

# SOUTHERN HEMISPHERE *SYMBIOCLADIUS* (DIPTERA, CHIRONOMIDAE) AND THEIR MAYFLY HOSTS (EPHEMEROPTERA, LEPTOPHLEBIIDAE)

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In this study, all associations known from the southern hemisphere of *Symbiocladius* KIEFFER, 1925 (Diptera, Chironomidae, Orthoclaadiinae) with their mayfly (Ephemeroptera, Leptophlebiidae) hosts are reviewed. All life stages of the new species *Symbiocladius renatae* from southern Chile are described. Keys to all species of *Symbiocladius* from the southern hemisphere are given. Biogeographic distributions and phylogenetic relationships are discussed. The population dynamics of *Symbiocladius renatae* sp. nov. and its host *Meridialaris diguillina* (DEMOULIN) are given for a 2-year period at the type locality, the Estero Pirén in southern Chile.

## *SYMBIOCLADIUS* / EPHEMEROPTERAN ASSOCIATIONS

The discovery of *Symbiocladius renatae* sp. nov. brings to three the number of *Symbiocladius* species known from the southern hemisphere. A second South American species, *S. wygodzinskyi* ROBACK, 1965, was the first member of the genus described outside of the Holarctic. The third austral form is *S. aurifodinae* HYNES, 1976 from Australia. The three recognized *Symbiocladius* species in the northern hemisphere, the North American *S. chatahoocheensis* CALDWELL and *S. equitans* (CLAASSEN), and the Palaearctic *S. rhithrogenae* (ZAVREL), are currently considered to represent a different subgenus from their southern congeners.

Fig. 1 summarizes the known records of South American *Symbiocladius* species against the combined distributional area of their confirmed Leptophlebiid hosts (PESCADOR & PETERS, 1987, also recorded *Massartellopsis irrarrazavali* - but no *Symbiocladius* - from a few high Andean sites in Bolivia). Included are only those collections verified to species by the junior author. PESCADOR & PETERS (1987) report a number of additional findings from several localities in central to south-central Chile, including occurrences of *Symbiocladius* on *Meridialaris laminata* (ULMER) from Nuble province (Region XIII), but these samples were not available for the present study.

Table 1 lists the specific records in southeastward geographical order of their localities. For further information on individual sites see the sections on «Material» and «Ecology» below, and - where applicable (Table 1) - CAMPOS *et al.* (1984).

South American *Symbiocladius* are found over most of the area inhabited by their mayfly hosts (Fig. 1). Although the two parasite species may inhabit watersheds in close geographical proximity (e.g. Table 1: locality numbers 8 & 9, or 18 & 21), they apparently do not occur

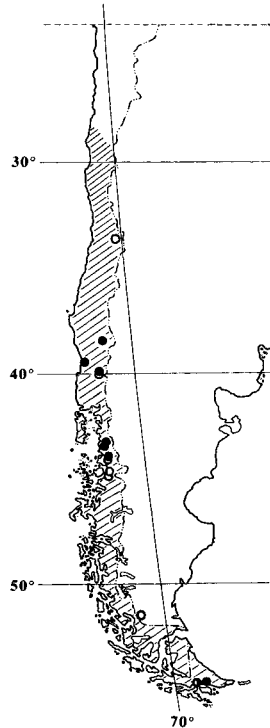
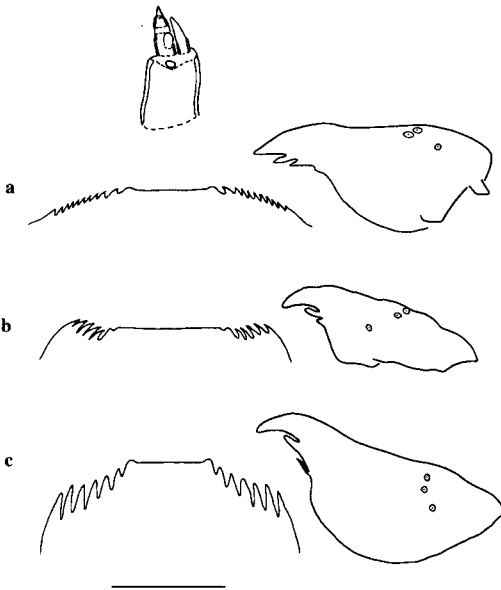


Fig. 1. Verified distributions of South American *Symbiocladius* species and their hosts. Hatched area: all Leptophlebiid hosts combined (after PESCADOR & PETERS, 1987); Closed circles: *S. renatae* sp. nov.; Open circles: *S. wygodzinskyi* ROBACK.

sympatrically in the strictest sense. ROBACK'S (1965) type material of *S. wygodzinskyi* contains specimens of *renatae* sp. nov. as well. However, since the two species in Roback's material generally separate according to different collection sites, the one exception of locality nrs. 19 & 20 (Table 1) is highly likely the result of a poorly labelled, composite sample («20-28 January»).

It is not known, what factors govern the survival of either species at any particular site, the outcome of possible habitat competition, or - for that matter - host preference where more than one potential host species is present. For example, among the many specimens of *S. renatae* sp. nov. from the Estero Pirén system (loc. nrs. 3-6), the authors have seen only a very few early instar larvae on nymphs of *Meridialaris chiloeense*, although the latter is usually even more abundant than the preferred host, *M. diguillina* (see section «Ecology», and GONSER, 1990). On the other hand, *M. chiloeense* appears to be the exclusive host at temperate rainforest and more southern sites, even though both other confirmed hosts are common there as well (PESCADOR & PETERS, 1987).



**Fig. 2.** Larval structures of austral *Symbiocladius* species. a: *S. renatae* sp. nov., antenna, edges of mentum, and mandible; b: *S. aurifodinae* HYNES, edges of mentum, and mandible; c: *S. wygodzinskyi* ROBACK, edges of mentum, mandible. Scale: 25 µm.

