

AMERICAN MUSEUM *Novitates*

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, NY 10024

Number 3457, 18 pp., 43 figures

October 28, 2004

Leech Collections from Chile Including Two New Species of *Helobdella* (Annelida: Hirudinida)

MARK E. SIDDALL¹ AND ELIZABETH BORDA²

ABSTRACT

Twelve species of leeches were collected from Reserva Nacional Yerba Loca, near Santiago, IX Región de la Araucanía and X Región de los Lagos, Chile. Included were representatives of the unusual Chilean taxa *Americobdella valdiviana*, *Mesobdella gemmata*, and two species of *Patagoniobdella*, each of whose phylogenetic placement and classification has been problematic. Eight species of Glossiphoniidae were found, including two new species in the genus *Helobdella*. *Helobdella wodzickiorum*, n.sp. possesses a large, prominent atrium and male sperm ducts extending to somite XXIII, whereas *Helobdella pichipanan*, n.sp. has micromorphic male genitalia, a weakly developed atrium, and ejaculatory ducts that extend only to XII/XIII. The phylogenetic positions of *A. valdiviana*, *M. gemmata*, and *Patagoniobdella* species are discussed.

INTRODUCTION

Southern Chile comprises one of the world's most unusual temperate ecozones beginning at 39°S, with the Araucaria forests at the northern edge of Region X (Región de los Lagos) through the Valdivian coastal rainforests and South to Gondwanian forests dominating in Tierra del Fuego. Consequently, Chile is home to one-third of the world's remaining temperate primary forest. Region X, in the vicinity of Valdivia, is marked by

a geological history of megathrust subduction, volcanism, and pleistocene glaciations which collectively have sculpted a complex landscape with the greatest concentration of freshwater west of the Andes. More than 90% of the biodiversity in this region is endemic and constitutes the highest species diversity among the world's temperate forests.

Chilean leeches have received an unusual amount of attention in the last 150 years. The first published record of leeches in South America was Emile Blanchard's (1849) trea-

¹ Division of Invertebrate Zoology, American Museum of Natural History (e-mail: siddall@amnh.org).

² Division of Invertebrate Zoology, American Museum of Natural History (e-mail: eborda@amnh.org).

tise included in the third volume of Claudio Gay's *Historia fisica y politica de Chile* in which four species were described: *Blenobdella depressa*, *Glossiphonia triserialis*, *Hirudo cylindrica*, and *Hirudo gemmata* (now these are *Haementeria depressa*, *Helobdella triserialis*, and the latter two are synonyms of *Mesobdella gemmata*). Major contributions that followed include Phillippi's (1872) discovery of the anatomically unusual *Americobdella valdiviana* and its later frequent scrutiny (Blanchard, 1917; Moore, 1924; Cabellero, 1956), the rediscovery and reassessment of *Mesobdella gemmata*, one of few New World haemadipsids (Grube, 1871; Blanchard, 1893; Weber, 1915), and a series of contributions by Raphaël Blanchard. The latter (no relation to Emile) had his interest in South American leeches piqued when he received (anonymously) a leech apparently taken from a nutria (*Myocastor coypus*: Rodentia) and which proved to be a species of *Theromyzon* (Blanchard, 1892b; Ringuet, 1947). Additional material received by him, particularly from Wilhelm Michaelsen's expedition to Chile in 1892 and 1893, contributed to several new species (Blanchard, 1893, 1896, 1900, 1917) and a growing realization that the temperate latitudes of Chile harbored an unusually high diversity of leeches, particularly those of the nonsanguivorous genus *Helobdella* (see also Moore, 1911).

Beginning in 1944, Raul Ringuet turned his attention from branchiuran fish parasites to the freshwater leech diversity of South America, which, in part, concerned the trans-Andean relationships of Chilean and Argentinian taxa. Two seminal contributions summarized contemporary knowledge of that hirudifauna. Ringuet (1944a) catalogued 360 leech specimens in the Museo de La Plata, and provided detailed internal anatomical descriptions for species that had not previously been dissected (Ringuet, 1944b). After detailing Argentinian spider fauna and ichthyofauna into the 1960s, Ringuet continued to make major contributions to knowledge of leeches in the last 10 years of his life, culminating in a trip to Santiago in 1979 and one of his last publications: a complete synopsis of Chile's known leech diversity (Ringuet, 1985a).

In the southern summer of 2001 we engaged in an expedition to the Región de los Lagos with an aim to collect the two unusual Valdivian leeches, *Americobdella valdiviana* and *Mesobdella gemmata*, and incorporate them in ongoing molecular phylogenetic work (Borda and Siddall, 2004). Our collection efforts also focused on inland freshwater drainages closer to the cordillera and not previously investigated (or not readily accessible) by Michaelsen in an effort to more fully characterize the endemic diversity of this region in advance of its steady disappearance. Moreover, this constitutes the first photographic documentation of Chilean hirudifauna.

MATERIALS AND METHODS

Leeches were collected from 17 localities in Chile. Collections were made in the Santuario de la Naturaleza Yerba Loca, east of Santiago on 18 February 2001, as well as in the IX Región de la Araucanía and X Región de los Lagos between 39°07'30"S and 42°47'23"S from 19 February 2001 to 6 March 2001. Collection methods included examination of the underside of rocks and submerged debris along shorelines of lakes and streams, wandering bare-legged in humid forests, as well as overturning logs and digging into the topsoil in those forests.

Leeches were relaxed with the gradual addition of ethanol and were either fixed in 10% formalin buffered with CaCl₂ and later transferred and stored in 70% ethanol or fixed in 95–100% ethanol until used for DNA extraction. Specimens were photographed alive with a Nikon 990 digital camera. Preserved animals were examined and photographed using a Nikon SMZ-U stereomicroscope with a SPOT-RT (Diagnostic Instruments, Inc.) digital camera.

To assess the genetic variation of color morph varieties in *Americobdella valdiviana*, the nuclear 18S rDNA gene was amplified and sequenced both for a terrestrial (dark maroon) specimen and for an aquatic (light gray) specimen. Tissue from the caudal sucker was used in order to minimize the possibility of contamination from prey DNA found in the gastric and intestinal regions. The DNeasy Tissue Kit (QIAGEN Inc., Va-

lencia, CA) was used for tissue lysis and DNA purification. PCR amplification of nuclear 18S rDNA was accomplished by obtaining fragments with primer pair combinations "AL", "CY", and "BO", yielding three overlapping double-stranded DNA fragments of approximately 600 base pairs (bp) each in length (Apakupakul et al., 1999). Amplification reaction mixtures for gene fragments used Ready-To-Go PCR Beads (Amersham Pharmacia Biotech, Piscataway, NJ), 1 μ l of each 10 μ M primer, 2 μ l DNA template, and 21 μ l RNase-free H₂O (total volume, 25 μ l). All amplification reactions were performed in a GeneAmp PCR System 9700 (P E Applied Biosystems) as follows: heated to 94° C for 5 min, followed by 35 cycles of 94° C (15 sec), 44° C (20 sec), and 70° C (90 sec) and a final extension at 72° C (7 min). Amplification products were sequenced in both directions. Each 8 μ l sequencing reaction mixture included 2 μ l BigDye (Applied Biosystems, Perkin-Elmer Corporation), 2 μ l of dye "extender" buffer (1 M Tris, pH 9; 25 mM MgCl₂), 2 μ l of 1 μ M primer and 2 μ l of gene amplification product. Samples were sequenced in a GeneAmp PCR System 9700 for 30 cycles at 96° C (10 sec), 50° C (10 sec), and 60° C (4 min). Sequences were purified by 70% isopropanol/70% ethanol precipitation to remove primers and unincorporated dyes and were electrophoresed in an ABI Prism 3700 sequencer (Applied Biosystems).

RESULTS

Twelve species of leeches were collected of which two are new to science. Half were nonsanguivorous species of *Helobdella* and two were principally terrestrial in habit. The only species found at only one collection locality was the new species of *Helobdella* from Santuario de la Naturaleza Yerba Loca.

ORDER ARHYNCHOBDELLIDA BLANCHARD,
1894

SUBORDER ERPOBDELLIFORMES CABALLERO,
1952

FAMILY AMERICOBDELLIDAE (CABALLERO,
1956)

Americobdella valdiviana (Phillippi, 1872)
Figures 1–6

One partial specimen (AMNH 4301, Annelida) free living, taken from Parque Oncol

(CV01–15), at 495 m, 39°42'27.1"S, 78°18'28.2"W, 28 February 2001, dug up by shovel in two pieces, with earthworm in gut, dark gray ventrally to maroon dorsally when alive, fixed and stored in 100% ethanol. One intact specimen (AMNH 4302, Annelida) 137 mm in length, free living at Fundo Buenaventura near Hueyelhue (CV01–16), approximately 39°45'S, 73°08'W, 2 March 2001, from under rock in stream, slate gray ventrally and dorsally with faint yellow mid-dorsal line when alive that disappeared upon fixation in 100% ethanol. Additional material examined includes a large pale gray specimen and a smaller dark specimen preserved in formalin at the Universidad Austral in Valdivia.

