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Systematics and phylogeny of the genus *Trophon* Montfort, 1810 (Gastropoda: Muricidae) from Patagonia and Antarctica: morphological patterns

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KEY WORDS: *Trophon,* Systematics, biogeography, comparative morphology.

ABSTRACT The systematics and phylogeny of species commonly included under the genus *Trophon* from Patagonia and Antarctica were studied. A bibliographic survey established the existence of over 100 specific names that have been proposed for living and fossil representatives of the genus *Trophon* from the study area. The following questions were addressed: How many valid species belonging to the genus *Trophon* live nowadays in Patagonia and Antarctica? Which were their real geographic ranges? Which valid genera of Trophoninae are represented in the study area? Is the subfamily Trophoninae a monophyletic group?
The specimens studied were drawn from the collections of the Museums of, La Plata and Buenos Aires, (Argentina), and the National Museum of Natural History, Smithsonian Institution, (USA). Material collected along the entire Patagonian coast was also included. Approximately 1,000 specimens, in more than 600 lots, were compared with the holotypes housed in several European and American institutions. Radular, anatomical and shell characters were used to redefine each species. Preliminary results of this analysis yielded 33 valid species that have been previously described and at least five new species. Two basic different morphological patterns are proposed using gross anatomy, accesory salivary glands and radular features. The morphological arrangement suggested that the Patagonian species group and the Antarctic species group heretofore considered to be in the same genus, are probably polyphyletic. The Patagonian group showed close relationships among its representatives.The species belonging to the Antarctic group are less known and further studies will probably show that this group includes representatives of different clades.

RIASSUNTO Sono qui studiate la sistematica e la filogenesi delle specie comunemente incluse nel genere *Trophon* dalla Patagonia e dall'Antartide. Una revisione dei dati bibliografici dimostra l'esistenza di oltre 100 nomi specifici proposti per rappresentanti fossili e viventi del genere *Trophon* dall'area di studio. Le seguenti questioni vengono esaminate: quante specie valide appartenenti al genere *Trophon* vivono attualmente in Patagonia e in Antartide? Qual'è la loro reale distribuzione geografica? Quali generi validi di Trophoninae sono rappresentati nell'area di studio? La sottofamiglia Trophoninae è un gruppo monofiletico?
Gli esemplari studiati originano dale collezioni dei musei di La Plata and Buenos Aires, (Argentina), e dal National Museum of Natural History, Smithsonian Institution, (USA). Materiale raccolto lungo l'intera costa patagonica è stato inoltre incluso. Circa 1000 esemplari, in oltre 600 lotti, sono stati comparati con gli olotipi conservati in varie istituzioni europee ed americane. Caratteri anatomici, radulari e conchiliari sono stati impiegati nella ridefinizione delle specie. I risultati preliminari di tale analisi hanno prodotto evidenze per 33 specie valide già descritte, e per almeno cinque specie non descritte. Due pattern morfologici distinti sono proposti sulla base dei dati anatomici generali, ghiandole salivari accessorie e caratteristiche radulari. La classificazione morfologica proposta suggerisce che il gruppo di specie patagoniche e quello di specie antartiche, finora considerati appartenenti al medesimo genere, siano probabilmente polifiletici. Le specie patagoniche hanno mostrato un considerevole livello di affinità tra di loro. Le specie appartenenti al gruppo antartico sono meno conosciute, e ulteriori ed approfonditi studi sono necessari, e probabilmente mostreranno che questo gruppo include rappresentanti di diversi cladi.

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INTRODUCTION

The genus *Trophon* was originally proposed for *Buccinum geversianus* Pallas, 1774 an extremely variable species whose real range includes both coasts of southern South America. Shell characters in this species are highly variable, and together with its widespread geographical range have brought about an extraordinary proliferation of names. VOKES (1991) included 14 different specific names which had been used only for *Trophon geversianus*, most of them synonymous. Vokes herself restricted the genus to *Trophon* s.s., with two species, also drawing attention to the presence in the area of the genera *Xymenopsis* Powell, 1951 (with two species) and *Fuegotrophon* Powell, 1951 (with one species). The 26 different names given to these three species has hindered the accurate interpretarion of their relationships. Most work on systematics of *Trophon* has been based on shell morphology, while anatomical data have been so far badly misappraised.

As a fossil *Trophon* can be identified in Patagonian rocks of an age as early as at least the early Eocene. IHERING (1907) mentioned nearly 15 species included in *Trophon s. l.*. However, modern revisions could possibly modify this arrangement substantially.