In Australia, *S. aurifodinae* HYNES is known only from associations with nymphs of an unnamed species, *Austrophlebioides* (sensu CAMPBELL & SUTER, 1988) sp. «A3», a formal description of which is in press (I. Campbell, pers. comm.). Other species of *Austrophlebioides* are apparently not affected, nor are the representatives of further potential host genera in the *Meridialaris* lineage (R. Marchant, S. Schreiber, pers. comms.).

While nymphs of *Austrophlebioides* can be found in a much more extensive region along the eastern/southeastern Australian mainland, as well as on Tasmania (PETERS & CAMPBELL, 1991), *S. aurifodinae* as yet has been recorded only from rivers and streams associated with the foothills and mountains in an area stretching roughly from Melbourne to west of Canberra (HYNES, 1976; L. Brundin, P. Cranston, T. Soldán, unpubl. records). Thus, *S. aurifodinae* appears to be distinctly restricted, both in host spectrum and geographic distribution, when compared to the two South American *Symbiocladius* species.

By contrast, two of the northern hemisphere *Symbiocladius* species, *Symbiocladius rhithrogenae* (ZAVREL) and *Symbiocladius equitans* (CLASSEN) are each recorded from both a vastly more expansive distributional area, and a considerably larger set of potential host species (SOLDÁN, 1978; JACOBSEN, 1995; TOKESHI, 1995).

*Symbiocladius renatae* SPIES, sp. nov.  
(Figs 2a, 3a-b, 4, 5a, c)

*Symbiocladius wygodzinskyi* ROBACK, 1965: 115. (partim)

*Etymology.* The species name has been chosen to honour the immense contributions of Mrs. Renate Gonsler, whose unfailing support and active assistance added indispensable quality and meaning to this study.

*Larva (4th instar)*

*Size.* At pupation ca. 4-6 mm long.

*Colour* (in alcohol). Head mostly light to medium brown, dorsal aspect with four whitish longitudinal stripes due to sutures along frontoclypeal apotome and narrow unpigmented strips from behind antennae to posterior; mouthparts (esp. mandibles) and antennae surrounded by darker sclerotization; postoccipital margin dark brown. Body usually mostly brown, in prepupal specimens (esp. thorax) often with blueish tinges and extensive unpigmented regions from internal tissue development; anterior and posterior parapod claws brown to dark brown.

*Head.* Maximum height (at posterior end of head capsule) much greater than length, the latter especially short ventrally (from anterior edge of mentum to postoccipital margin).

Table 1. Localities of verified records for South American *Symbiocladius* species.

Loc. Nr.	Country	Region	Province	Source	Site	Host	Symbiocladius
1	Chile	Metrop.	Santiago	«estero cordillera» <sup>1</sup>	«Los Maitenes, 1500m asl» <sup>1</sup>	<i>Mass. irrazavali</i> (DEM.)	wygodzinskiyi ROB.
2		IX	Malleco	Rio Cautín	5 km S of Curacautín	<i>Mer. diguillina</i> (DEM.)	<i>renatae</i> n. sp.
3			Cautín	arroyo to Rio Pirén	7 km above Rio Queule	<i>Mer. diguillina</i> (DEM.)	<i>renatae</i> n. sp.
4				Rio Pirén	7 km above Rio Queule	<i>Mer. diguillina</i> (DEM.), <i>Mer. sp.?</i>	<i>renatae</i> n. sp.
5				Rio Pirén	4 km above Rio Queule	<i>Mer. diguillina</i> (DEM.)	<i>renatae</i> n. sp.
6				Rio Pirén	near confl. to Rio Queule	<i>Mer. diguillina</i> (DEM.)	<i>renatae</i> n. sp.
7		X	Valdivia	Rio Chan-Chan	at confl. to Lago Neltume	<i>Mer. diguillina</i> (DEM.)	<i>renatae</i> n. sp.
8				Rio Blanco («B»)	near confl. to Rio Enco	<i>Mer. chiloeense</i> (DEM.)	<i>renatae</i> n. sp.
9				Rio Blanco («A»)	near confl. to Rio Currinque	<i>Mer. chiloeense</i> (DEM.)	wygodzinskiyi ROB.
10			Palena	arroyo to Lago Yelcho	2 km E of La Cabana	? (drift sample)	<i>renatae</i> n. sp.
11				Rio Frio <sup>2</sup>	10 km N of Rio Palena <sup>2</sup>	<i>Mer. chiloeense</i> (DEM.)	<i>renatae</i> n. sp.
12		XI	Aisén	Rio Aura <sup>2</sup>	near confl. to Rio Palena <sup>2</sup>	<i>Mer. chiloeense</i> (DEM.)	<i>renatae</i> n. sp.
13				Rio Los Cesares <sup>2</sup>	5 km N of Lago Risopatrón <sup>2</sup>	<i>Mer. chiloeense</i> (DEM.)	wygodzinskiyi ROB.
14				Rio Queulat <sup>2</sup>	10 km SE of Canal Puyuguapi <sup>2</sup>	<i>Mer. chiloeense</i> (DEM.)	wygodzinskiyi ROB.
15				Rio Cisnes <sup>2</sup>	15 km NE of Puerto Cisnes <sup>2</sup>	<i>Mer. chiloeense</i> (DEM.)	wygodzinskiyi ROB.
16		XII	Magallanes	«Chorillo de la Piedra» <sup>1</sup>	?	<i>Mer. chiloeense</i> (DEM.)	wygodzinskiyi ROB.
17	Argentina	-	Santa Cruz	«Rio Turbitio» <sup>3</sup>	?	<i>Mer. chiloeense</i> (DEM.)	wygodzinskiyi ROB.
18		-	T. del Fuego	«Rio Tristen» <sup>3</sup>	«Ushuaia» <sup>3</sup>	<i>Mer. chiloeense</i> (DEM.)	wygodzinskiyi ROB.
19		-	T. del Fuego	?	«Ushuaia» <sup>3</sup>	<i>Mer. chiloeense</i> (DEM.)	wygodzinskiyi ROB.
20		-	T. del Fuego	?	«Ushuaia» <sup>3</sup>	<i>Mer. chiloeense</i> (DEM.)	<i>renatae</i> n. sp.
21		-	T. del Fuego	Rio Tierra Mayor	at road to Puerto Harberton	<i>Mer. chiloeense</i> (DEM.)	<i>renatae</i> n. sp.