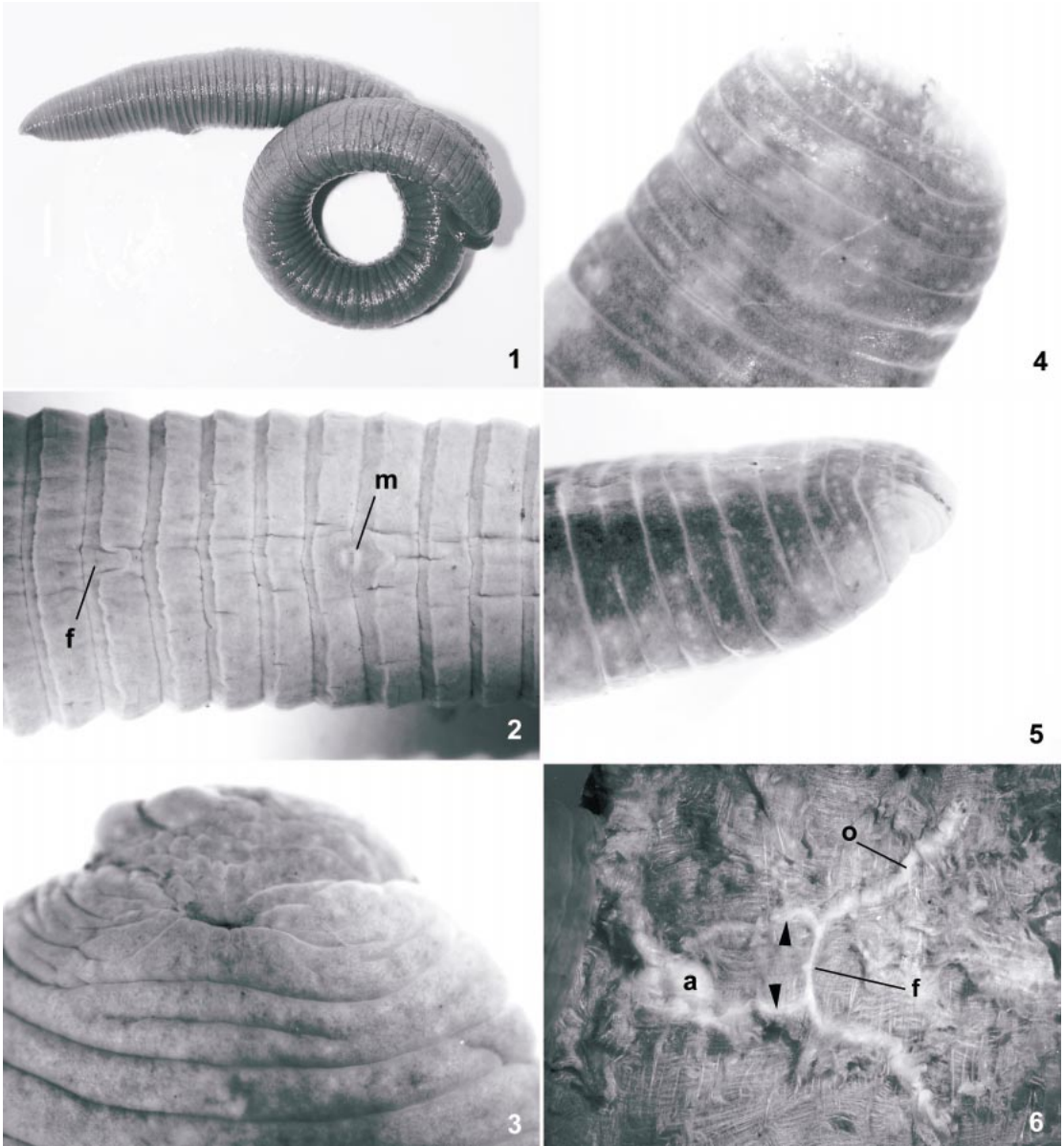
This species, though rare, is large and robust (fig. 1), and easily recognizable. Male gonopore in furrow at XI b5/b6 and female gonopore in furrow at XII b5/b6 (fig. 2). Though reported by Moore (1924), no eyespots were observed in the live leech (figs. 4, 5) or following fixation. Nephropores in ventral annulus b5, midbody annuli with an irregular tendency toward subdivision at margins (fig. 2). There are no postanal annuli (fig. 3). Although the parenchymal spaces are difficult to dissect due to the extensive connective tissue, we observed the bilobed male atrium, caecate ovisacs, and the longitudinal connecting conduit between male and female median reproductive apparatus (fig. 6). Small ribosomal subunit sequences were identical for leeches from these two localities (GenBank accession number AY425461).

SUBORDER HIRUDINIFORMES CABALLERO,
1952

FAMILY XEROBDELLIDAE MOORE, 1946

Mesobdella gemmata (E. Blanchard, 1849)
Figures 7–14

Three specimens (AMNH 4303, Annelida) fixed in 100% ethanol and three specimens (AMNH 4304, Annelida) fixed in 10% formalin, collected from exposed skin prior to or while bloodfeeding, 528 m, Chan-Chan Alto (CV01–13), 39°33'49.7"S, 73°12'23.9"W, 26 February 2001, in humid forest and near roadside pools of water where frogs were calling and mating. One specimen (AMNH 4305, Annelida) fixed in 100% ethanol, at Fundo Bue-

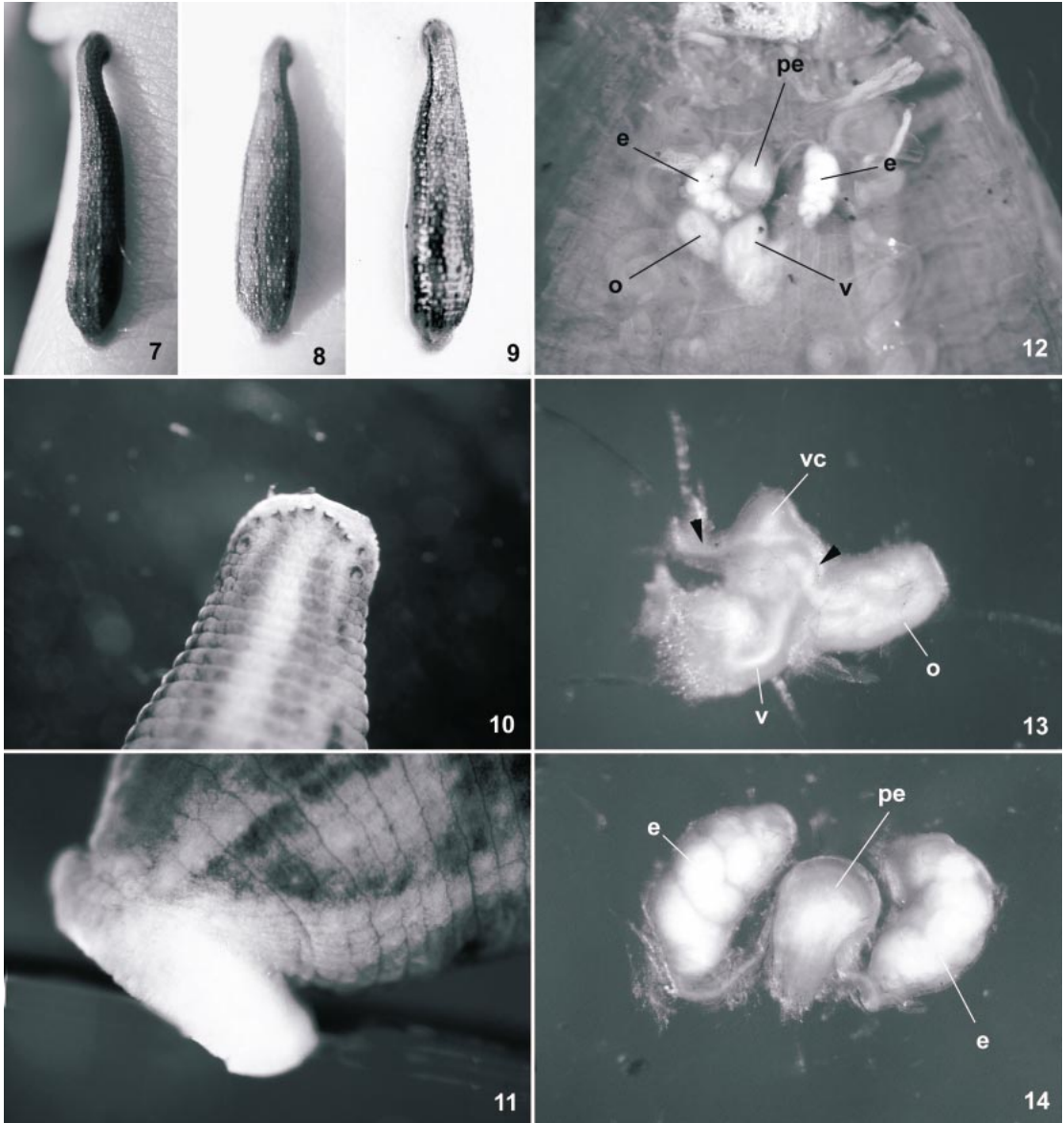


Figs. 1–6. *Americobdella valdiviana*. **1.** Whole specimen approximately 20 cm in length from the Universidad Austral. **2.** Ventral view of female (f) and male (m) gonopores. **3.** Dorsal view of caudal somites in which there are no annuli between the anus and the sucker. **4.** Dorsal view of cephalic somites in live specimen from Hueyelhue. **5.** Lateral view of cephalic somites in live specimen from Hueyelhue. **6.** Dissection of clitellar somites revealing the atrial region (a), ovisacs (o), female gonopore (f), and the conducting tissue (arrowheads) between the oviducts and male median reproductive apparatus.

naventura near Hueyelhue (CV01–16), approximately 39°45'S, 73°08'W, 2 March 2001.

Dorsum variable tawny brown to deep

brown field when alive with darker longitudinal pigment patterns following paramedial and marginal ridges especially posteriorly (figs. 7, 8, 9). Cephalic somites slightly wid-



Figs. 7–14. *Mesobdella gemmata*. 7, 8, 9. Live specimens from Chan-Chan Alto feeding on the second author. 10. Dorsal view of cephalic somites. 11. Lateral view of caudal somites in which no respiratory auricle is visible. 12. Dissection of clitellar somites revealing the median reproductive apparatus including the penis sheath (pe), epididymes (e), vaginal sac (v), and an ovary (o). 13. Female median reproductive apparatus exhibiting independent oviducts (arrowheads) and a small vaginal caecum (vc). 14. Male median reproductive apparatus showing the stout penis and sheath (pe) and associated epididymes (e).

ened at V with five pairs of eyespots, one on each of II, III, IV, V, and VI (fig. 10). Mid-body somites triannulate. Posteriolateral respiratory auricles absent (fig. 11). Male gon-

opore on annulus XI a3 very near furrow of XI a2/a3 ; female gonopore in furrow at XII/XIII. Median reproductive apparatus micromorphic (fig. 12) with male penis sheath in

XII a1 and a2, entirely anterior to female organs (fig. 12). No common oviduct. Paired oviducts short, inserting ventrally into vagina in XII a3. Ovisacs ovoid in XII a3. Vagina initially in XIII a1 but recurved anteriorly well into XII a3 and with short caecum anterior to oviductal insertion point (fig. 13). Ejaculatory ducts thin with short preatrial loop between base of penis sheath and epididymes (fig. 14). Epididymes in XII a1 and a2.