A bibliographic survey established the existence of over 100 specific names that have been proposed for living and fossil representatives of the genus *Trophon* from the study area (see apendix 1).

The last good account of the genus *Trophon* from Antarctica was accomplished by POWELL in 1951 and 1958. He described one genus, two subgenera and four new species. Powell included for the first time, illustrations of the radula and protoconch of several species, despite of previous THIELE'S (1904) illustration of the radula of *T. albolabratus* Smith. These illustrations clearly point out several different radular morphologies. However, the quality of the drawings never allowed an accurate comparison with the other representatives.

Recent attempts (NUMANAMI, 1996; HOUART, 1997; 1998) to include the antarctic species of this genus worked basically by default for all the fusiform lamellose shells with tricuspid rachidian radulae teeth regardless of their real affinities. Comparative studies on the soft anatomy and radulae on Antarctic representatives of the subfamily Trophoninae are wanted.

In this paper the following questions are addressed: How many valid species belonging to the genus *Trophon* live nowadays in Patagonia and Antarctica? Which are their real geographic ranges? Which valid genera of Trophoninae are represented in the study area? Is the subfamily Trophoninae a monophyletic group?

MATERIAL AND METHODS

The specimens studied were drawn from the collections of the Museums of La Plata (MLP) and Argentino de Ciencias Naturales (MACN), Buenos Aires, (Argentina), and the National Museum of Natural History, Smithsonian Institution (USNM), Washington, D.C. (USA). Material collected along the entire Patagonian coast was also included. Approximately 1,000 specimens, in more than 600 lots, were compared with the holotypes, paratypes and syntypes housed in several European and American institutions.

Most of the material are from the United States Antarctic Program (USAP) housed at USNM. This material belongs basically to the expeditions of three ships: RV/ Hero, RV/ Eltanin and RV/Siedlecki. Additional specimens are from several Antarctic expeditions of the Argentine Republic, deposited at the MACN. Finally, several lots were studied at the Zoological Institute and Museum, Hamburg (ZMH) and Senckenberg Museum, Frankfurt (SMF), most of them belonging to the expeditions of the ships RV/Walther Herwig and RV/Polarstern.

The animals, all preserved in alcohol, were dissected to extract the radulae and to illustrate the gross anatomy of the anterior parts of the digestive system including salivary glands, accessory salivary glands and stomach when it was available. In addition, the morphology of the penes and female external organs are presented, some of them processed with critical point dry.

The radulae were prepared according to the method described by SOLEM (1972) and observed under the scanning electron microscope (SEM). All pictures were digitalized with a digital scanning camera and processed with the software Adobe Photoshop v. 6.01.

RESULTS

The study of the material allows the following systematic arrangement:

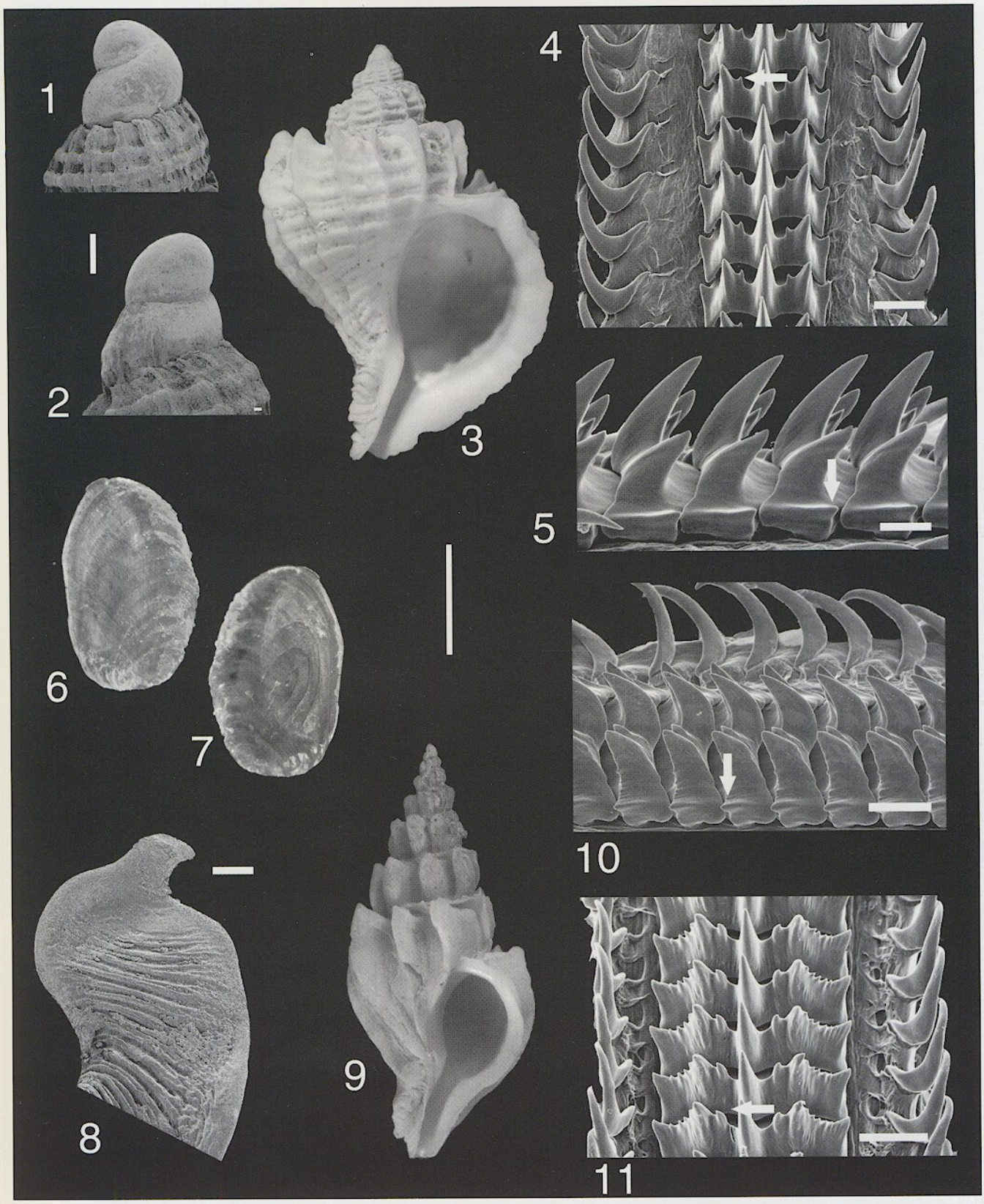
Trophon
T. geversianus (Pallas, 1774)
T. plicatus (Lightfoot, 1786)
T. pelseneeri (Smith, 1915)
T. bahamondei McLean & Andrade, 1982
T. iarae Houart, 1998
T. acanthodes Watson, 1882

"T." malvinarum Strebel, 1908
"T." ohlini Strebel, 1904
"Murex" clenchi Carcelles, 1953