References: <sup>1</sup>PESCADOR & PETERS (1987); <sup>2</sup>CAMPOS *et al.* (1984); <sup>3</sup>ROBACK (1965)

Eyespots strongly reduced to absent. Frontoclypeal apotome with slender midsection, both end regions widened, but strongly narrowing toward apices; posterior end of apotome not reaching as far posterior as separate ends of dorso-lateral parts of head capsule; 3 pairs of setae anteriorly (near mandibles and antennae), 1 pair near mid apotome, and further posterior 1 pair on or just lateral of frontoclypeal sutures. Each side of labrum with a row of 2 short (max. 10  $\mu$ m), simple setae (SI, SII?), a slender peg or spine (up to 5  $\mu$ m), and a posterior, narrow blade (max. 12  $\mu$ m long). Pecten epipharyngis of 3-5 apically combed hooks, and 3-4 further ventral, slightly larger, hooked brushes each bearing 2 apical rows of comb teeth; ungula present; premandibles absent. Antenna (Fig. 2a) 4-segmented; AR on male larvae 1.5-2.0 (M=1.7; n=5), on female specimens 1.25-1.75 (M=1.4; n=5); segment 1 with 1-2 annular to short peg-like structures on margin of apical surface, ring organ not evident; segment 2 proximally with a pair of short bulbs on opposite sides (Lauterborn organs?); blade basally sclerotized, about as long as segment 2. Mandible (Fig. 2a) with pointed apical, and 2 inner teeth, the latter similar in size and shape; seta subdentalis and seta interna absent; ventro-lateral surface with 3 setae, each arising in a circular unpigmented area. Maxilla with palp and lacinia each reduced to a small, circular area partially enclosed by narrow sclerotization, and each with several very short, peg-like structures. Mentum (Fig. 2a) U-shaped, with a transverse antero-medial edge (20-30  $\mu$ m wide), and obliquely longitudinal rows of 8-10 lateral teeth each; first lateral teeth slightly larger than others, and often

less acute, the adjacent ends of the median edge sometimes slightly set off and anteriorly produced relative to remaining edge; the antero-ventral mentum corners often show structures resembling narrow ventromental plates. 1 pair of setae submenti present; ventro-lateral of mandible 2 closely set setae, further lateral and dorsal 3 setae in a widely spaced triangle. Postoccipital margin ventrally with pair of strong projections.

**Body.** Anterior parapods mostly fused; claws in extensive, medially contiguous, transverse patch; claw size increasing from very short spinules anteriorly and medially to large, apically combed hooks postero-laterally. Body segments each with several short (up to 15  $\mu$ m) setae spread around all sides. Procerci, anal, and supraanal setae absent. Anal tubules may exist in form of a pair of very low, bulbous protrusions sometimes visible dorsal of posterior parapods. Posterior parapods short, separate, in postero-terminal position, basally each with 3 short setae; claws of each parapod in an elongate, weakly curved patch roughly parallel to longitudinal body axis, each patch consists of an irregular, single row of ca. 20 large, low, long-tipped hooks - often with a few small comb teeth on inner contour - embedded in small points and hooklets mostly (esp. medially) grouped in short rows.

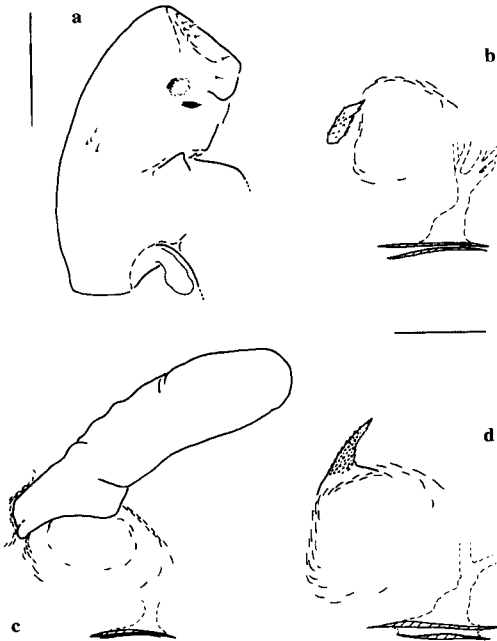
### Pupa

**Size.** Pupae ca. 3-5.5 mm long; Wing sheath lengths of exuviae (measured from sclerotized anterior wing root to tip) ranging for male specimens from 1.4-1.6 mm (locality nr. 4; see Table 1) to 1.8 mm (loc. nr. 10), for female exuviae from 1.5-1.7 mm (loc. nr. 4) to 2.3 mm (loc. nr. 21).

**Colour** (in alcohol). Depending on degree of adult development, ranging between prepupal coloration (with blueish and weakly pigmented areas) to near adult coloration. In later pupal stages, head, thorax, and wing pads brown, abdomen lighter with inhomogeneous tergal pigment; Exuviae also variable: in early pharate specimens with pigment limited to light brown cephalo-thorax areas, and narrow anterior and lateral borders of abdominal tergites; exuviae from drift uniformly brown; abdomen always with conspicuous submedian adhesion marks (2 pairs dorsally, 1 pair ventrally).

**Head.** Frontal warts, cephalic tubercles, frontal and post-orbital setae absent. Pedicel sheath without median spur or projection, with weak apical pearl row (strongly reduced to absent on female specimens). Prefrons between eyes on midline with 1 or more small, blunt to subacute, irregularly sclerotized ridges or tubercles. Clypeo-labrum with conspicuous darker pigment.