FAMILY SEMISCOLESCIDAE SCRIBAN AND
AUTRUM, 1934

Patagoniobdella variabilis (Blanchard,
1900)

Figures 15–19, 22–24

Two specimens (AMNH 4308, Annelida) fixed in 100% ethanol and one dissected specimen (AMNH 4309, Annelida) fixed in 10% formalin, free living, collected from underside of rocks, 137 m, Lago Villarica (CV01–06), 39°16'39.6"S, 71°58'47.4"W, 21 February 2001. One free-living specimen collected from under submerged branch on shoreline of Lago Huerquehue (CV01–09), 1411 m, 39°07'36.9"S, 71°41'45.4"W, 22 February 2001, fixed in 100% ethanol (AMNH 4310, Annelida) and dissected. The latter specimen was unusual in that the dorsum and dorsal surface of the caudal sucker were centrally black and with broad marginal longitudinal zones of emerald-green pigment when alive (fig. 15).

Dorsum typically dark reddish-brown with medial and paramarginal longitudinal zones of light brown pigment patches when alive (fig. 16). Cephalic somites with five pairs of pyriform eyespots arranged in parabolic arc on uniannulate somites II, III, IV, and on first annulus of biannulate somites V and VI (figs. 17, 18). Gonopores separated by 1/2 + 2 + 1/2 annuli, male gonopore on annulus XII b1, female gonopore on annulus XII b5 (fig.

19). Testisacs at interganglionic intervals. Anteriormost testisacs at XIV/XV are unpaired (i.e., two testisacs at interval), whereas those at XV/XVI through XXIII/XXIV appear as doublets on each side (figs. 22, 24). Ascending male sperm ducts (i.e., “vasa deferentia”) lateral to testisacs, thin and fragile in specimens from Lago Villarica but robust in specimen from Lago Huerquehue (figs. 22, 24). Tightly coiled proximal sperm ducts (i.e., “epididymes”) in XIV and XV, both sets arranged to the left of penis sheath with ejaculatory ducts entering “prostate” glandular region of penis sheath at XVI without procurrent posterior loop (fig. 22). Base of penis sheath at XIX. Female reproductive anatomy arranged principally to the right of midline (fig. 23). Vaginal sac ends at XIII; common oviduct without procurrent loop and returning anteriorly along vaginal sac to a single globular ovisac in XII. Gastric tissue and intestines unbranched. Gastric/intestinal sphincter in XIX. Two annuli between anus and caudal sucker.

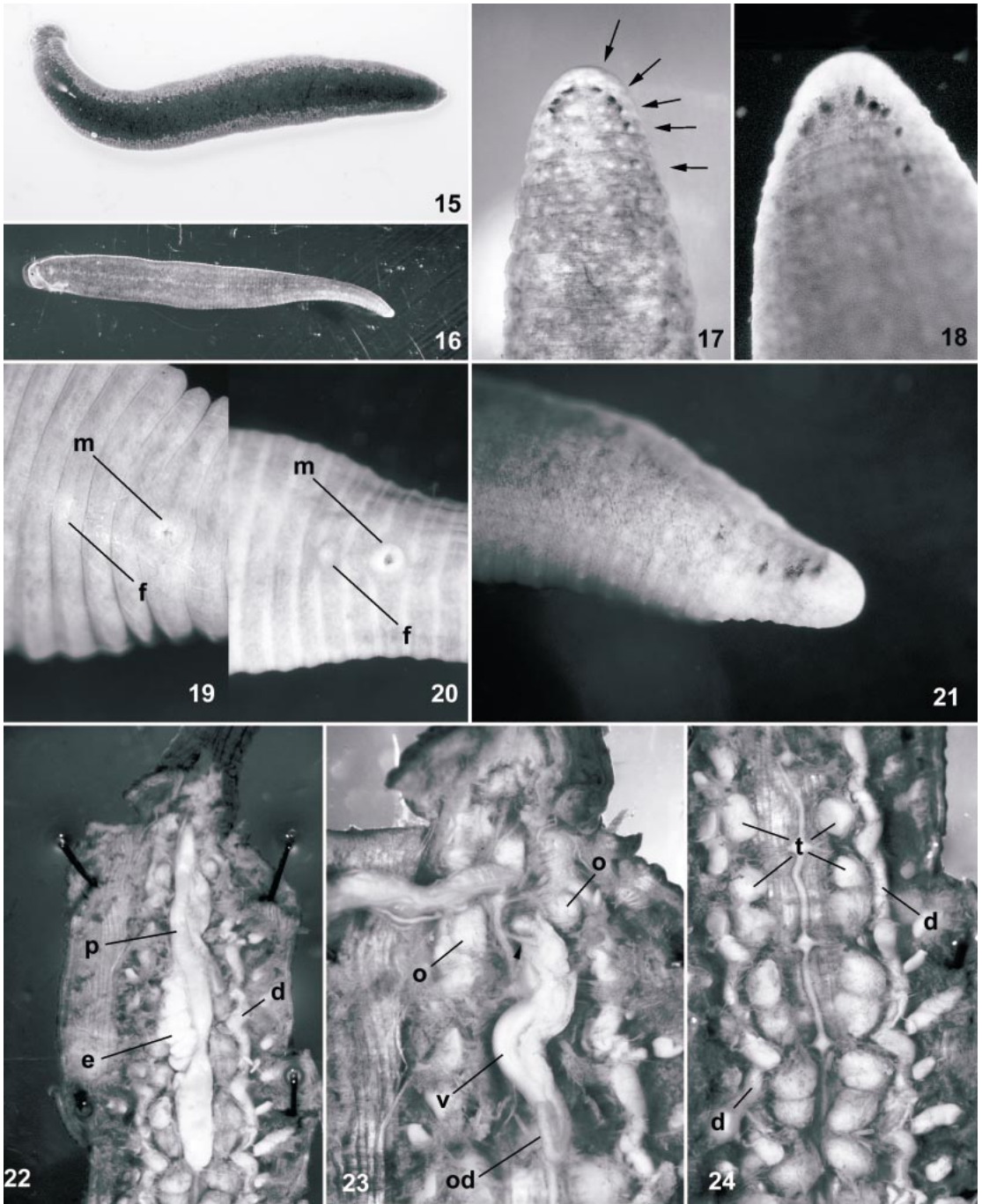
Patagoniobdella fraterna Ringuelet, 1976
Figures 20, 21

One specimen (AMNH 4306, Annelida) fixed in 100% ethanol and one specimen (AMNH 4307, Annelida) fixed in 10% formalin, free living, collected from underside of submerged branches at 214 m, Lago Neltume (CV01–03), 39°46'32.3"S, 71°57'27.7"W, 20 February 2001.

Dorsum similar to *P. variabilis*, dark reddish-brown with medial and paramedial longitudinal zones of light brown pigment patches when alive. Cephalic somites with five pairs of irregular eyespots arranged in parabolic arc on uniannulate somites II, III, IV, and on first annulus of biannulate somites V and VI (fig. 21). Male gonopore on annulus XII b1; female gonopore on annulus

→

Figs. 15–24. *Patagoniobdella* species. **15.** Live specimen of *Patagoniobdella variabilis* from Lago Huerquehue; the lighter pigment zones were emerald-green. **16.** *Patagoniobdella fraterna* from Lago Neltume; the darker pigment zones were brick-red. **17.** Dorsal view of cephalic somites of *Patagoniobdella variabilis* from Lago Huerquehue showing the five pairs of eyespots (arrows). **18.** Dorsal view of cephalic somites of *Patagoniobdella variabilis* from Lago Villarica. **19.** Ventral view of clitellar somites of *Patagoniobdella variabilis* from Lago Huerquehue. **20.** Ventral view of clitellar somites of *Patago-*



niobdella fraterna from Lago Neltume. **21.** Lateral view of cephalic somites of *Patagoniobdella fraterna* from Lago Neltume. **22.** Midbody dissection of *Patagoniobdella variabilis* from Lago Huerquehue showing the long penis and sheath (p) with a single mass of associated epididymes (e) and the lateral robust ascending sperm ducts (d). **23.** Ovisacs (o), common oviduct (od), and vagina (v) of *Patagoniobdella variabilis*. **24.** Ascending sperm ducts (d) lateral to the testisacs (t) of *Patagoniobdella variabilis*.

XII a2 (i.e., separated by $1/2 + 1 + 1/2$ annuli; fig. 20). Testisacs at interganglionic intervals. Antermost testisacs at XIV/XV are paired (i.e., four testisacs at interval), as are those at XV/XVI through XXIII/XXIV, which appear as doublets on each side. Ejaculatory duct between epididymes and penis sheath with posterior procurent loop.

ORDER RHYNCHOBDELLIDA BLANCHARD,
1894

FAMILY GLOSSIPHONIIDAE VAILLANT, 1890

Haementeria gracilis (Weyenberg, 1833)
Figure 25

One specimen (AMNH 4311, Annelida) fixed in 100% ethanol collected from the first author's left ankle at Laguna de los Lotos, Isla Teja, Valdivia (CV01-12), 13 m, $39^{\circ}47'58.6''S$, $73^{\circ}15'45.7''W$, 24 February 2001.

One pair of eyespots. Gonopores separated by two annuli. Midbody annuli dorsally subdivided. Two pairs of longitudinal rows of major papillae on dorsum on a1 associated with circular unpigmented zones.

Theromyzon propinquium Ringuélet, 1947
Figure 26

Three specimens (AMNH 4312, Annelida) fixed in 10% formalin and three specimens (AMNH 4336, Annelida) fixed in 100% ethanol, collected from overturned rocks at 214 m, Lago Neltume (CV01-03), $39^{\circ}46'32.3''S$, $71^{\circ}57'27.7''W$, 20 February 2001. One specimen (AMNH 4313, Annelida) fixed in 10% formalin, collected from overturned rock at Lago Panguipulli (CV01-04), $39^{\circ}38'39.2''S$, $72^{\circ}19'31.4''W$, 20 February 2001. One specimen (AMNH 4314, Annelida) fixed in 70% formalin, collected from overturned rock at Lago Villarica (CVO1-06), $39^{\circ}16'39.6''S$, $71^{\circ}58'47.4''W$, 21 February 2001. One specimen (AMNH 4315, Annelida) fixed in 100% ethanol, collected from overturned rock at Lago Tinquilco (CV01-07), $41^{\circ}47'20.0''S$, $71^{\circ}50'52.8''W$, 21 February 2001. One specimen (AMNH 4316, Annelida) fixed in 100% ethanol, collected from overturned rock at Miraflores, Chiloé (CV01-18) $42^{\circ}47'23.5''S$, $73^{\circ}51'12.3''W$, 6 March 2001.

