The identity of *Waldo parasiticus* (Dall, 1876) and description of *Waldo trapezialis* new species (Bivalvia: Galleomatoidea)

Diego G. Zelaya  
Cristián Ituarte  
Division of Invertebrate Zoology  
Museo de La Plata  
1900 La Plata, Buenos Aires  
ARGENTINA  
dzelaya@museo.fenym.unlp.edu.ar

**Abstract**

The epibiotic bivalve *Waldo parasiticus* (Dall, 1876), originally described as a leptonid species, is redescribed and figured on the basis of shell morphology, soft-part anatomy and reproduction. The complete synonymy of *W. parasiticus* is given, and a lectotype is designated and figured. *Waldo trapezialis* new species from South Georgia Islands is described and illustrated. The genus *Waldo* Nicol, 1966 is recognized as valid and redescribed.

Additional key words: Antarctica, bivalves, *Lepton parasiticum*.

**Introduction**

*Lepton parasiticum* Dall, 1876, was described based upon specimens living as “commensals” on irregular echinoids collected at the Kerguelen Islands. Dall’s (1876) original description was adequate, but without illustration. Soot-Byen (1959) reported and figured *Lepton cf. parasiticum* from southern Chile, and Arnaud (1964) reported *L. parasiticum* from Adelia Land, Antarctica, and the Kerguelen Islands. Moreover, four species with similar shell features and habitat were described from Antarctic and Subantarctic waters: *Lepton costulatum* Martens, 1885, *Scioberetia australis* Bernard, 1895, *Solecardia antarctica* Hedley, 1911, and *Montacuta christenseni* Grieg, 1929. Their descriptions were based mainly on shell characters, and most of them were imprecise. With the sole exception of *S. antarctica* reported by Mühlenhard-Siegel (1989) and Linse (1997), none of them have been found again after their original description. At present, as previously noted by Dell (1990), “the relationship of *Lepton* [= *Waldo*] *parasiticum* with similar species living in association with echinoderms remains uncertain”.

*Waldo parasiticus* has been listed under different neoleptonid genera: *Lepton*, *Notolepton*, *Neolepton*, and *Neodelaisia* (Dall, 1876; Arnaud, 1964; Osorio and Bahamonde, 1970 and F. R. Bernard, 1983, respectively). By studying the types of *Lepton parasiticum*, Nicol (1966) found differences in shell sculpture and hinge characters sufficient to propose *Waldo*, as a new genus of Neoleptonidae. In a systematic revision of the Neoleptonidae, Salas and Gofas (1998) excluded *Lepton parasiticum* from that family, suggesting that this species most likely belongs to the Montacutidae or Galleomatoidea.

In the present paper, the placement of “*Lepton* parasiticum” Dall in the genus *Waldo* is confirmed, and new data on anatomy, shell characters, reproductive biology, and host specificity are given. In addition, *Waldo trapezialis* new species is described.

**Materials and Methods**

The specimens used in this study were collected by the R/V *EDUARDO L. HOLMBERG* during the 1995 cruise to South Georgia Islands (Figure 1) and the R/V *POLARSTERN* during the 2002 Latin American Polarstern Study (LAMPOS). Specimens were studied and figured using scanning electron microscopy (SEM); shell measurements were recorded using a stereoscopic microscope equipped with micrometer eyepiece (for all calculations mean and standard deviations are given). Several alcohol-preserved specimens of *Waldo parasiticus* new species were processed for histology by decalcification in a Railliet-Henry’s solution, followed by dehydration, embedding in Paraplast®, sectioning (7 μm thickness) and staining with hematoxylin-eosin (Gabe, 1968).