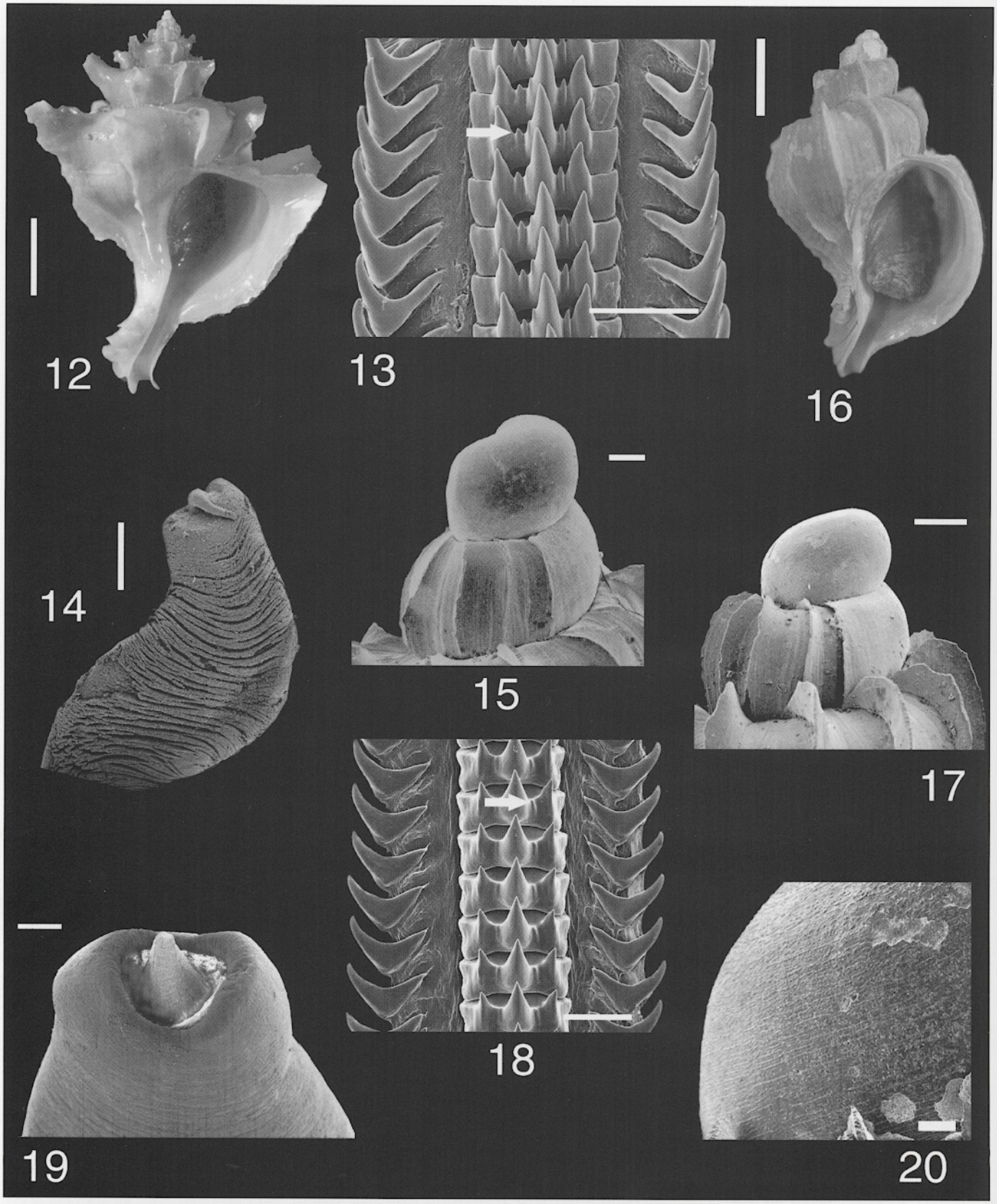
Polar *"Trophon"*
T. mawsoni Powell, 1957
T. leptocharteres Oliver & Picken, 1984
T. macquariensis Powell, 1957
T. nucelliformis Oliver & Picken, 1984
T. cribellum Strebel, 1908
T. cuspidarioides Powell, 1951
T. septus Watson, 1882
T. scolopax Watson, 1882
T. scotianus Powell, 1951
T. coulmanensis Smith, 1907
T. shackletoni Hedley, 1911
T. paucilamellatus Powell, 1951
T. declinans Watson, 1882
T. longstaffi Smith, 1907
T. minutus Melvill & Standen, 1907

Table I. Geographic distribution of Trophon species from Southern South America and Antarctica. O=South Orkney; K= Kerguelen; G= South Georgia; M=Macquarie Is.

Magellanic species	Insular species	Circumantarctic
T. geversianus (Pallas)	*Trophon cribellum* Strebel (G)	*Trophon coulmanensis* Smith
T. plicatus (Lightfoot)	*T. albolabratus* Smith (K)	*T. drygalskii* Thiele
T. pelseneeri (Smith)	*T. brevispira* Martens (G)	*T. echinolamellatus* Powell
T. bahamondei McLean & Andrade	*T. distantelamellatus* Strebel (G)	*T. minutus* Melvill & Standen
T. iarae Houart	*T. macquariensis* Strebel (G)	*T. enderbyensis* Powell
T. malvinarum Strebel	*T. mawsoni* Powell (M)	*T. minutus* Melvill & Standen
T. acanthodes Watson	*T. scolopax* Watson (K)	*T. longstaffi* Smith
	T. septus Watson (K)	*T. scotianus* Powell
"T". ohlini Strebel	*T. cuspidarioides* Powell (G)	*T. shackletoni* Hedley
"Murex" clenchi Carcelles	*T. eversoni* Houart (K?)	*T. nucelliformis* Oliver & Picken
	T. leptocharteres Oliver & Picken (O)	*T. declinans* Watson
		T. paucilamellatus Powell



Figures 1-11. Patagonian *Trophon* 1-7. *Trophon geversianus* (Pallas, 1774), MLP 27201, Puerto Golondrina, Ushuaia, Tierra del Fuego. 1-2. Two side views of the protoconch, scale bar = 500 µm. 3. Shell apertural view, Scale bar = 1 cm. 4. Dorsal view of radular ribbon, arrow heads internal denticle of lateral cusp of rachidian tooth, scale bar = 50 µm. 5. Lateral view of rachidian teeth, arrow heads single marginal cusp, scale bar = 30 µm. 6-7. Operculum, external (6) and internal (7) views, scale bar = same as 3. 8-11. *Trophon plicatus* (Lightfoot, 1786). 8. Penis, critical-point dried, scale bar = 400 µm. 9. Shell apertural view, scale same as in 3. 10. Lateral view of rachidian teeth, arrow heads single marginal cusp scale bar = 50 µm. 11. Dorsal view of radular ribbon, arrow heads internal denticle of lateral cusp of rachidian teeth scale bar = 50 µm.