**Thorax** (Fig. 3a). Antepronotum on each side with 1-2 low dorsal tubercles similar to those on prefrons, and with 3-6 fine dorsal to median setae, plus 0-2 setae in far ventral and sometimes relatively posterior positions (Fig. 3a); max. seta length ca. 30  $\mu$ m. Suture area with very little granulation. Precorneal setae absent. Thoracic horn (Fig. 3b) situated immediately dorsal of a large, roundish humeral mound; thoracic horn sclerotized, with numerous surface denticles and serrations, horn mostly straight and of even circumference, but with a short, acute apex bending over humeral mound at a shallow angle to horn stem; thoracic horn length 40-70  $\mu$ m. Anterior tracheae of each thorax side uniting to a short common stem reaching integument just posterior to humeral mound (Fig. 3b); tracheal opening reinforced with



**Fig. 3.** Pupal structures of austral *Symbiocladius* species. a, b: *S. renatae* sp. nov.; c: *S. aurifodinae* HYNES; d: *S. wygodzinskyi* ROBACK; a: Thorax, lateral view (wing pad partially omitted); b-d: Thoracic horn, humeral mound, and terminus of tracheal stem. Scales: a 500  $\mu$ m; b-d 50  $\mu$ m.

pair of parallel sclerotized bars. 4 dorsocentral setae near suture, due dorsal from sclerotized wing root (Fig. 3a); three very reduced, the fourth max. 40  $\mu\text{m}$  long, fine; the latter usually positioned furthest from the posterior, but occasionally located ventral of, and between Dc<sub>2</sub> and Dc<sub>3</sub>. Prealar tubercles or setae absent. Wing sheath tip without nose or pearl row. Fore and mid leg sheaths with the tarsi simply curved along wing sheath tip; hind tarsal sheaths folded twice, their apices pointing in direction opposite to those of other legs.

**Abdomen.** Strongly narrowing toward posterior, median width of segment VIII 35-45% of segment II width. Armament consisting of minute to small points exclusively, the latter usually grouped in loose to linked rows of several points each; pattern somewhat variable, may be partially reduced, maximum expression as follows: Tergum I (TI) with pair of antero-lateral patches next to median recess of segment contour; TII with postero-lateral patches (points directed to anterior), and very weak rudiments in antero-lateral tergite corners; TIII-VII with anterior transverse bands reaching onto paratergites, and with extensive postero-lateral patches sending narrower bands to median (the latter bands medially interrupted on TIII-IV, fused on TV-VII); posterior usually slightly larger than anterior points, orientation of posterior points turning from direction to anterior in the lateral patches to posterior direction medially; TVIII with anterior and posterior transverse bands, with postero-lateral patches of anteriorly directed points, posterior band medially interrupted on female specimens; TIX with small central patch. Conjunctives bare. Sterna (St) I-VII with postero-lateral patches, and StII-VII with median extensions of these patches analog to but thicker than in above tergal pattern; StI with rudimentary antero-lateral patches; StII with antero-medial patch; StIII with a large triangular patch of weak shagreen extending from along anterior sternite margin to the posterior bands; on subsequent sterna the latter pattern is progressively modified by reduction of the postero-medial extent, but development of lateral arms of the anterior shagreen band, eventually reaching the postero-lateral patches on StVII+VIII; StVIII like TVIII with a posterior band of points exclusively directed to posterior, medially widely interrupted on female pupae; StIX bare. Dorsal setae (numbers for one segment side each) TI-VII: 5; TVIII: 1 anterior, 1-2 postero-medial, and 0-1 postero-lateral; TIX: 3, incl. 1 in postero-lateral position. Lateral setae all very short, segmt. I: 1 dorsal; II-VII: 1 each dorsal and ventral, near mid segment, often very close to folded pleura; VIII: 1 each dorsal and ventral, in posterior position. Ventral setae StI-VIII: 5; StIX: 0. 1 O-seta each present on paratergites (pT) II-VII, near median pT margin on II, further lateral on subsequent segments. Pedes spurii B (PsB), and discrete PsA absent. Female StVIII postero-medially with conspicuous unpigmented lobes accommodating adult gonapophyses VIII; female StIX distinctly shorter than TIX. Anal lobes present on male specimens only, as a pair of short, unpigmented, medially separate lobes posterior to TIX, each with 2 short (8-10  $\mu\text{m}$ ) but sturdy setae postero-medially. Male genital sheaths pigmented, ca. 3 times as long as TIX. Female genital sheaths unpigmented.

### Male imago

**Colour (in alcohol).** Rather uniformly brown to dark brown, dorsal regions of head, pedicels, and apical

abdominal segment darkest, thoracic vittae not distinct, abdominal segments I-VIII slightly lighter, terga II-VII with faintly darker median and lateral longitudinal stripes.

**Head.** Temporal setae absent, 2 pairs of very short setae on coronal triangle. Frontal tubercles absent. Antenna with 13 flagellomeres (fl), fl<sub>2</sub> shortest, fl<sub>1</sub> length slowly increasing toward fl<sub>12</sub>, AR = 0.75-0.79 (n=5); tips of long plume setae not overreaching antennal apex, fl<sub>13</sub> distally with short setae only, sensilla chaetica absent; groove present from fl<sub>4</sub>-13. Eyes without dorso-medial extension; eye setae length up to ca. twice facet height. Tentorium nearly straight, without any distinct widening or projection. Cibarial pump elongate rectangular, cornua little projecting (comp. Fig. 5c). Originating between antero-lateral corner of cibarial pump and torma on each side a narrowly triangular sclerite with serrate antero-medial margin (mandible?); further distal, another, more digitiform sclerite (lacinia?). Clypeus bare, much wider than long. Palp (Fig. 5c) with one elongate (140-180  $\mu\text{m}$ ), mostly unpigmented but apically darkened free palpomere; setose, other sensory structures not evident.

**Thorax.** Strongly produced anteriorly, head in relatively ventral rather than anterior position. Anteprenotal lobes widest laterally, very narrowly meeting; 6-12 dorsal to median setae, lateral anteprenotals rarely present (max. 1 each). Postpronotum anterior of spiracle with 0-3 setae; 25-40 dorsocentral setae in bi- to multi-serial strip from posterior humeral region almost to scutellum; 2-6 prealar setae usually in a fairly widely spread cluster; posterior anepisternum II with 3-6 dorsal to median setae; acrostichal, supraalar and scutellar setae absent. All thoracic setae short (max. 30-40  $\mu\text{m}$ ). Remnants of humeral pit outlined by slightly stronger microtrichiae. Scutal tubercle absent. Postnotum with median furrow, except anteriorly.