Additional specimens from the National Museum of Natural History, Washington (USNM), and others obtained from dried samples of echinoids housed at the collection of Invertebrates, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (MACN) were studied. Type specimens of *Lepton parasiticum* (USNM), and *Montacuta christenseni* from Bergen Museum, Norway (BM), were studied. The type material of *Scioberetia australis* (consisting of fragments of one shell, two 1 mm-long juveniles and a series of histolog-
Waldo parasiticus (Dall, 1876) (Figures 2–22)

Lepton parasiticus Dall, 1876: 45–46.
Lepton costulatum Martens, 1855: 94; Martens and Pfeffer, 1856: 115 (South Georgia Islands).
?
Solecardia antarctica Hedley, 1911: 4, pl. 1, fig. 5; Mühlenhard-Siegel, 1989: 164, pl. 3, fig. 28; Linsè, 1997: 55, pl. 2, figs. 1–3 (Cape Royds).
Montacuta christenseni Grieg, 1929: 14 (Admiralty Bay, South Shetland Islands).
Neolepton parasiticum.—Osorio and Balamonde, 1970: 221.
Waldo parasiticus.—Nicol, 1966: 59–61, pl. 8, fig. 5 and pl. 9, figs. 5–7.

Description: Shell small (maximum shell length 4.1 mm), moderately inflated (mean shell width/shell height ratio 0.6 ± 0.06, n = 11). Shell extremely thin, whitish, translucent, shiny. Shell outline ovate, elongate (shell height/shell length ratio: 0.69 ± 0.04, n = 11), slightly inequilateral, beaks subcentral, not prominent (Figures 2–4). Anterior end rounded and slightly projecting, posterior end truncate (less markedly in juveniles), slightly oblique (Figures 4, 5). Dorsal margin straight or slightly and evenly arcuate, posterior margin straight, ventral margin slightly and evenly curved, crenulate. Valves gaping ventrally and at anterior and posterior ends (Figures 8–10). Nepionic shell (approximately 470 μm length), inflated, forming a rounded cup (Figure 11), clearly demarcated by a commarginal rim (Figure 12). Shell surface sculptured with 30–35 relatively well-marked radial ribs and irregular commarginal ribs, both fading towards the beaks. Radial ribs often very evident in small-sized specimens, tending to fade in adults. Hinge edentulous in adults. Ligament internal, strong; external periostracal ligament present (Figures 13–16).

D-shaped larvae with two well-developed lamellar lateral teeth in the right valve, the anterior long and slen-
Figures 4–12. *Waldo parasiticus* from South Georgia Islands, MLP 6505. 4. Outer view of an adult specimen. 5. Outer view of a juvenile. 6. Lateral view of a living specimen showing the anterior extension of the mantle border. 7. Ventral view of a specimen showing the anterior mantle projections and paired tentacles along the ventral mantle border. 8. Anterior shell gap. 9. Ventral shell gap. 10. Posterior shell gap. 11. Detail of the nepionic shell. 12. Detail of the zone between nepionic shell and dissoconch. Scale bars: Figures 4–10 = 1 mm; Figures 11–12 = 100 μm.
Figures 13-19. Waldo parasiticus. 13-15. Isla de Los Estados, MACN 22219; 16-19. South Georgia Islands, MLP 6505. 13. Inner view of a left valve. 14, 15. Details of the hinge. 16. Inner view showing the internal ligament. 17. Inner view of the right valve of a larva removed from adult. 18. Right valve of a larva, detail of the hinge. 19. Left valve of a larva, detail of the hinge. L: internal ligament. Scale bars: Figure 13 = 1 mm; Figures 14-15, 17-19 = 100 μm; Figure 16 = 500 μm.