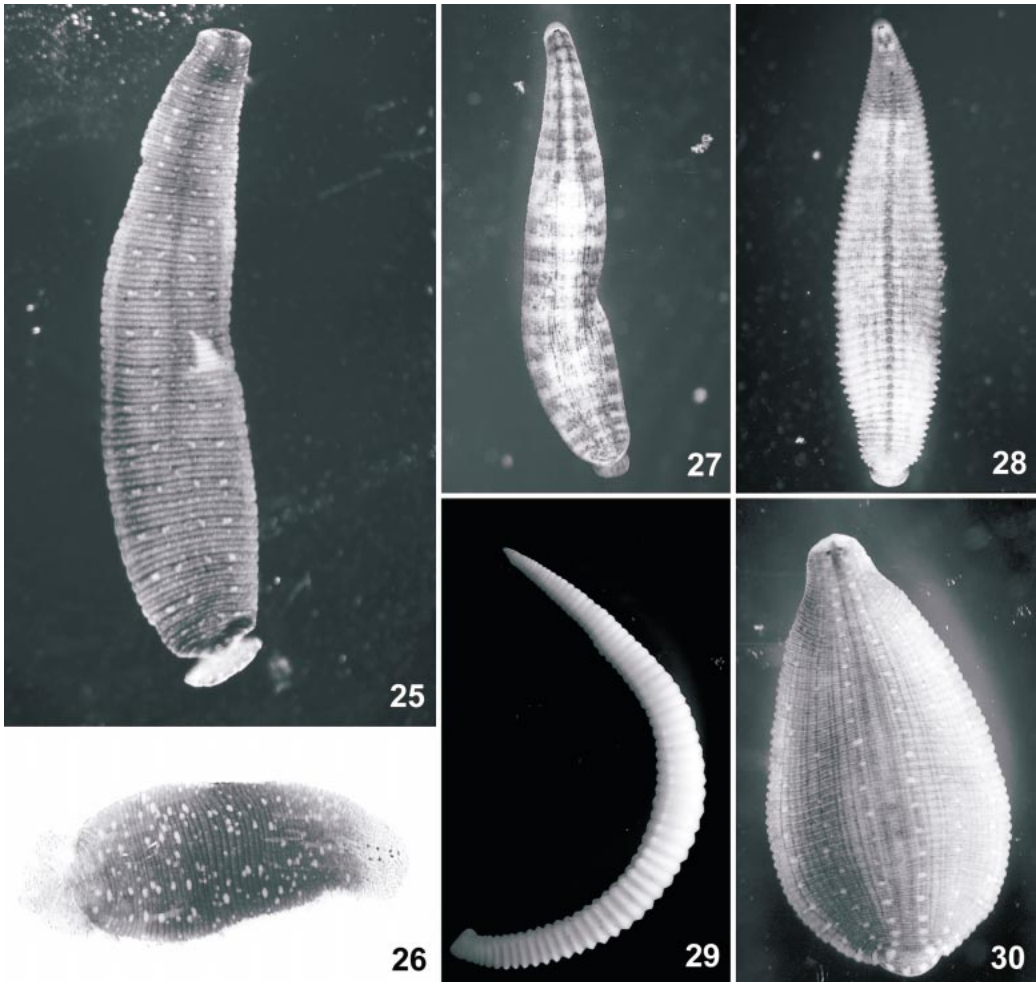
Four pairs of eyespots. Gonopores separated by three annuli. When alive, dorsum with olive green chromatophores and numerous irregular patches of orange pigment that appear to mostly follow four longitudinal rows repeating in each somite. Caudal sucker very clear with scattered olive green chromatophores and marginal arc of orange pigmented spots.

REMARKS: Several weeks after detailing the anatomy of the European *Theromyzon tessulatum* (see Blanchard, 1892a), Blanchard (1892b) received a leech that appeared to be identical to the European duck leech from an anonymous donor in Chile. Believing the Chilean specimens to be the same species, Blanchard (1892b) considered several hypotheses regarding this unusually disjunct distribution: that it was transported on migratory birds, that it was introduced via domesticated ducks, or that it was introduced via moist soils on aquatic plants. Later Ringuélet (1978) determined that early accounts of this species in Chile and Argentina were attributable to *Theromyzon propinquium* Ringuélet, 1947, which is distinct from the European species in terms of live color patterns and internal anatomy (Ringuélet, 1947).

Helobdella duplicata Moore, 1911
Figure 27

Nine specimens (AMNH 4317, Annelida) fixed in 100% ethanol and 15 specimens (AMNH 4318, Annelida) fixed in 10% formalin, collected from underside of rocks at Lago Panguipulli (CV01-04), $39^{\circ}38'39.2''S$, $72^{\circ}19'31.4''W$, 20 February 2001. Twelve specimens (AMNH 4319, Annelida) fixed in 100% ethanol and 16 specimens (AMNH 4320, Annelida) fixed in 10% formalin, collected from underside of rocks at Lago Panguipulli (CV01-05), $39^{\circ}38'38.3''S$, $72^{\circ}19'24.0''W$, 20 February 2001. Three specimens (AMNH 4321, Annelida) fixed in 10% formalin, collected from under rocks at 137 m, Lago Villarica (CV01-06), $39^{\circ}16'39.6''S$, $71^{\circ}58'47.4''W$, 21 February 2001.

One pair of eyes. Gonopores separated by one annulus. Nuchal glands without scute on VIII a1. Midbody annuli subdivided with transverse metameric darker coloration on



Figs. 25–30. Several glossiphoniid leeches. **25.** *Haementeria gracilis*. **26.** *Theromyzon propinquum* (live). **27.** *Helobdella duplicata*. **28.** *Helobdella simplex*. **29.** *Helobdella michaelsoni*. **30.** *Helobdella cordobensis*.

a1. A pair of broad paramedial zones of approximately six fine longitudinal lines.

Helobdella simplex Moore, 1911
Figure 28

Fifty specimens (AMNH 4322, Annelida) fixed in 100% ethanol and 15 specimens (AMNH 4323, Annelida) fixed in 10% formalin, collected from underside of rocks at Lago Panguipulli (CV01–04), 39°38'39.2"S, 72°19'31.4"W, 20 February 2001. Six specimens (AMNH 4324, Annelida) fixed in 100% ethanol and six specimens (AMNH 4345, Annelida) fixed in 10% formalin, col-

lected from underside of rocks at Lago Panguipulli (CV01–05), 39°38'38.3"S, 72°19'24.0"W, 20 February 2001. Eleven specimens (AMNH 4325, Annelida) fixed in 100% ethanol and 19 specimens (AMNH 4326, Annelida) fixed in 10% formalin, collected at 137 m, Lago Villarica (CV01–06), 39°16'39.6"S, 71°58'47.4"W, 21 February 2001. Two specimens (AMNH Annelida 4327) fixed, collected from under rocks at Lago Tinquilco (CV01–07), 41°47'20.0"S, 71°50'52.8"W, 21 February 2001.

One pair of eyes. Gonopores separated by one annulus. Margins of midbody annuli ren-

dering serrated appearance. One row of medial papillae on each annulus of postgenital somites.

Helobdella michaelsoni Blanchard, 1900
Figure 29

Six specimens (AMNH 5253, Annelida) fixed in 100% ethanol and two specimens (AMNH 5249, Annelida) fixed in 10% formalin, collected from underside of rocks at Lago Calafquen (CV01-02), 39°29'26.2"S, 72°08'50.1"W, 19 February 2001. Seven specimens (AMNH 5256, Annelida) fixed in 100% ethanol and six specimens (AMNH 5252, Annelida) fixed in 10% formalin, collected from underside of rocks at Lago Neltume (CV01-03), 39°46'32.3"S, 71°57'27.7"W, 20 February 2001. One specimen (AMNH 5254, Annelida) and 29 specimens (AMNH 5255, Annelida) fixed in 100% ethanol and four specimens (AMNH 5250, Annelida) and six specimens (AMNH 5251, Annelida) fixed in 10% formalin, collected at Lago Panguipulli (CV01-06), 39°38'39.2"S, 72°19'31.4"W, 20 February 2001. One specimen (AMNH 5257, Annelida) fixed in 100% ethanol, collected from under rocks at 137 m, Lago Villarica (CV01-06), 39°16'39.6"S, 71°58'47.4"W, 21 February 2001.

Body thin and elongate. Caudal sucker terminal. Atria piriform with strongly curved anterior cornua. Male sperm ducts very thick and recurving at XVI. Ovaries short and lobate, to XIII only. No papillae. No nuchal glands. Gastric tube without postcaeca. Pigmentation is highly variable from colorless to irregular fine brown speckling. This species appears to have a remarkable variation in Chile from the very stout to extremely thick and vermiform representatives.

Helobdella cordobensis Ringuelet, 1943
Figure 30

Three specimens fixed in 10% formalin (AMNH 4342, Annelida) from 207 m, Lago Calafquen (CV01-02), 39°29'26.2"S, 72°08'50.1"W, 19 February 2001. Three specimens fixed in 10% formalin (AMNH 4343, Annelida) and two fixed in 100% ethanol (AMNH 4344, Annelida) from 214 m,

Lago Neltume (CV01-03), 39°46'32.3"S, 71°57'27.7"W, 20 February 2001.

Dorsum with three pairs of rows of white spots. Three pairs of inconspicuous rows of papillae between white spots. Fourteen pairs of longitudinal lines of pigment. Venter has major pair of paramedial stripes, with minor lateral longitudinal striping. Sucker is ventrally directed. Proboscis extends to XIII, with thick salivary ducts at base and diffuse salivary cells in parenchyma extending from X to XVI/XVII. Esophagus very short. Four pairs of digitate gastric caeca, plus a pair of postcaeca. Four pairs of corrugated intestinal caeca. Atria weakly developed. Ejaculatory ducts recurved in XVII. Ovaries broad and long, extending to XIX.