Wing (no unfolded specimen available). Membrane macrotrichia absent. Squama with 16-30 setae in partially double row.

Legs (no fully hardened specimen available; n=6). Tibial spurs, tibial combs, elongate beard, and sensilla chaetica absent. Fore leg with relatively shortest femur, longest tibia (fe<sub>2</sub> > fe<sub>3</sub> > fe<sub>2</sub>; ti<sub>1</sub> > ti<sub>3</sub> > ti<sub>2</sub>). LR1 ca. 0.47-0.50; LR2 ca. 0.42-0.45; LR3 ca. 0.44-0.47. Fourth tarsal segment (ta<sub>4</sub>) always longer than ta<sub>5</sub>. Claw with 2-3 long, seta-like spines at base, apically cupped with a series of fine comb teeth around the tip. Empodium coarsely feathered, curving to about mid claw.

**Abdomen.** Segments II-VIII with tergal setae limited to a pair of sublateral groups of 5-12 setae each on TII, progressively fewer on subsequent segments.

Hypopygium (Fig. 4). Anal tergite bands and anal point absent. TIX with extensive, postero-medial field of 20-45 short (ca. 20  $\mu\text{m}$ ) setae. Laterosternite IX indistinct. Proctiger microtrichiose, with deep postero-medial emargination. Transverse sternapodeme (Fig. 4a) evenly arched, without anterior projections; phallapodeme with 2 major bends against horizontal plane, distinctly widened over posterior two thirds of length. Virga absent. Pars ventralis present as a low, microtrichiose ridge along vertical surface between gonocoxites (Figs 4b, c), running from a narrow, undelimited ventral origin to a point at its dorsal end. Gonocoxite densely setose; with a large, round, median lobe marginally free of microtrichiae, but ventrally

bearing several setae; ventral of the distal end of the large lobe with another small (often indistinct) lobe; medio-basally, adjacent to pars ventralis, with a sometimes slightly elevated patch of microtrichiae each arising from a shallow pit (Fig. 4c). Gonostylus of about even circumference throughout, little curved; apex with low, lamellar rim, and shallow median bowl harboring 1-2 straight setae similar to other stylus setae (Figs 4a, c); megasetae and crista dorsalis absent.

*Female imago* (identical to male except as follows)

*Head* (Fig. 5c). Antenna with 6 very sparsely setose flagellomeres (fl), fl2 shortest; AR=0.47-0.71 (n=5); scapus usually with 1-2 + 1 ventral and median setae, respectively.

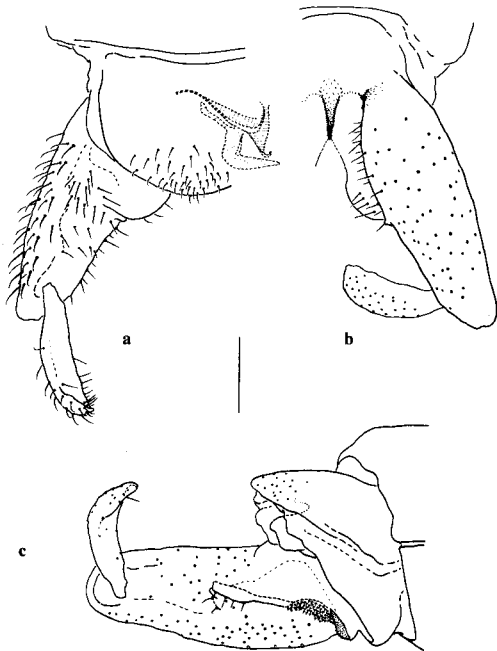
*Thorax*. Each side with 4-10 dorsal to median, 0-1 lateral antepronotal setae; 0-2 postpronotals; 25-35 dorsocentrals; 2-12 prealars; 0-3 setae on posterior anepisternum II. Wing (no unfolded specimen available). Squama with 14-40 setae.

*Legs* (no fully hardened specimen available; n=5). LR1 ca. 0.42-0.45; LR2 ca. 0.37-0.40; LR3 ca. 0.42-0.45. Fourth tarsal segment (ta4) always shorter than ta2. Claw apically simple, pointed.

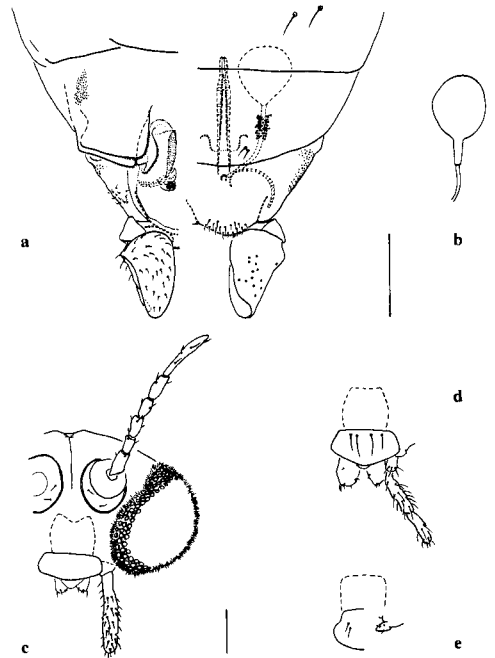
*Abdomen*. Terga II-VIII with pair of sublateral groups of 10-28 setae each on TII, progressively fewer on subsequent segments.