Figures 12-20. Antarctic *Trophon* 12-15. *Trophon paucilamellatus* Powell, 1951, USNM 897576,. 12. Shell apertural view, scale bar = 1 cm. 13. Dorsal view of radular ribbon, arrow heads internal denticle rising from the base of rachidian tooth, scale bar = 100 µm. 14. Penis, critical-point dried, scale bar = 500 µm. 15. Protoconch, scale bar = 200 µm. 16-20. *Trophon scotianus* Powell, 1951. 16. Shell apertural view, scale bar = 1 cm. 17. Protoconch, scale bar = 200 µm. 18. Dorsal view of radular ribbon, arrow heads obsolete intermediate denticle between lateral and central cusp of rachidian teeth, scale bar = 200 µm. 19. Tip of the penis, critical-point dried, scale bar = 400 µm. 20. Protoconch, detail showing the spiral ornamentation, scale bar = 60 µm.

T. drygalskii Thiele, 1912
T. brevispira Martens, 1885
T. distantelamellatus Strebel, 1908
T. enderbyensis Powell, 1958
T. echinolamellatus Powell, 1951
T. eversoni Houart, 1997
T. albolabratus Smith, 1875
T. mucrone Houart, 1991
T. veronicae Pastorino, 1999

Coronium
C. coronatum (Penna-Neme & Leme, 1978)
C. elegans Simone, 1996
C. oblongum Simone, 1996

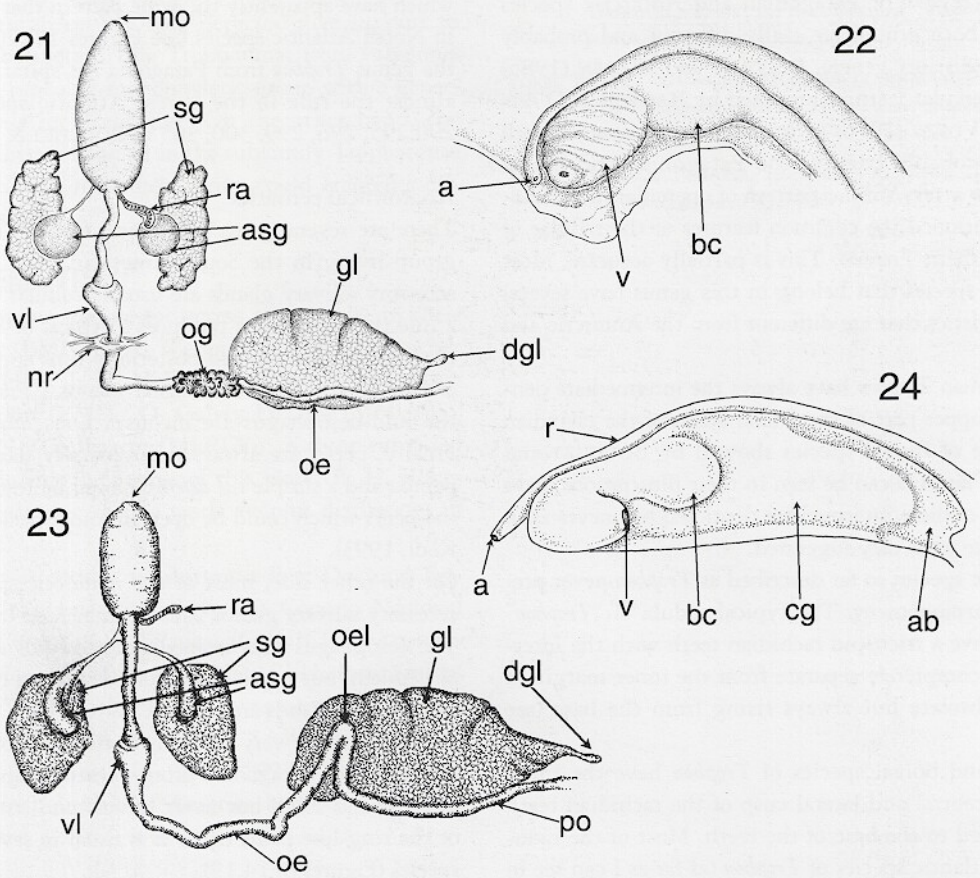
Fuegotrophon
F. pallidus (Broderip in Broderip & Sowerby, 1833)
F. amettei (Carcelles, 1946)