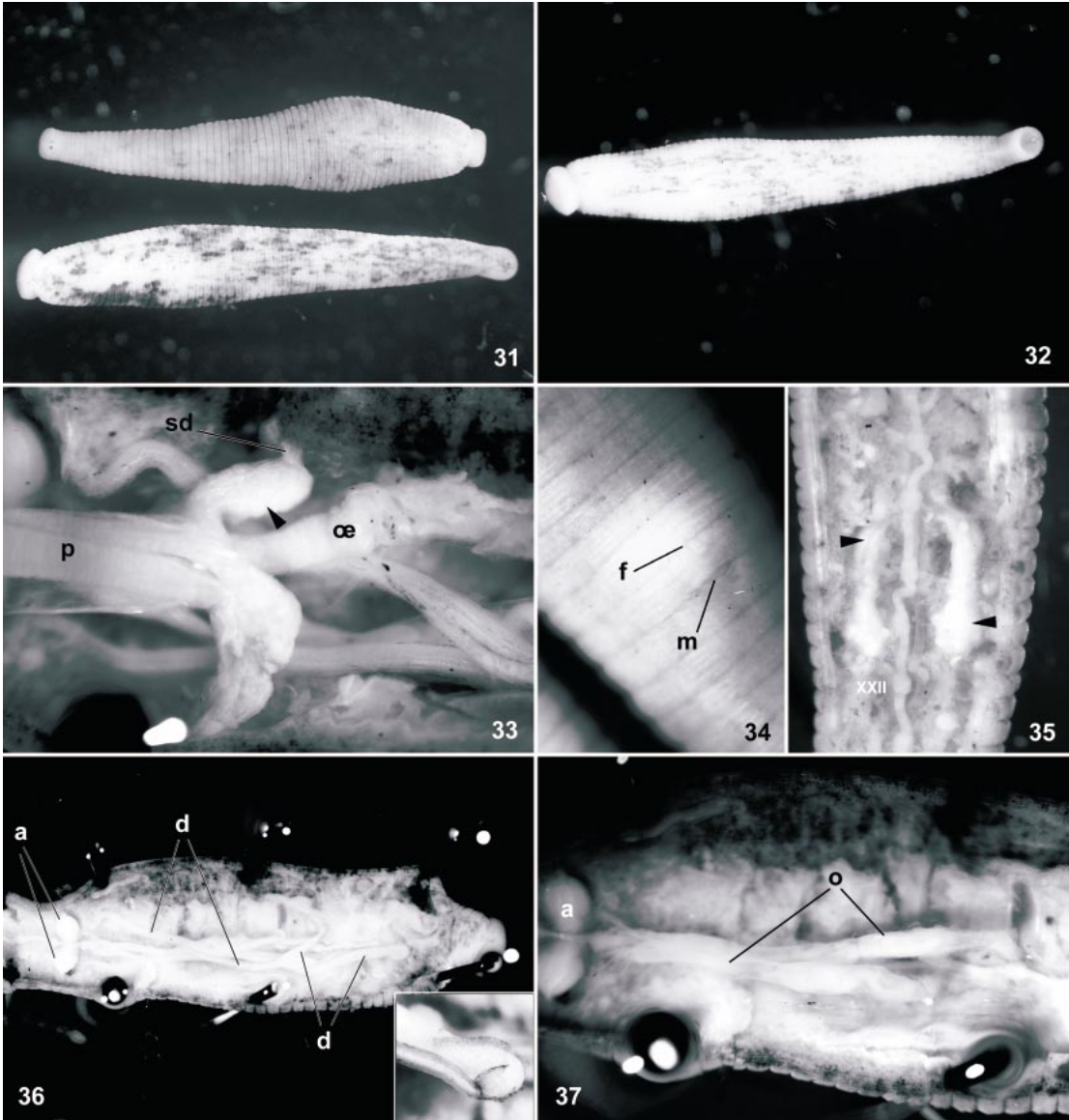
REMARKS: *Helobdella cordobensis*, which may previously have been confused with *Batrachobdella gemmata*, as they look remarkably similar dorsally (Blanchard, 1900), was originally a subspecies in the *Helobdella triserialis* group (Ringuelet, 1943a). Like other members of this group, it has four digitate gastric caeca differing from the typical 5 caeca found for other members of the genus. The Chilean representatives of the species differ somewhat from those at the type locality in terms of external pigmentation and their slightly longer ejaculatory ducts (to XVII instead of XVI).

Helobdella wodzickiorum, new species
Figures 31-37

HOLOTYPE: Collected from underside of rocks in streams Santuario de la Naturaleza Yerba Loca (CV01-01), 2259 m, 33°18'S, 70°17'W, 18 February 2001, fixed in 10% formalin (AMNH 4338, Annelida). Body 12 mm in length and 1 mm wide.

PARATYPES: Fifteen specimens fixed in 100% ethanol (AMNH 4339, Annelida) and 14 specimens fixed in 10% formalin (AMNH 4340, Annelida), collected at Santuario de la Naturaleza Yerba Loca (CV01-01), 2068 to 2259 m, 33°18'S, 70°17'W, 18 February 2001.

DESCRIPTION: Dorsum irregularly mottled pale tawny brown to white field (fig. 31). Venter irregularly mottled as in dorsum (fig. 32). Annuli not subdivided. Sucker terminal (figs. 31, 32). Neither nuchal scute nor



Figs. 31–37. *Helobdella wodzickiorum*, n.sp. **31.** Two specimens demonstrating dorsal appearance and variability. **32.** Ventral appearance. **33.** Base of proboscis (p) at junction with esophagus (œ) where small salivary glands (arrowheads) surround the salivary ductule bundle (sd) draining parenchymal salivary cells. **34.** Female (f) and male (m) gonopores on venter. **35.** Gastric postcaeca (arrowheads) viewed ventrally. **36.** Dorsal view of male median reproductive apparatus showing the prominent atria (a) and extremely long sperm ducts (d) for which the ascending and descending portions are markedly different in diameter (inset). **37.** Elongate ovisacs (o).

glands present in VIII. One pair of eyespots on III. Base of proboscis at XIII/XIV (fig. 33). Salivary glands at base of proboscis in XIV and with diffuse parenchymal salivary cells (fig. 33). Gastric tract tubular and acae-

cate. Postcaeca to XXII (fig. 35). Four intestinal caeca. Ejaculatory ducts insert into atria dorsolaterally (fig. 36); recurve at XXII. Descending and ascending portions with distinct transition in XXII (fig. 36 inset). Atria bul-

bous and directed laterally (figs. 36, 37). Long, tubular ovisacs extending to XIX (fig. 37).

REMARKS: Species of *Helobdella* with irregularly mottled dorsal pigmentation include *Helobdella paranensis* (Oka, 1930), *Helobdella similis* Ringuelet, 1942 (see Ringuelet, 1942a, 1985b), and *Helobdella nunununojensis* Siddall, 2001. Both *H. similis* and *H. nunununojensis* also share several internal features with *H. wozzickiorum*, like the tubular crop lacking caeca, and short postcaeca (Ringuelet, 1985b; Siddall, 2001b). Each of *Helobdella bolivianita* Siddall, 2001, *H. nunununojensis*, *Helobdella cryptica* (Ringuelet, 1978), and *H. paranensis* have the unusual glandular salivary tissue around the salivary ducts that drain cells in the parenchyma. *Helobdella bolivianita*, however, has a scute at VIIIa1/a2 (Siddall, 2001a) and *H. nunununojensis* has a very small caudal sucker (Siddall, 2001b) and would not be readily confused with *H. wozzickiorum* even on external anatomy. Whereas several species of *Helobdella* have ovaries as long as those seen in *H. wozzickiorum*, like *H. cordobensis* (fig. 30), no other species in the genus has a larger male reproductive anatomy with the large prominent atria and male sperm ducts extending all the way to somite XXIII.

ETYMOLOGY: The species is named for Wojtek Wozzicki and Kathryn Gregory-Wozzicki who conveyed us to the Yerba Loca Reserve for what should have been only a pleasant afternoon hike in the Andes but also unintentionally became our first collection locality.

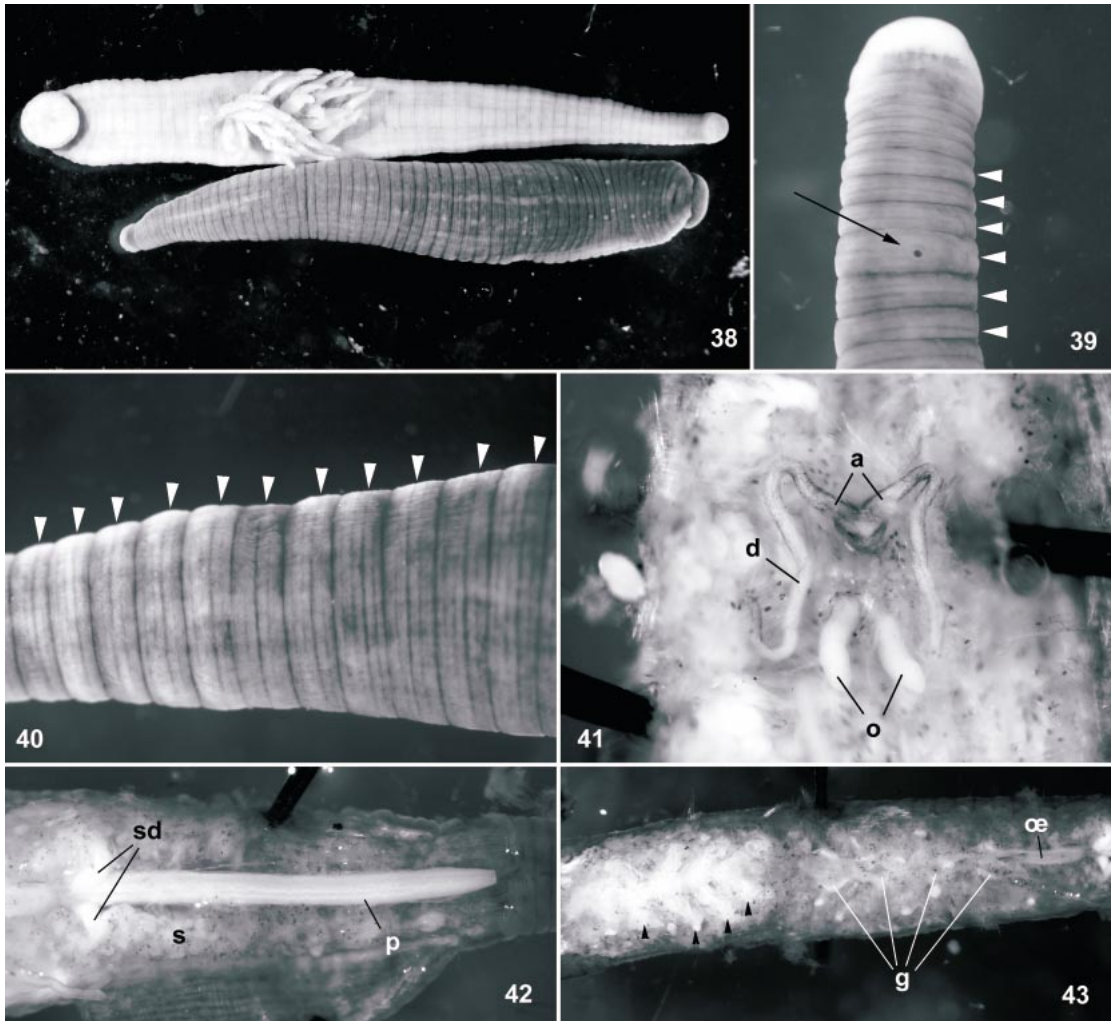
Helobdella pichipanan, new species
Figures 38–43