*Genitalia* (Fig. 5a). Tergite (T) VIII with 2-3 pairs of setae scattered posteriorly. Sternite (St) VIII without setae, but with pair of antero-lateral fields of surface granulation. Vaginal area relatively wide (ca. 1/3 of posterior StVIII

width), delimited on each side by a roundedly right-angled ventral corner, and a more dorsal one projecting slightly further to posterior; its lateral walls excavated under a ventral ledge of StVIII, its roof on a strong incline from antero-ventral to postero-dorsal. Gonapophyses VIII of each body side originating from a common base forming a ventral ridge parallel to posterior walls of vaginal area; ventrolateral lobe large, curving to far dorsal and anterior; dorsomesal lobe extending to dorsal of spermathecal eminence, where it ends in a membranous lobe containing an apodeme curving to medio-oral; membrane present as a wide, U-shaped sclerite with curved ends (Fig. 5a, right). Apodeme lobe (?) a narrow sclerite lateral of distal end of dorsomesal lobe. Labia with apico-ventral microtrichia. Notum shorter than seminal capsule length, and shorter than rami. Seminal capsule 140-180 µm long x 125-160 µm wide, sclerotized; spermathecal ducts (Fig. 5a, right) almost straight, basally lined with «special secretory cells» (SAETHER, 1980). Coxosternapodemes with median ends separate, curving to posterior. Gonocoxite IX with antero-lateral to ventral surface granulation, and with 7-13 mostly postero-ventral setae; dorso-median edge delineated by an apodeme (Fig. 5a, right), but fused to TIX. TIX with 15-24 setae, mostly along posterior margin. Segment X with macrotrichiae only, without projecting postgenital plate. Cerci large, antero-ventral projection short and wide, outer cercal surfaces with evenly spread setae of about equal length (up to 40 µm).



**Fig. 4.** Adult male hypopygium of *Symbiocladius renatae* spec. nov.; a: Dorsal; b: Ventral; c: Lateral view, left gonocoxite and gonostylus removed. Scale: 100 µm.



**Fig. 5.** Adult female structures of austral *Symbiocladius* species. a, c: *S. renatae* spec. nov.; b, d: *S. wygodzinskyi* ROBACK; e: *S. aurifodinae* HYNES. a: Genitalia (left: ventral, right: dorsal aspect); b: Seminal capsule and spermathecal duct; c: Head, frontal view; d-e: cibarial pump, clypeus, and labial palp. Scales: a-b 200 µm; c-e 100 µm.

*Taxonomic remarks*

A practical character for separating still attached pupae of *S. renatae* sp. nov. and *wygodzinskyi* ROBACK exists in the position of the larval exuvial head capsule relative to the pupal abdomen. While in the new species the larval head capsule was invariably found tucked under the host's fore wing pad, and adjacent to abdominal segments V/VI of the pupa, the head capsules of *S. wygodzinskyi* larvae are always found in more posterior positions on the host, next to pupal segments III/IV.

Although a large part of ROBACK's (1965) type series of *S. wygodzinskyi* is here transferred to *renatae* sp. nov. (see below under «Paratypes»), his simultaneous descriptions of *wygodzinskyi* are not affected, since the respective individual specimens Roback's morphologies are based upon are true *S. wygodzinskyi*.

*Material* (compare Table 1)

Types (unless otherwise specified: leg. T. Gonsler (TG); slide-mounted in Euparal; host nymph of *Meridialaris diguillina* (Demoulin) in alcohol; at Zoologische Staatssammlung (ZSM), Munich, Germany).

Holotype: associated larval exuviae (Lex), pupal exuviae (Pex), pharate male (phM); Chile, Region IX, Prov. Cautín, Arroyo to Estero Pirén ca. 7 km above confl. with Rio Queule, from female nymph (fN), leg. T. Gonsler; 19/X/1985; deposited (along with host) at ZSM.

Allotype: assoc. Lex, Pex, phar. female (phF); Chile, Reg. X, Prov. Valdivia, Rio Chan-Chan at confluence to Lago Neltume, from fN, 27/II/1984, leg. T. Gonsler; at ZSM (incl. host).

Paratypes: Locality nr. 3 (holotype locality) - 2 L, 1 Lex, Pex, phM, 24/III/1985; - 2 L, 28/IV/1985; - 1 L from fN, 1 Lex, Pex, phM from fN, 4/II/1986, in coll. T. Gonsler (TG). Loc. nr. 4 - 1 Lex, Pex, phM, 24/IV/1984; - 1 Lex, Pex, phF, 25/V/1984; - 1 Lex, Pex, phF from fN, 7/XII/1984; - 1 Lex, Pex, phM, 22/II/1985, in coll. TG; - 1 L from fN, 1 L from fN of *Meridialaris* sp.? (partially slide-mounted), 24/III/1985; - 1 L from fN of *Meridialaris* sp.?, 14/IX/1985; - 1 L from fN, 15/IV/1986. Loc. nr. 5 - 1 L from fN, 18/XII/1985; 1 Lex, Pex, phF from fN, 14/IV/1986, in coll. TG. Loc. nr. 8 - 1 Lex, Pex, phM on mN of *Meridialaris chiloeense* (DEM.), 2/III/1984; NOTE: 2 slides (Lex, adult abdomen mounted separately). Loc. nr. 10 - 2 male Pex, 1 adult male drowned during emergence, 25/II/1986, leg. M. Spies. Loc. nr. 11 - 3 L from 1 fN each of *Meridialaris chiloeense* (DEM.), 15/III/1984. Loc. nr. 12 - Lex (of phM in Pex; see under 'Further records') from fN of *Mer. chiloeense* (DEM.), 15/III/1984. Loc. nr. 20 (published type locality of *S. wygodzinskyi* ROBACK (1965: 116, 118): «Ushuaia», 20-28/II/1960, leg. P. Wygodzinsky; all from 1 fN each of *Mer. chiloeense* (DEM.) - 1 Lex, Pex, phF, slide-mounted in Euparal, at American Museum of Natural History, New York (AMNH); 1 Lex, Pex, phF, slide-mounted (host N incl.) in Hoyer's medium, at Academy of Natural Sciences, Philadelphia (ANSP); 1 Lex, Pex, phM, in alcohol, at AMNH. Loc. nr. 21 (4 km E of road «Ruta 3» to Ushuaia) - 1 Lex, Pex, phF from fN of *Mer. chiloeense* (DEM.), 15/II/1986, in coll. TG.

