santacrucensis*, the reticulum presents a development more irregular than in the previous species; the ridges are thinner, the denticulation less prominent and the height of the denticles less than 5 microns. The relationship between the egg diameter and the number of cells is 20:1.

In the case of *B. leonensis*, the model fades even more and the cells are not well-delimited because of an incomplete formation of the ridges. The ridge vertices end in rather pyramidal formations that are not denticles and their height is 4.2 microns. It is obvious that *B. santacrucensis* presents a central position among the three species as regards the development of the cortical reticulum.

Moreover, it is interesting to emphasize the fact that the Patagonian *Branchinecta* have such a similar modeling in the outer covering, whereas in other species the eggs can be easily identified by this characteristic. Maybe this is due to the fact that the Patagonian group has suffered a rather recent species separation and the pressure of selection favors the acquisition of an egg whose sculpture widens the contact area with the substratum, considering the severe climatic conditions characterized by strong winds of the region.

As regards the Thamnocephalidae from Argentina, the two registered species, *D. cervicornis* and *D. brasiliensis* are different because of the egg size and the sculpture of the outer layer. In the first one, the diameter is 0.2632 mm and the second is 0.2304 mm. The cells are very large in both species; they are well-delimited and the outer covering presents no visible pores and no denticles. In the case of *C. cervicornis*, the development of the outer covering is more complex than in the *D. brasiliensis*. The differences can be seen in the form of the cells and in the ridge size, length and thickness.

In the case of the Chirocephalidae, the species that represented this family in Argentina is *P. salinicola*. The studies made by Mura et al. (op. cit.) and the present

work allow to establish differences at a generic and specific level of the analyzed characteristic.

As regards the egg size, *P. salinicola* has an intermediate situation between *Chirocephalus salinus* Daday, 1910, and *C. diaphanus* Prévost, 1820. The sculpture of the outer layer also presents important variations between both genera with respect to the cell size and form and the characteristics of the delimiting ridges.

According to the results, we consider that the simultaneous analysis of the egg diameter and the morphology of the outer layer using the MEB constitutes a very useful methodology to determine genera and species of anostracans.

This allows us to know the specific identity of the material in case only ovigerous females are found and makes it possible a correct identification, even when only resting eggs are present in samples corresponding to freshwater bodies either dried or not.

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