HOLOTYPE: Collected from underside of submerged branches on shoreline at Lago Chico (CV01–08), 1239 m, 39°08'33.3"S, 71°42'44.1"W, 22 February 2001, fixed in 10% formalin (AMNH 4328, Annelida). It is 39 mm in length and 7.0 mm in width. Dorsum dark gray to brown with pale beige longitudinal middorsal zone; venter pale with two pairs of black paramedial lines.

PARATYPES: One specimen at Lago Tinquico (CV01–07), 41°47'20.0"S, 71°50'52.8"W, 21

February 2001, fixed in 100% ethanol (AMNH 4329, Annelida). Three specimens fixed in 100% ethanol (AMNH 4330, Annelida) and five fixed in 10% formalin (AMNH 4331, Annelida), from Lago Chico (CV01–08), 1239 m, 39°08'33.3"S, 71°42'44.1"W, 22 February 2001. Eleven specimens fixed in 100% ethanol (AMNH 4332, Annelida) and 11 specimens fixed in 10% formalin (AMNH 4333, Annelida) from Lago Huerquehue (CV01–09), 1411 m, 39°07'36.9"S, 71°41'45.4"W, 22 February 2001. One specimen fixed in 100% ethanol (AMNH 4334, Annelida) and three fixed in 10% formalin (AMNH 4335, Annelida), from Lago Patos (CV01–010), 1467 m, 39°07'30.0"S, 71°42'14.6"W, 22 February 2001. Two specimens fixed in 100% ethanol (AMNH 4336, Annelida) and one with brood fixed in 10% formalin (AMNH 4337, Annelida), from Lago Verde (CV01–011), 1285 m, 39°08'07.2"S, 71°42'31.0"W, 22 February 2001.

DESCRIPTION: Dorsum dark gray median to light brown/beige paramedially with pale beige broad middorsal longitudinal zone (fig. 38). One pair of dorsal continuous paramedial faded black stripes. Two to three pairs of discontinuous dark and light rows of pigment within the continuous stripes and six or more pairs of discontinuous dark and light rows of marginal to continuous stripes. Two to three pairs of dark transverse lines per annulus. Some dorsal papillation towards posterior end (fig. 38). Venter pale beige with two pairs paramedial faded black stripes (fig. 38). Anterior and posterior sucker of same pale beige color; caudal sucker subterminal. Marginal longitudinal black stripes ventrally. In juveniles, dorsal paramedial stripes conspicuously dark and continuous. Pale, dorsal longitudinal zone, not conspicuous. No dorsal posterior papillation. Inner pair of ventral paramedial stripes prominent and continuous; outer pair discontinuous. Annuli weakly subdivided (figs. 39, 40). Nuchal gland present on VIII a1/a2 (fig. 39). One pair of eyes on III. Base of proboscis at XIII. Thick salivary ducts at base of proboscis with parenchymal salivary cells; diffuse (fig. 42). Gastric tract tubular with weak caecal bulges midsomite; one pair of postcaeca present and four pairs of intestinal caeca (fig. 43). Go-



Figs. 38–43. *Helobdella pichipanan*, n.sp. **38.** Ventral (top) surface of adult with 33 attached juveniles, and dorsal surface (bottom) of another adult. **39.** Dorsal view of cephalic somites showing the position of the nuchal gland (arrow) and the subdivision of annuli (arrowheads). **40.** Subdivision of annuli (arrowheads) in clitellar and midbody somites. **41.** Median reproductive apparatus with diminutive atria (a), sperm ducts (d), and ovisacs (o). **42.** Dissection of anterior somites revealing the long proboscis (p) and salivary ductule bundle (sd) draining parenchymal salivary cells (s). **43.** Alimentary canal comprising the esophagus (\o), weakly defined gastric caeca (g), and intestinal caeca (arrowheads).

nads micromorphic. Male atria very weakly developed, nearly absent (fig. 41). Ejaculatory ducts extend only to XII/XIII. Ovisacs extend only to XII/XIII (fig. 41).

REMARKS: Several leeches in South America possess a glandular region at VIIIa1/a2, the same position at which *Helobdella stagnalis* (among others) exhibits a hardened scute. Each of these, *H. duplicata*, *H. diploides*, *H. simplex*, *Helobdella ringueleti* Sid-

dall, 2001, and *H. nunununojensis*, is readily distinguished from *H. pichipanan*. *Helobdella duplicata* has pronounced dorsal metameric banding (fig. 27) and *H. simplex* (fig. 28) has the obvious middorsal row of papillae on all annuli (Moore, 1911). The caudal sucker of *H. nunununojensis* is much smaller than the body width (Siddall, 2001b). Like *H. ringueleti*, differences from *H. diploides* could be difficult to discern on the

basis of external anatomy alone. Although *H. diploides* also has subdivided annuli, it does not have a dorsal pigment pattern (Ringuelet, 1948). The dorsal and ventral pigmentation of *H. ringueleti* and *H. pichipanan* is nearly identical, and both species have subdivided annuli. Even on dissection the two species similarly lack prominent gastric caeca save for the postcaeca, and have small ovaries residing in XII only (Siddall, 2001b). However, these two differ markedly in the male reproductive anatomy. In fact, no other species of *Helobdella* has male genitalia that are smaller, an atrium that is as weakly developed, or sperm ducts that are less extensive.

ETYMOLOGY: The name (pron. pee chee pah nahn) is Mapuche for small male genitalia.

DISCUSSION

The diversity and endemism of neotropical hirudifaua, attributed to the limited dispersal range of the majority of its species, is well known (Moore, 1911, 1924; Weber, 1915; Pinto, 1923; Ringuelet, 1944a, 1985a, 1985b; Richardson, 1969; Soós, 1966; Sawyer, 1986; Siddall, 2001a, 2001b), and continues to be reflected in the collections made during this expedition. There are over 30 described *Helobdella* species from South America alone, in particular from Argentina, Bolivia, Brazil, Chile, Paraguay, Peru, and Uruguay. The recent synonymy of other glossiphoniid genera with *Helobdella* (i.e., *Adaetobdella*, *Acritobdella*, *Desmobdella*, and *Gloiobdella*; Siddall and Borda, 2003) increases that number to approximately 40 species, including recent descriptions of new *Helobdella* species from Bolivia (Siddall, 2001a, 2001b).

These collections and the resulting genetic sequence and morphological data from each of *Americobdella valdiviana*, *Mesobdella gemmata*, and *Patagoniobdella* species have been essential in resolving key phylogenetic questions about relationships among arhynchobdellid groups (Borda and Siddall, 2004). From a systematic standpoint, the phylogenetic placement and classification of each of these species had been problematic. This is a consequence of each having unusual life-history strategies, and possessing morphological characteristics that apparently deviate from other members of traditionally estab-

lished arhynchobdellid families and genera (Forbes, 1890; Blanchard, 1893, 1917; Moore, 1911, 1924; Cordero, 1937; Ringuelet, 1945, 1954, 1985a, 1985b; Richardson, 1969, 1971, 1976; Sawyer, 1986). The combination of a new phylogenetic framework (Borda and Siddall, 2004) and the morphological details above permits clarification of their systematic position among the Hirudiniida.

Americobdella

In the original description (Phillippi, 1872), the monotypic *Americobdella valdiviana* was classified as an erpobdellid (Phillippi, 1872) because it was a predator and had rudimentary jaws, typical of erpobdellid leeches (Weber, 1915; Blanchard, 1917; Harant, 1929). Phillippi (1867) remarked on its resemblance “to the European *Trocheta* in both appearance and habit”. Moore (1924: 43) argued that this comment caused “all subsequent writers to be misled”, and he recommended reclassifying *Americobdella* in the distichodont series of Hirudinidae, because several external characteristics pointed directly to an affinity with the Hirudinidae. Caballero (1956) placed *A. valdiviana* in its own family, but still classified it with the Hirudiniformes, where it remained (Ringuelet, 1985a, 1985b; Sawyer, 1986). The unstable classification of *A. valdiviana* can be attributed to its being reminiscent of an ancestral arhynchobdellid leech, retaining morphological traits and habitat preferences seemingly transitory between rhynchobdellid and arhynchobdellid leeches. Most significant is the presence of the intergonadal conducting tubules, connecting the male atrium and the female ovarian ducts, typically found in rhynchobdellid piscicolid leeches. As a result, Moore (1924; see also Ringuelet, 1954; Soós, 1966) proposed that *A. valdiviana* belonged to an ancestral lineage that originated before other arhynchobdellid groups. Likewise, Siddall and Burreson’s (1995, 1996) phylogenetic analyses based on morphology and life-history data found that *A. valdiviana* was in a transitional position between the two major groups of leeches (i.e., Rhynchobdellida and Arhynchobdellida). Recent phylogenetic work by Borda and Siddall (2004),

using combined morphological and molecular data, indicates that *A. valdiviana* is more closely related to the erpobdelliforms (i.e., *Barbronia* spp., *Erpobdella* spp.), and not the hirudiniforms as previously suggested (Moore, 1924; Ringuélet, 1944a, 1976, 1985a, 1985b; Caballero, 1956; Sawyer, 1986). As the most basal lineage of the erpobdellid leeches, it should be formally removed from the Hirudiniformes and placed under the Erpobdelliformes, together with the families Erpobdellidae and Salifidae.