Further verified records (unless otherwise specified: leg. T. Gonsler; in alcohol, in coll. TG): Locality nr. 2 - 1 Lex, Pex, phF from fN, 19/IV/1984. Loc. nr. 3 (holotype locality) - 1 Lex on fN, 25/IV/1984; - 2 L, 1 Lex, Pex, phF, 24/III/1985; - 3 L, 1 Lex, Pex, phF, 1 Lex, Pex, phM, 1 Lex on fN, 1 Lex, Pex, phM on fN, 28/IV/1985; - 1 L from fN, 1 Lex, Pex, phF from mN, 1 Lex, Pex, phM from fN, 19/X/1985 (holotype sample). Loc. nr. 4 - from 1 fN each: 6 L, 1 Lex, 1 Lex, Pex, phF, 1 Lex, Pex, phM, and 1 Lex, Pex, phM from mN, 24/IV/1984, at ZSM; - 2 Lex, Pex, phF from 2 fN, 25/IV/1984, at ZSM; - 1 Lex, Pex, phF from mN, 7/XII/1984; - 2 L, 1 Lex, Pex, phM, 22/II/1985; - 1 Lex, Pex, phF on mN, 24/III/1985; - 1 Lex, Pex, phM, 28/IV/1985; - 1 L on fN, 1 Lex, Pex, phM on fN, 1 Lex, Pex, phM on mN, 18/XII/1985; - 1 L, 6/III/1986; - 2 L, 1 Lex, Pex, phF on mN, 1 Lex, Pex, phM on fN, 14/IV/1986; - 1 L on fN, 1 Lex, Pex, phF on fN, 1 Lex, Pex, phF on mN, 15/IV/1986, at ZSM. Loc. nr. 5 - 2 L, 1 Lex, 1 female P, 1 Lex, male P on fN, 1 Lex, Pex, phM, on mN, 23/III/1985; - 1 L on fN, 19/XI/1985; - from 1 fN each: 5 L, 1 Lex, Pex, phM, and 1 L, 1 Lex, Pex, phF, on 1 mN each, 18/XII/1985; - 1 Lex, Pex, phM on mN, 14/IV/1986. Loc. nr. 6 - 1 L on mN, 25/IV/1984. Loc. nr. 7 (allotype locality) - 1 Lex, Pex, phF on fN, 27/II/1984. Loc. nr. 8 - 1 L on fN of *Meridialaris chiloeense* (DEM.), 2/III/1984. Loc. nr. 11 - on 1 fN of *Mer. chiloeense* (DEM.) each: 1 empty shroud, 9 L, 1 Lex, Pex, phM, 15/III/1984. Loc. nr. 12 - 1 phM in Pex on fN of *Mer. chiloeense* (DEM.), 15/III/1984. Loc. nr. 21 (4 km E of road «Ruta 3» to Ushuaia) - 1 L from fN of *Mer. chiloeense* (DEM.), 15/II/1986.

*Differential diagnosis*

The high number of lateral teeth on the larval mentum, the presence of a pupal thoracic horn, and the microtrichiose eyes of the adults suffice to separate the new species from all known northern hemisphere congeners. Among the three described southern hemisphere species in the genus, *Symbiocladius renatae* sp. nov. is distinguished by the characters given in the keys below.

KEYS TO THE SPECIES OF *SYMBIOCLADIUS* OF THE SOUTHERN HEMISPHERE*Larvae*

- Mentum with 8-10 teeth in each lateral row (Fig. 2a).  
Mandible with inner teeth about equal in size and shape (Fig. 2a) *S. renatae*
- Mentum with 5-6 lateral teeth on each side. Proximal inner tooth of mandible distinctly smaller than its neighbor 2.
- Proximal inner tooth of mandible long and slender (Fig. 2c). Mentum with relatively narrow median, and large lateral teeth (Fig. 2c) *S. wygodzinskyi*
- Proximal inner tooth of mandible short and stout (Fig. 2b). Mentum with relatively wide median, and smaller lateral teeth (Fig. 2b) *S. aurifodinae*

*Pupae*

- 1. Thoracic horn ca. 250-350 µm long, its flexible surface without denticles (Fig. 3c) *S. aurifodinae*
- Thoracic horn less than 150 µm long, sclerotized, with numerous surface denticles 2.
- 2. Thoracic horn evenly curved, gradually narrowing from wide base to acute apex (Fig. 3d) *S. wygodzinskiyi*
- Thoracic horn no wider at origin than near middle, basally straight, apical part bent at a shallow angle (Fig. 3b) *S. renatae*

*Adult males*

- 1. 3 separate free palpomeres (as in Fig. 5d). Thoracic dorsocentral setae strong, ca. 100-150 µm long, arising from conspicuous unpigmented areas. Tibial spurs present. Gonostylus with at least 1 apical megaseta *S. wygodzinskiyi*
- 1 free palpomere. Thoracic dorsocentral setae weak, no longer than 50 µm, not set in distinct unpigmented areas 2.
- 2. Free palpomere large, elongate (as in Fig. 5c). Tibial spurs absent. Gonostylus (Fig. 4) never with apical megasetae *S. renatae*
- Free palpomere small, globose (as in Fig. 5e). Tibial spurs present. Gonostylus with several apical megasetae *S. aurifodinae*

*Adult females*

- 1. 3 separate free palpomeres (Fig. 5d). Thoracic dorsocentral setae strong, ca. 100-150 µm long, arising from conspicuous unpigmented areas. Tibial spurs present. Spermathecal duct basally enclosed in elongate neck of seminal capsule (Fig. 5b) *S. wygodzinskiyi*
- 1 free palpomere. Thoracic dorsocentral setae weak, no longer than 50 µm, not set in distinct unpigmented areas. Seminal capsule without extended neck (Fig. 5a), spermathecal duct basally lined with numerous special secretory cells (SAETHER, 1980) 2.
- 2. Free palpomere small, globose (Fig. 5e). Tibial spurs present. Sternite VIII with numerous setae. Cerci bearing conspicuous, interlocking ventro-medial seams of strong setae *S. aurifodinae*
- Free palpomere large, elongate (Fig. 5c). Tibial spurs absent. Sternite VIII bare (Fig. 5a). Setation of cerci not as above *S. renatae*