Xymenopsis
X. corrugata (Reeve, 1848)
X. muriciformis (King & Broderip, 1832)
X. subnodosa (Gray, 1839)
X. buccinea (Lamarck, 1816)

Tromina
T. dispectata Dell, 1990

Boreotrophon
B. verrillii (Bush, 1893)
B. aculeata (Watson, 1882)

This arrangement includes all living species considered valid up to now described in the family Trophoninae from South America and Antarctica. There are several remarks to take into account. *Murex clenchi* is only known by three specimens without soft parts including holotype and paratype. Protoconch and



Figures 21-24. Diagrammatic schemes of the alimentary and paleal female reproductive systems. 21. *Trophon paucilamellatus* Powell, 1951. anterior portion of the alimentary system. 22. *T. equinolamellatus* paleal reproductive female organs. 23. *Trophon plicatus* (Lightfoot, 1786), anterior portion of the alimentary system. 24. anterior portion of the alimentary system.
a = anus; ag = albumen gland; ap = anal papilla; asg = accessory salivary gland; bc = bursa copulatrix; cg = capsule gland; dgl = ampulla of gland of Leiblein; gl = gland of Leiblein; mo = mouth; nr = nerve ring; oe = oesophagus; og= oesophageal glands ("Framboisse glands"); oel: oesophageal loop; po= posterior oesophagus; r = rectum; ra = radula; sg = salivary gland; v = vagina; vl = valve of Leiblein.

ultrastructure of the shell suggests that it belongs to the genus *Trophon*, however, the radula will have the last word about it. Something similar occurs with *T. malvinarum* which is only known by the holotype and a few dry specimens.
Trophon ohlini was originally described under this genus by Strebel. However, the radula and the protoconch are actually very different from all the other species. It will probably belong to a different genus.
The analysis of the radulae and gross anatomy of most of the species up to now described suggests the presence of two basic morphological types. I selected two representatives species as an example of both morphological arrangements: *Trophon geversianus* (Figures 23 and 24) from the Magellanic Malacological Province and *Trophon paucilamellatus* from Antarctic and circumantarctic waters (Figures 21 and 22).

DISCUSSION

Radular remarks

BOUCHET and WARÉN (1985) in the first attempt to study, with modern criteria, the species included in the genus *Trophon* from the Northern Atlantic considered no heavy taxonomic differences among the species from Northern and Southern Hemisphere. However, a close review of Patagonian and Antarctic species demonstrate that both groups are really different and probably belongs to several distinct genera. BOUCHET and WARÉN (1985) mentioned the opercular features proposed by RADWIN & D'ATTILIO (1976) and VOKES (1976) as insufficient to separate both groups. This is probably true for the Patagonian and boreal species which show a very similar pattern of opercular morphology. They also mentioned the common features of the radulae of Northern and Southern *Trophon*. This is partially accurate. Most of the Patagonian species that belong in this genus have several common characteristics that are different from the Antarctic and Boreal ones.
Radulae of Patagonian *Trophon* have always the intermediate denticle in the inner upper part of the lateral cusps of the rachidian teeth. The radulae of Boreal species showed by BOUCHET and WARÉN (1985), as far as it can be seen in their illustrations, have different positions of these intermediate denticles, but never as in *T. geversianus* despite what they suggested.

All the antarctic species so far described as *Trophon* never present this radular arrangement. The typical radula of "*Trophon*" from Antarctica have a tricuspid rachidian teeth with the intermediate denticles completely separate from the inner margin of lateral cusps or obsolete but always rising from the base (see Figures 13, 18).

The antarctic and boreal species of *Trophon* have the inner denticle between central and lateral cusp of the rachidian teeth always free, attached to the base of the teeth. Most of the radulae of Northeast Atlantic species of *Trophon* (as far as I can see in BOUCHET and WARÉN'S revision (1985) have a broad attachment of the marginal teeth.