Phillippi (1872) provided conflicting information regarding the habitat preference of *A. valdiviana*. In his description he noted that *A. valdiviana* was a species living in damp earth and feeding on earthworms. However, the specimens he examined were collected in "ditches of mill races" and from a brook. Corroborating this were descriptions of the species suggesting external color variation to be associated with habitat preference (Weber, 1915; Moore, 1924; Ringuélet, 1985a, 1985b). Weber (1915) described terrestrial specimens collected from Corral as being dorsally dark gray, with a uniform yellowish-gray venter. Moore (1924) received specimens "collected in damp earth in Valdivia" (p. 30) and a letter from a Professor Monteleagre Randolph describing an aquatic *Americobdella* (= *Phillippia*) that was "blue-slate [in color] and bears only one red stripe on the back" (p. 29, footnote). On our expedition, a terrestrial dark gray to maroon specimen (found in the midst of consuming an oligochaete) and an aquatic slate-gray specimen with a yellow mid dorsal line were collected. These collections are at variance with color types associated with a specific habitat. Regardless, the fact that 18S rDNA sequences were found to be identical for both specimens suggests that *A. valdiviana* is neither exclusively terrestrial nor aquatic, but rather amphibious in habit. The variation in color pattern and habitat preference could be age specific or developmental; darker specimens appear to be smaller in size than their lighter counterparts.

The presence or absence of eyes in *A. valdiviana* has been a matter of speculation (Weber, 1915; Blanchard, 1917; Pinto, 1923; Moore, 1924; Ringuélet, 1985a, 1985b; Sawyer, 1986). *Americobdella valdiviana* was de-

scribed by Phillippi (1872) as lacking eyes, a diagnostic character for the species in subsequent reports (Weber, 1915; Blanchard, 1917; Pinto, 1923). The lack of eyes was recognized as being associated to a partial subterranean habitat preference similarly found in other burrowing, blind oligochaete predators in the genera *Trocheta* and *Cylicobdella* (Phillippi, 1872; Weber, 1915). To the contrary, Moore (1924: 33) suggested that "this leech has always been considered to be eyeless, and my first examination led to the same conclusion. However, under intense lighting . . . there is no difficulty in making out . . . several whitish areas within small deeply pigmented fields which are evidently eyes." Consequently, other authors followed this revision and even illustrated the presence of six pairs of eyes or "eyelike organs" (Ringuélet, 1944a, 1985a, 1985b; Sawyer, 1986). However, examination of the live specimen suggests once again that *A. valdiviana* in fact does not have eyes.

Mesobdella

The terrestrial sanguivore *Mesobdella gemmata* was traditionally classified a haemadipsid (Blanchard, 1893, 1900; Ringuélet, 1942b, 1943b, 1944a, 1985a; Sawyer, 1986) based on gross morphological characters (i.e., ocular arch; wide dorsal median field; position of first nephropores; Richardson, 1971) and life-history strategies (i.e., terrestrial and sanguivorous). These apparent affinities suggested that *M. gemmata* shared a common ancestry with the terrestrial Indo-Pacific leeches (Blanchard, 1893, 1917; Caballero, 1940; Ringuélet, 1943b, 1944c; Sawyer, 1986), but its geographic distribution, in Chile, and apparent shared reproductive homologies with South American hirudinids (e.g., *Oxyptychus* species) suggested otherwise (Richardson, 1969; Ringuélet, 1972).

Moore (1946) proposed a subfamily Xerobdellinae to include *M. gemmata* with members of other terrestrial genera, such as *Xerobdella* Frauenfeld, 1868 from Europe, and the Mexican *Diestecostoma* Vaillant, 1890. He believed these shared a resemblance in the position of nephropores and the absence of auricles (Moore, 1946). Xerobdellinae was synonymized with Diestecosto-

matidae (Ringuet, 1954), but later Ringuet (1972) established the family Mesobdellidae to the exclusion of the genera *Xerobdella* and *Diestecostoma*. Ringuet (1972) created the family Mesobdellidae in light of Richardson's (1969, 1971) comparative work showing affinities with Neotropical aquatic sanguivores (i.e., *Oxyptychus* spp.) and included only the South American taxa, *Mesobdella* spp. and *Nesophilaemon skottsbergi*, the latter from the Juan Fernandez archipelago. Richardson (1971: 218) suggested the external "haemadipsine-like features" to be a secondary adaptation to terrestriality, whereas the "systems which have not come under the influence of this habit, the female median region and the simple form and paramedial position of the anterior region of the male paired duct, [are] unlike the auriculate land-leeches."

Recent phylogenetic work (Trontelj et al., 1999; Borda and Siddall, 2004) supports the divergence of a second terrestrial sanguivorous lineage separate from the IndoPacific haemadipsids. Further studies including additional representative taxa from the genera *Mesobdella* and *Xerobdella* (i.e., *Mesobdella lineata*, *Mesobdella notohilica*, *Xerobdella anulata*, and *Xerobdella prealpina*), as well as other New World terrestrial genera, *Diestecostoma* and *Nesophilaemon*, could resolve their phylogenetic relationships and therefore lead to the redefinition of previously proposed families (Ringuet, 1953, 1972, 1982; Harant and Grassé, 1959; Soós, 1966).

Patagoniobdella

The family Semiscollecidae Scriban & Auctum, 1934 was emended by Ringuet (1972) to include the genera *Semiscollex* Kingberg, 1867 and *Patagoniobdella* Ringuet, 1972. Currently (Ringuet, 1985b), the genus *Semiscollex* includes five species (*S. intermedius* Ringuet, 1942, *S. juveniles* Kingberg, 1867, *S. notatus* Cordero, 1937, *S. similis* Weyenbergh, 1879, and *S. zonatus* Oka, 1930) and the genus *Patagoniobdella* includes three species (*P. adomonia* Ringuet, 1976, *P. fraterna*, and *P. variabilis*). Ringuet (1972) established the genus *Patagoniobdella* for *Semiscollex variabilis*, which has two pairs of testisacs per interganglionic space and thick

ejaculatory ducts. Otherwise, external morphological characters, digestive track, and reproductive organs are much like in *Semiscollex* species.

Members of Semiscollecidae variously have been classified among the erpobdelliforms or the hirudiniforms (Weyenbergh, 1879; Blanchard, 1896; Ringuet, 1954), but have mostly been associated with the family Haemopidae (Moore, 1911; Ringuet, 1944a, 1944b, 1954; Richardson, 1969; Sawyer, 1986). Blanchard (1896) anticipated that these South American predators were not closely related to other hirudinids and had them in their own subfamily (Semiscollecinae). Ringuet (1954: 5; see also Blanchard, 1896; Moore, 1911; Richardson, 1969) pointed to the apparent "mixture" of characteristics such as "las conspicuas papilas cutaneas y otros detalles mas son como en los Erpobdellidos", but with hirudinid eyes, basically hirudinid anatomy, and a haemopid alimentary tract. Richardson (1969) suggested there were differences in reproductive morphology (i.e., acaecate vagina) in the semiscollecids compared to haemopid leeches, but he still tentatively retained them in the Haemopidae. In the most recent classification, Sawyer (1986) placed the semiscollecids under Haemopidae, but under the subfamily Semiscollecinae, to distinguish the South American genera *Cyclobdella*, *Orchibdella*, *Patagoniobdella*, and *Semiscollex*, from the North American haemopids. On the other hand, Ringuet (1985a, 1985b), in his final contributions, adhered to his earlier classification (Ringuet, 1972). The inclusion of representative semiscollecids, *Semiscollex similis* from Bolivia and the two *Patagoniobdella* species described here, in Borda and Siddall's (2004) phylogenetic analysis has shed some light on their phylogenetic and systematic position within Arhynchobdellida. They appear to share common ancestry with the South American *Oxyptychus* species and North American *Macrobdella* species and not with the haemopids at all. The latter were found in a separate lineage together with the medicinal leeches, typified by the genus *Hirudo* and allies. Therefore, we formally resurrect the family Semiscollecidae as defined by Ringuet (1972).

ACKNOWLEDGMENTS

This work would have been impossible without the generosity and support of our friends in Chile, especially Patricio and Ani Torres as well as Wojt Wodzicki and Kate Gregory- Wodzicki. We thank Rebecca Budinoff, Kirsten Jensen, Louise Crowley, Kenneth Macdonald, and Megan Harrison for their comments on drafts of the manuscript. Several individuals counseled the senior author against naming *Helobdella pichipanan* after a person (e.g., *H. pichipanan*). This work was supported by a Partnerships for Enhancing Expertise in Taxonomy (PEET) Grant from the National Science Foundation (BIO-DEB 0119329) as well as by the Louis and Dorothy Cullman Program in Molecular Systematic Studies and by the Ambrose Mo-nell Foundation.