Anatomy: Mantle margins free for about the 3/5 of its length, fused at posterior end forming a relatively short presiphonal suture. Only the exhalant aperture, extended in a short siphon, present (Figure 3). Mantle border extending beyond shell margin, covering the surface of the valves. The free edges of the mantle extend anteriorly and upwards forming a partly closed channel serving as a temporary inhalant "siphon" (Figures 6, 7). Ventral mantle border with long and stout cylindrical tentacles: 1 unpaired tentacle (just over the exhalant siphon) and 7 paired tentacles, alternate or opposite (5 pairs at sides of the pedal aperture, 1 at the point of mantle border fusion, and 1 posterior to the mantle border fusion, on the presiphonal suture) (Figures 3, 7). Only one, the inner, demibranch present, ascending lamella shorter than the descending one, with few interlamellar junctions; the suprabranchial space serves as brood space (Figures 20-22). Foot cylindrical (short when retracted) with a blunt heel and well-marked byssal groove running along the ventral foot surface. A strong byssal gland lo-
Parasiticum (USNM verely christenseni (BM 54°27' W, numerous 54°18' S, 5 filaments. 470 Isla Estero 1996 1). 1959); Antarctica: Adelia Land, Antarctica: (MACN 18715); several loose valves, Isla de los Estados (MACN 22219); 10 specimens, 54°27' S, 35°41' W, South Georgia Islands, 249-256 m, 12 April 2002 (MLP 6729); 4 specimens, 60°59' S, 43° 27' W, South Orkneys Islands, 399-402 m, 22 April 2002 (MLP 6731) (Figure 1).

Distribution: Antarctic and Subantarctic waters, 50-470 m.

Remarks: Diagnostic characters of Waldo parasiticus are: the extremely thin shell, gaping ventrally and at anterior and posterior ends, beaks with a well-marked neoplastic shell, adult hinge edentulous with internal ligament, shell surface sculptured with radial ribs and commarginal ribs, and expanded mantle border covering the outer shell surface bearing long and stout tentacles.

The syntypes of Montacuta christenseni (despite being strongly decalcified) were found to be identical in shell morphology and soft part anatomy to Waldo parasiticus. Smaller syntypes differed slightly in having strongly marked radial ribs.

The original description of Lepton costulatum Martens, 1885, and its redescription by Martens and Pfeffer (1886) are rather poor and lack illustrations. Despite this, they are informative enough to indicate that L. costulatum is conspecific with W. parasiticus. Unfortunately, the types of L. costulatum, originally housed at Museum für Naturkunde, Berlin (ZMB 37468), seem to be lost (M. Glaubrecht, in litt., June 2001).

Solecardia antarctica Hedley, 1911, a species reported from the Antarctic Region, is also similar to W. parasiticus and, based on the information given by the original description and figure, they seem to be conspecific, as previously suggested by Arnaud (1964).

Lepton costulatum and Montacuta christenseni were previously proposed as synonyms of Lepton parasiticum by Soot-Ryen (1959).

Biological observations: Waldo parasiticus is a di-ocious species. Females produce large, non-planktrophic yolky eggs, which are incubated in the space limited by the descending lamella of the inner demibranch and the visceral mass. Larvae, occurring free in the volume of the brooding space, were found in April and November in specimens larger than 1.5 mm. A maximum number of 157 D-shaped larvae (0.45/0.5 mm length × 0.4/0.5 mm width), all in the same developmental stage, were found in a maternal individual of 2.7 mm long. Waldo parasiticus lives as an epibiont, secured by the byssus to the spines in the ambulacral areas of numerous irregular Antarctic and circumantarctic Schizasteridae echinoids (Table 1). The epibiotic behavior in association with large invertebrates (referred to as symbiosis, commensalism or parasitism by different authors) is characteristic of many Galeommatoidea. While the
vast majority of galeommatids have been reported to live on crustaceans, members of the Montacutidae were mainly reported associated with irregular echinoids (Coan et al., 2000; Mikkelsen and Bieler, 1992; Ponder, 1968; Deroux, 1961; Popham, 1940).

Species erroneously identified as Waldo parasiticus: Mortensen (1943) reported specimens of “white mussels” attached to spines of the echinoid Sterechinus diadema from Kerguelen Islands; these specimens were later reported by Arnaud (1964) as Notolepton parasiticum. However, Mortensen’s (1943) figures suggest that the specimens likely belong to Lissarca notorcadensis Melville and Standen, 1907. Powell (1957) erroneously reported specimens of a true Neoleptonidae as Notolepton parasiticum (Dall). Speci-
Table 1. Echinoid species reported as hosts for Waldo parasiticus.