Based on radular features the whole *Trophon* group from Patagonia is very homogeneous. All the species included in this group have the following common radular features (Figures 4-5, 10-11):

1-intermediate denticle attached to the upper height of the internal edge of the lateral cusp of the rachidian teeth;
2-single marginal denticle in the external edge of the base of the rachidian teeth;
3-the attachment area of the marginal teeth are always (no exception) narrow,
thin and the free part of the same thickness,
4-the central cusp of the rachidian is always thin and larger than the laterals.

Conchological remarks

Conchological features are so variable that I considered them secondary. However, the protoconch is actually very different and permits the division in at least both two clearly defined groups. Most of the Patagonian representatives have a slightly asymmetrical protoconch in relation with the axis (Figures 1-2) which is mostly perpendicular to the shell axis in the Antarctic group. There is no ornamentation in Patagonian *Trophon,* whereas most of the boreal species have a delicate pattern of irregular cords. The antarctic species have in general no ornamentation in the protoconch either with only three exceptions: *T. scotianus* Powell, 195, *T. drygalskii* Thiele, 1912 and *T. paucilamellatus* Powell, 1951 which have apparently the same pattern that it could be observed in North Atlantic species (see Figures 17, 20). No protoconch of the genus *Trophon* from Patagonia has spiral ornamentation, as is almost the rule in the boreal Atlantic species (see figs. 289, 290,295, 296, 299, 300, 305 in BOUCHET & WARÉN, 1985).

Anatomical remarks

There are several gross anatomical features that characterize the group living in the South American coast. Where known, the accessory salivary glands are usually tubular ("kidney-shape"). As a rule the oesophagus produces a typical oesophageal loop before the valve of Leiblein and posteriorly runs appresed to the left side of this gland. The oesophageal glands ("Framboisse" glands) in the mid-oesophagus are inconspicuous, not externally visible. Finally, penes are always dosoventrally flattened, with a large papilla and a simple *vas deferens* closed by the overlapping sides of the penis which could be open in some species (*e.g. T. geversianus*, Kool, 1993).
On the other side, most of the Antarctic species have spherical accessory salivary glands usually embedded in the salivary glands. The oesophagus runs immediately towards and under the gland of Leiblein, but previously a very developed (visible to naked eye) oesophageal glands are present.
Penes are in fact very different in most of both groups of species. However, the Patagonian group presents papillae, large and long, or short and small but never conical and rising from the middle or the ring-like penis tip as it is usual in several of the Antarctic species (Figures 8, 14,19).
The palial oviduct arranged as in *Trophon geversianus* is the generalized morphology for the Patagonian species (HARASEWYCH, 1984). As an example of the antarctic representatives, *Trophon scotianus* has a broad pallial oviduct and the bursa copulatrix oval, globose with several layers of tissue before leads to the vaginal opening.

Geographical remarks

Table I shows living *Trophon* species arranged according to their geographical distribution, forming three groups of species: Magellanic, Circumantarctic and Insular ones. Probably, because of the particular reproductive biology (embryos develops inside the egg-capsule without plancktonic larvae) the distribution of the species are truly restringed. There is no interchange between Patagonia and Antarctica species. Several species are endemic (*e.g. Trophon macquariensis*, *T. albolabratus* etc). Others have an extensive distribution as *T. geversianus*. However, no Antarctic species occurs in Patagonia and viceversa

Concluding remarks

KOOL (1993) demonstrated that *Trophon geversianus* (Pallas, 1774) is closely related to *Nucella lapillus* and *Ocenebra erinacea*. He suggested that this relationship is even closer within this two taxa and the type species of Trophoninae (*T. geversianus*) than with other representatives included in the subfamily. He already suspected that Trophoninae is not a monophyletic group and some of its members may belong to a new group. *Trophon geversianus* (Pallas, 1774) and most of the Patagonian representatives of the subfamily (around 10 species) are closely related among them. Radulae and anatomical features here depicted give support to this statement. Furthermore, living Trophoninae from Patagonia form a compact and probably monophyletic group with a generous amount of fossils representatives.On the other hand, the Antarctic species hitherto included in the subfamily Trophoninae show several features that in the near future could granted a different systematic position.