REFERENCES

- Apakupakul, K., M.E. Siddall, and E.M. Burre-son. 1999. Higher-level relationships of leeches (Annelida: Clitellata: Euhirudinea) based on morphology and gene sequences. *Molecular Phylogenetics and Evolution* 12: 350–359.
- Blanchard, E. 1849. Annelides. In D. C. Gay (ed-itor), *Historia fisica y politica de Chile*. Zoologia, Paris 3: 43–50.
- Blanchard, R. 1892a. Description de la *Glossiphonia tessellata*. *Memoirs de la Société Zool-ogique de France* 5: 56–88.
- Blanchard, R. 1892b. Présence de la *Glossiphonia tessellata* au Chile. *Actes de la Société Sci-entifiques du Chile* 2: 177–187.
- Blanchard, R. 1893. Sur une sangsue terrestre du Chili. *Comptes Rendus des Seances de l'Academie des Sciences* 116: 446–447.
- Blanchard, R. 1896. Viaggio del Dott. A. Borelli nella Republica Argentina e nel Paraguay. 21. Hirudinées. *Bollettino dei Musei di Zoologia ed Anatomia comparata, Universita di Torino* 11: 1–24.
- Blanchard, R. 1900. Hirudineen. In *Hamburger Magalhaensische Sammelreise* 3: 1–20. Ham-burg.
- Blanchard, R. 1917. Monographie des Hémadip-sines (Sangsues terrestres). *Bulletin de la Soci-été de Pathologie Exotique* 10: 640–675.
- Borda E., and M.E. Siddall. 2004. Arhynchobdel-lida (Annelida: Oligochaeta: Hirudinida): phy-logenetic relationships and evolution. *Molecu-lar Phylogenetics and Evolution* 30: 213–225.
- Cabellero, E.H. 1940. Nuevo genero y especie de Hirudíneos perteneciente a la subfamilia Hae-madipsinae. XV. Sobretiro de los Anales del In-stituto de Biología (México) 11: 573–583.
- Cabellero, E.H. 1956. Hirudíneos de México XX: Taxa y nomenclatura de la clase Hirudinea has-ta generos. Sobretiro de los Anales del Instituto de Biología (México) 27: 179–202.
- Cordero, E.H. 1937. Los hirudíneos del Nordeste del Brasil, I. Especies recogidas por Clemente Pereira en 1933 y por el autor en 1935. *Anais da Academia Brasileira de Ciências* 9: 13–26.
- Forbes, S.A. 1890. An American terrestrial leech. *Bulletin Illinois State Laboratory of Natural History* 3: 119–120.
- Grube, A.E. 1871. Beschreibungen einiger Egel-arten. *Archiv für Naturgeschichte* 37: 87–121.
- Harant, H. 1929. Essai sur les Hirudinées. *Ar-chives de la Societe des Sciences Medicales et Biologique de Montpellier* 19: 615–683.
- Harant, H., and P.P. Grassé. 1959. Classe des An-nélides Achètes ou Hirudinées ou Sangsues. In P. P. Grassé (editor), *Traité de Zoologie Masson*, Paris 5:471–593.
- Moore, J.P. 1911. Hirudinea of southern Patagon-ia. *Reports of the Princeton University Expe-dition to Patagonia, 1896–1899* 3: 669–689.
- Moore, J.P. 1924. The anatomy and systematic po-sition of the Chilean terrestrial leech, *Cardea vadiviana* (Phillippi). *Proceedings of the Acad-emy of Natural Sciences of Philadelphia* 76: 29–48.
- Moore, J.P. 1946. Leeches (Hirudinea) from the Hawaiian Islands, and two new species from the Pacific region in the Bishop Museum col-lection. *Occasional Papers Bernice P. Bishop Museum* 18: 171–191.
- Moore, J.P. 1952. Professor A. E. Verrill's fresh-water leeches—a tribute and a critique. *Notulae Naturae (Philadelphia)* 245: 1–15
- Oka, A. 1930. Sur un nouveau genre d'Hirudinées provenant de l'Amérique du Sud. *Proceeding of the Imperial Academy (Tokyo)* 6: 239–242.
- Phillippi, R.A. 1872. *Macrobodella*, ein neues Ges-lecht der Hirudineen. *Zeitschrift für gesam-mten Naturwissenschaften* 2: 439–442.
- Pinto, C. 1923. Ensaio Monographico dos Hiru-dineos. *Revista do Museu Paulista. Sao Paulo* 13: 853–1118.
- Richardson, R.L. 1969. A contribution to the sys-tematics of the hirudinid leeches, with descrip-tion of new families, genera and species. *Acta Zoologica Academiae Scientiarum Hungaricae* 15: 97–149.
- Richardson, R.L. 1971. The relationship of the terrestrial jawed sanguivorous g. *Mesobdella* to the neotropical hirudiniform leeches (Hirudi-noidea). *Proceedings of the Linnean Society of New South Wales* 95: 215–220.
- Richardson, R.L. 1976. On the nature of the gen-

- ital primordial and their role in the development of the reproductive systems in Hirudinea. *Acta Zoologica Academiae Scientiarum Hungaricae* 22(1-2): 155-63.
- Ringuelet, R.A. 1942a. Descripciones preliminares de nuevos hirudíneos Argentinos. *Notas Museo de La Plata* 7: 217-227.
- Ringuelet, R.A. 1942b. Sobre dos hirudíneos del sur de Chile: *Mesobdella gemmata* (E. Bl.) y *Helobdella similis* Ring. *Physis* 19: 364-378.
- Ringuelet, R.A. 1943a. Sobre la morfología y variabilidad de *Helobdella triserialis* (Em. Bl.) (Hirudinea, Glossiphoniidae). *Notas del Museo de La Plata* 8: 215-240.
- Ringuelet, R.A. 1943b. Sobre dos hirudíneos del sur de Chile. *Mesobdella gemmata* (E. Bl.) y *Helobdella similis* Ring. *Physis* 19: 364-378.
- Ringuelet, R.A. 1944a. Sinopsis sistemática y zoogeográfica de los Hirudíneos de la Argentina, Brasil, Chile, Paraguay y Uruguay. *Revista del Museo de La Plata. Sección Zoología* 3: 163-232.
- Ringuelet, R.A. 1944b. Los hirudíneos Argentinos de los géneros *Helobdella* R. Bl., *Batracobdella* Vig., *Cylicobdella* Gr. y *Semiscollex* Kinb. *Revista del Museo de La Plata. Sección Zoología* 4: 5-94.
- Ringuelet, R.A. 1944c. Notas sobre hirudíneos neotropicales. *Hygrobdeella palaезi* Cab. curiosa sanguijuela terrestre Mexicana. *Notas del Museo de La Plata* 74: 167-177.
- Ringuelet, R.A. 1945. Hirudíneos del Museo de la Plata. *Revista del Museo de La Plata. Sección Zoología* 4: 95-137.
- Ringuelet, R.A. 1947. Notas sobre Hirudíneos neotropicales. III: *Theromyzon propinquus* nov. sp. de la Argentina. *Notas del Museo de la Plata, Zoología* 12: 217-222.
- Ringuelet, R.A. 1948. Notas sobre Hirudíneos neotropicales V: Especies de la Republica del Paraguay. *Notas del Museo de La Plata* 13: 213-244.
- Ringuelet, R.A. 1953. Notas sobre Hirudíneos neotropicales VII: Un nuevo Haemadipsido del género *Mesobdella* Blanch. *Notas del Museo de La Plata* 16: 187-193.
- Ringuelet, R.A. 1954. La clasificación de los Hirudíneos. *Notas del Museo de la Plata* 17: 1-15.
- Ringuelet, R.A. 1972. Nuevos taxia de hirudíneos neotropicales con la redefinición de Semiscollecidae y la descripción de Cyclobdellidae fam. nov. y Mesobdellidae fam. nov. *Physis* 31: 193-201.
- Ringuelet, R.A. 1976. Clave para las familias y géneros de sanguijuelas (Hirudinea) de aguas dulces y terrestres de Mesoamérica y Sudamérica. *Limnobiología* 1: 9-19.
- Ringuelet, R.A. 1978. Nuevos géneros y especies de Glossiphoniidae Sudamericanos basados en caracteres ecto y endosomáticos (Hirudinea, Glossiphoniiformes). *Limnobiología* 1: 269-276.
- Ringuelet, R.A. 1982. Nesophilaemonidae Nov. Fam. De Hirudiniiformes Haemadipsoides. *Neotropica* 28: 3-6.
- Ringuelet, R.A. 1985a. Sinopsis de los hirudíneos de Chile (Annelida). *Boletín de la Sociedad de Biología de Concepción* 56: 163-179.
- Ringuelet, R.A. 1985b. Fauna de agua dulce de la Republica Argentina, Volumen XVII Annelata, Fascículo 1 Hirudinea. Buenos Aires: Fundación para la Educación, la Ciencia y la Cultura, 321 pp.
- Sawyer, R.T. 1986. *Leech biology and behavior*. Oxford: Clarendon Press, 1065 pp.
- Siddall, M.E. 2001a. Leeches of Laguna Volcán, Bolivia, including a new species of *Helobdella* (Clitellata: Hirudinea). *American Museum Novitates* 3313: 1-11.
- Siddall, M.E. 2001b. Hirudinea from the Apolobamba in the Bolivian Andes, including new species of *Helobdella* (Clitellata: Hirudinea). *American Museum Novitates* 3341: 1-14.
- Siddall, M.E., and E. Borda. 2003. Phylogeny and revision of the leech genus *Helobdella* (Glossiphoniidae) based on mitochondrial gene sequences and morphological data and a special consideration of the *triserialis* complex. *Zoologica Scripta* 32: 23-33.
- Siddall, M.E., and E.M. Burreson. 1995. Phylogeny of the Euhirudinea: independent evolution of blood feeding by leeches? *Canadian Journal of Zoology* 73: 1048-1064.
- Siddall, M.E., and E.M. Burreson. 1996. Leeches (Oligochaeta?: Euhirudinea), their phylogeny and the evolution of life history strategies. *Hydrobiologia* 334: 277-285.
- Soós, Á. 1966. Identification key to the leech (Hirudinoidea) genera of the world, with a catalogue of the species. II. Family: Semiscollecidae, Trematobdellidae, Americobdellidae, Diestecostomatidae. *Hirudinea. Acta zoologica Academiae Scientiarum Hungaricae* 12: 145-160.
- Trontelj, P., B. Sket, and G. Steinbrück. 1999. Molecular phylogeny of leeches: congruence of nuclear and mitochondrial rDNA data sets and the origin of bloodsucking. *Journal of Zoological Systematics and Evolutionary Research* 37: 141-147.
- Weber, M. 1915. *Monographie des hirudíneos Sud-Americanas*. Thèse por Docteur ès-Sciences, Université de Neuchâtel, Neuchâtel, France.
- Weyenberg, H. 1879. Algunas sanguijuelas o chancacas de la familia Gnathobdellidae y revista de esta familia. *Boletín de la Academia Nacional de Ciencias (Córdoba)* 3: 231-244.

Recent issues of the *Novitates* may be purchased from the Museum. Lists of back issues of the *Novitates* and *Bulletin* published during the last five years are available at World Wide Web site <http://library.amnh.org>. Or address mail orders to: American Museum of Natural History Library, Central Park West at 79th St., New York, NY 10024. TEL: (212) 769-5545. FAX: (212) 769-5009. E-MAIL: scipubs@amnh.org

Ⓢ This paper meets the requirements of ANSI/NISO Z39.48-1992 (Permanence of Paper).