<table>
<thead>
<tr>
<th>Species (original designations)</th>
<th>Host</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lepton parasiticum</td>
<td>Triphyllus sp.</td>
<td>Dall, 1876</td>
</tr>
<tr>
<td>Lepton costulatum</td>
<td>spatangoid echinoids</td>
<td>Martens, 1855; Martens and Pfeffer, 1886</td>
</tr>
<tr>
<td>Lepton sp.</td>
<td>Abatus caecernosus</td>
<td>Mortensen, 1910; Mortensen, 1936</td>
</tr>
<tr>
<td>Lepton parasiticum</td>
<td>Abatus agassizii</td>
<td>Thiele, 1912</td>
</tr>
<tr>
<td>Montacutia christenseni</td>
<td>Abatus caecernosus</td>
<td>Grie, 1929</td>
</tr>
<tr>
<td>Montacutia christensi</td>
<td>Abatus caecernosus</td>
<td>Mortensen, 1936</td>
</tr>
<tr>
<td>Lepton cf. parasiticum</td>
<td>Tripuyaester philippii</td>
<td>Soot-Ryen, 1939</td>
</tr>
<tr>
<td>Notolepton parasiticum</td>
<td>Abatus bidens</td>
<td>Arnaud, 1964</td>
</tr>
<tr>
<td>Waldo parasiticus</td>
<td>Abatus agassizii</td>
<td>present work</td>
</tr>
<tr>
<td>Waldo parasiticus</td>
<td>Tripuyaester excactus</td>
<td>present work</td>
</tr>
</tbody>
</table>

Waldo trapezialis new species
(Figures 23-28)

Description: Shell small (maximum shell length 2.9 mm), trapezoidal, somewhat inflated (shell width/shell height ratio: 0.73 ± 0.12, n = 7), relatively high (shell height/shell length ratio: 0.74 ± 0.03, n = 7); gaping widely at ventral margin and only slightly at anterior end (Figures 25, 27). Shell extremely thin, white, shiny. Shell inequilateral, slightly inequivalve (Figure 26). Beaks subcentral, slightly displaced forward (located at around 45% of shell length), not prominent (Figure 23). Neoponic shell (approximately 500 µm length) well-marked, inflated, forming a cup (Figure 24). Anterior end low, widely rounded, posterior end high, evenly arcuate. Dorsal margin markedly sloping forward, wide and evenly arcuate, ventral margin long, straight and smooth. Shell surface smooth. Hinge edentulous in adults. Internal ligament, strong, saddle-shaped (Figure 28), external periostracal ligament present.

Anatomy: Mantle margins free at about the 3/4 of its length, with large pedal aperture; posterior end of the mantle forming an exhalant aperture extended in a short siphon. Mantle border extended beyond the shell margin, covering at least partially the shell surface. At the anterior end, the free edges of the mantle extend to form a temporary inhalant structure, a partly closed channel directed upwards. Along the ventral border of the mantle 5 pairs of opposite long and stout cylindrical tentacles, present: 3 at sides of the pedal aperture, 1 at the point of mantle fusion, and 1 posterior to the fusion, on the presiphonal suture. Only one, the inner, demibranch present. Foot cylindrical with a blunt heel and well-marked bysal groove running along its ventral surface. A strong byssus gland located at the base of the foot heel secretes a multifilamentous byssus; each one of the byssus filaments provides anchorage to one spine of the host, an irregular echinoid.

Type locality: 54°18' S, 35°30' W, South Georgia Islands, 94 m (Figure 1).

Type material: Holotype (MLP 6728-1) (2.45 × 1.9 mm), 3 paratypes (MACN 35016) (2.9 × 2.0 mm, 1.7 × 1.35 mm and 1.6 × 1.25 mm) and 2 paratypes (MLP 6728-2) (2.45 × 1.8 mm and 2.9 × 2.2 mm) all from type locality, 8 April 1996; 1 paratype, 54°27' S, 35°41' W, South Georgia Islands, 249-256 m, 12 April 2002 (2.55 × 1.8 mm) (MLP 6730).