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Appendix 1. Proposed species names under the genus *Trophon* for South America and Antarctica

1. *acanthodes* Watson, 1882
2. *accuminatus* Strebel, 1904
3. *aculeatus* Watson, 1882
4. *acuminatus* Strebel, 1904
5. *albidus* Philippi, 1846
6. *albolabratus* Smith, 1875
7. *albus* Strebel, 1904
8. *amettei* Carcelles, 1946
9. *antarcticus* Philippi, 1868
10. *brevispira* Martens, 1885
11. *bruceana* Melvill & Standen, 1916
12. *brucei* Strebel, 1904
13. *buccineus* Lamarck, 1816
14. *bulbosa* Perry, 1811
15. *cancellarioides* Reeve, 1847
16. *cancellinus* Philippi, 1845
17. *candidatus* Mabille & Rochebrune, 1889
18. *cinguliferus* Pfeffer, 1887
19. *clenchi* Carcelles, 1953
20. *condensatus* Hedley, 1916
21. *corrugatum* Reeve, 1848
22. *coulmanensis* Smith, 1907
23. *coulmanensis multilamellatus* Numanami, 1996
24. *couthouyi* Strebel, 1904
25. *cribellum* Strebel, 1908
26. *crispus* Gould, 1849
27. *crispus* var. *burwoodianum* Strebel, 1908
28. *cuspidarioides* Powell, 1951
29. *declinans* Watson, 1882
30. *decolor* Philippi, 1845
31. *dispar* Mabille & Rochebrune, 1889
32. *dispectata* Dell, 1990
33. *distantelamellatus* Strebel, 1908
34. *drygalskii* Thiele, 1912
35. *echinolamellatus* Powell, 1951
36. *elegans* Strebel, 1904
37. *elongatus* Strebel, 1904
38. *enderbyensis* Powell, 1957
39. *falklandicus* Strebel, 1908
40. *fasciculatus* Hombron & Jacquinot, 1854
41. *fenestratus* Strebel, 1904
42. *fimbriatum* Martyn, 1784
43. *fimbriatus* Hupé in Gay, 1854
44. *foliaceum* Chemnitz, 1780
45. *foliaceus minor* Chemnitz, 1784
46. *foliatus* Schumacher, 1817
47. *geversianum* Pallas, 1774
48. *geversianus* var. *calva* Kobelt, 1878
49. *gouldi* Cossmann, 1903
50. *gracilis* Perry, 1811
51. *gradata* Ihering, 1897
52. *hoylei* Strebel, 1904
53. *hupeanus* Ihering, 1907
54. *iarae* Houart, 1998
55. *inflatus* Hombron & Jacquinot, 1854
56. *intermedius* Hupé in Gay, 1854
57. *laciniatum* Martyn, 1784
58. *lamellosus* Gmelin, 1791
59. *lebruni* Mabille & Rochebrune, 1889
60. *leptocharteres* Oliver & Picken, 1984
61. *liratus* Couthouy in Gould, 1849
62. *loebbeckei* Kobelt, 1878
63. *longstaffi* Smith, 1907
64. *macquariensis* Powell, 1957
65. *magellanicus* Gmelin, 1791
66. *malvinarum* Strebel, 1908
67. *mawsoni* Powell, 1957
68. *minutus* Melvill & Standen, 1907
69. *mucrone* Houart, 1991
70. *muriciforme* King & Broderip, 1832
71. *necocheanus* Ihering, 1907
72. *nucelliformis* Oliver & Picken, 1984
73. *obesus* Strebel, 1904
74. *ohlini* Strebel, 1904
75. *orbignyi* Carcelles, 1946
76. *ornatus* Strebel, 1904
77. *paessleri* Strebel, 1904
78. *paessleri* var. *turrita* Strebel, 1904
79. *pallidus* Broderip, 1833
80. *patagonicus* d'Orbigny, 1839
81. *pelecetus* Dall, 1902
82. *pelseneeri* Smith, 1915
83. *peruvianus* Lamarck, 1816
84. *philippianus* Dunker in Kobelt, 1878
85. *plicatus* Lightfoot, 1786
86. *plumbeus* Gould, 1852
87. *poirieria* Powell, 1951
88. *priestleyi* Hedley, 1917
89. *pseudoelongatus* Strebel, 1904
90. *ringei* Strebel, 1904
91. *roseus* Hombron & Jacquinot, 1854
92. *scolopax* Watson, 1882
93. *scotianus* Powell, 1951
94. *septus* Watson, 1882
95. *shackletoni* Hedley, 1911
96. *shackletoni paucilamellatus* Powell, 1951
97. *standeni* Strebel, 1904
98. *textiliosus* Hombron & Jacquinot, 1854
99. *unicarinatus* Philippi, 1868
100. *varians* d'Orbigny, 1839
101. *ventricosus* Molina, 1810
102. *veronicae* Pastorino, 1999
103. *verrillii* Bush, 1893
104. *violaceus* Mabille & Rochebrune, 1889