Distribution: South Georgia Islands.

Etymology: The name refers to the trapezoidal shell outline.

Remarks: Waldo trapezialis new species can be easily identified by its trapezoidal shell shape, smooth shell surface, and shell border not crenulated. W. trapezialis differs from W. parasiticus in having a more inflated, slightly inequivalve shell, with a long smooth and straight ventral margin, high broadly arcuate posterior end, and surface without radial sculpture or commarginal ribs. The neoponic shell is larger in W. trapezialis. W. trapezialis also differs from W. parasiticus in lacking the unpaired tentacle above the exhalant siphon.

The specimens of Waldo trapezialis new species studied were collected attached to loose spines of an irregular echinoid. We do not have at this point further details on the identification of the host species.

THE SYSTEMATIC POSITION OF WALDO

The genus Waldo was proposed by Nicol (1966) to include Lepton parasiticum Dall, and was tentatively assigned to the family Neoleptonidae. The presence of only one pair of demibranchs clearly exclude Waldo from the Neoleptonidae. Salas and Gofas (1998), in a revision of the genus Neolepton, suggested that Waldo parasiticus most likely belongs to the Montacutidae or Galeommatidae. However, the lack of hinge teeth in the adults, the presence of stout tentacles as mantle projections, and the dioecious condition are characters not previously reported for members of the Montacutidae. At
present there is not agreement on the suprageneric classification of the Galeommatoidea. Vokes (1980) recognized five families of Galeommatoidea: Kelliciidae, Erycinidae, Leptonidae, Montacutidae and Galeommatidae, while Coan et al. (2000), recognized only two galeommatoid families: Lasaeidae (which includes Montacutidae) and Galeommatidae. Due to this and to the lack of a clear definition of families, a decision about the suprageneric placement of Waldo is postponed.

Waldo parasiticus resembles Scioberetia australis F. Bernard, 1895, a species obtained from the ambulacral areas of the echinoid Tripylus excavatus from Cape Horn (southern South America). The species was never recorded again after its original description; however, Bernard's (1895a) record was subsequently repeated by Thiele (1912), Arnaud (1964), Osorio and Bahamonde (1970), F. R. Bernard (1983), and Böhme (1993). According to the generic diagnosis of the genus Scioberetia given by Thiele (1934), Waldo would be its synonym. However, from Bernard's (1895a) original description and from the study of the type material of S. australis (MNHN), it is clear that this genus differs from Waldo by the presence of a well-developed taxodont-like larval hinge teeth (Bernard, 1895a), the lack of byssus gland and by the absence of tentacles on the mantle border. The probable hermaphroditic condition discussed by Bernard (1895a–c) would be an additional differential character. In our opinion, both Scioberetia and Waldo should be considered as valid genera.

ACKNOWLEDGMENTS

The authors wish to thank D. Nahabedian for providing the specimens collected by the R/V EDUARDO L. HOLMGREN. We are grateful also to M. G. Harasewych and T. Nickens (National Museum of Natural History, Washington, DC, USA), V. Héros and P. Bouchet (Muséum National d'Histoire Naturelle, Paris, France), and J. A. Kongsrud (University of Bergen, Museum of Zoology, Bergen, Norway) who kindly facilitated the study of type specimens. M. Glaubrecht (Museum für Naturkunde, Berlin, Germany) kindly commented on the types of Lepton costulatum, and A. Tablado allowed access to the MACN collections. Michael Schrödl provided photographs of living specimens taken aboard the R/V POLARSTERN, and Rafael Urróelá (from the MLP Scanning Electron Microscopy unit) for his technical assistance and fine work with SEM photography; their help is also greatly appreciated. The authors are members of the National Research Council for Science and Technology (CONICET), Argentina. This work was partially supported by a grant from Fundación Antorchas to D. Z.

LITERATURE CITED