PHYLOGENY AND BIOGEOGRAPHY

The morphologies outlined above for *Symbiocladius renatae* sp. nov. considerably extend the known range of character expressions for all life stages of the genus. Specifically, adult features like the occurrence of setae on the female scapus, and on the postpronotum and posterior anepisternum II of both sexes, the

complete absence of tibial spurs and male gonostylar megasetae, or the presence of a pars ventralis on the male hypopygium, all appear to set the new species clearly apart from its relatives. However, unfortunately, none of the descriptions available on other *Symbiocladius* species reaches levels of detail comparable to the present study. For example, the obvious presence of thoracic horns on the pupae of *S. wygodzinskiyi* had been entirely overlooked, and vestigial partes ventrales appear to be present at least on all three austral members of the genus. Therefore, assessment of systematic and phylogenetic relationships, both within and across global hemispheres, has to be deferred until all species have been examined in equal detail. With these goals in mind, a full revision of the genus *Symbiocladius* is intended by the junior author.

On the other hand, the evidence gathered so far - most notably the pupal thoracic horns and adult eye macrotrichia: both always absent on northern specimens, but never missing on austral ones - supports ROBACK'S (1965) establishment of two separate subgenera, and related biogeographical implications. Specifically, preliminary comparisons have as yet produced no character, in which the Australian *S. aurifodinae* assumes a systematic position clearly intermediate between its Neotropical and Holarctic relatives. These results are consistent with the ranking of *Acletius*, the austral subgenus of *Symbiocladius*, among those faunal taxa exhibiting transantarctic distributions indicative of systematic roots beyond the final separation of Gondwanan remnant parts (ASHE *et al.*, 1987). The apparent absence of *Acletius* from southern Africa and New Zealand could possibly point to a time after the latter continents finally broke away from the austral supercontinent. The presumably Laurasian origins of the Heptageniidae, in recent time the practically exclusive hosts of Holarctic *Symbiocladius*, also seem to contradict pre-breakup Pangaeian dispersal of the parasites' ancestors.

On the other hand, the reported occurrence of *Symbiocladius* on *Thraulodes* in Arizona (MAYO, 1969), putative evidence for an alternative hypothesis of northward dispersal across the Central American land bridge (GONSER, 1990), has been discovered as based on generic misidentification of the involved chironomid (compare JACOBSEN, 1995). More importantly, recent populations are globally limited to cool-temper-



ate, amphitropical regions approximatively between the thirtieth and sixtieth parallels. Without additional information from new taxa or geographic records, only the outstanding systematic revision and phylogenetic analysis may lead to better explanations for the present-day distributions of *Symbiocladius* associations.

The fact that *Acletius* in South America are found on nymphs of both *Meridialaris* and *Massartellopsis*, and on these exclusively, gives added confirmation to the conclusion of PESCADOR & PETERS (1987) that these two genera are most closely related. The link established by the common presence of closely related parasites similarly reflects on South American/Australian relationships within the Atalophlebiinae, and especially the *Meridialaris* lineage.

## ECOLOGY

*Symbiocladius renatae* sp. nov. has been found in first to fifth order streams displaying a variety of habitat characteristics. Clear-water, relatively low-gradient, lower-elevation sites with mostly stony substrates are predominant (Table 1: locality nrs. 2-7). However, the list also includes higher velocity, temperate rainforest waters (loc. nrs. 10-12), a turbid stream with nearly completely clogged substrate interstitial spaces due to ash-laden runoff from a volcano (loc. nr. 8), and slightly brown water passing through coarse woody debris in a Patagonian lowland bog (loc. nr. 21). Wherever measured, instantaneous summer water temperatures never exceeded 20°C. The only thoroughly studied situation is that of the type locality (Estero Pirén 1984-'86; locality nrs. 3-6 in Table 1), where host-associated larvae have been found from September through May, and pupae from October through June (Fig. 7), with relatively few samples taken in mid-winter (July, August). The fact that all other records for the species fall within the months of January through March not necessarily reflects more than a combined sampling effort heavily skewed toward the southern summer.

## TYPE LOCALITY

The Estero Pirén is a first and second order stream in the coastal mountains of southern

Chile approximately 20 km south of the mouth of the Río Toltén. Its geographical location is 39° 21'-23' S, 73° 5'-12' W, where in 13 km it flows from 400 m a.s.l. at its source to almost sealevel at its mouth (Fig. 6). The stream is characterized by 3 distinct sections: 1) a steep headwater section with coarse substrate, heavily canopied by a «Valdivian coastal forest» (selva Valdiviana de la costa), the most species-rich plant community in Chile (HOFFMANN, 1982). 2) a midsection of 7 km length and an average gradient of 8‰ with cobbles and gravels as the main substrate. Through deforestation for agriculture and firewood the stream is only partially canopied here, the riparian vegetation consisting mainly of *Hypericum androsenum* (Hypericaceae), and some shrubs of *Amomyrtus luma* (Mirtaceae) and *Laurelia sempervirens* (Monimiaceae). The results presented in this paper are from this section. 3) the section below the confluence with the Estero Traiguén to its mouth in the Río Queule. In the course of 3 kms the stream meanders through a flat grassy floodplain already under tidal influence. The substrate consists mainly of sand and fine gravels.

The catchment lies in the «Piedra Laja» formation, composed mainly of metamorphosed basalt and diabases, and of mica slates. Therefore, the Estero Pirén is a soft-water stream, and the sediments consist mainly of stones and gravels that are flattened on two sides. Due to the proximity to the ocean and the mild climate, water temperatures fluctuate little and were not observed to fall below 9°C in the winter or exceed 19°C in the summer during the study period.

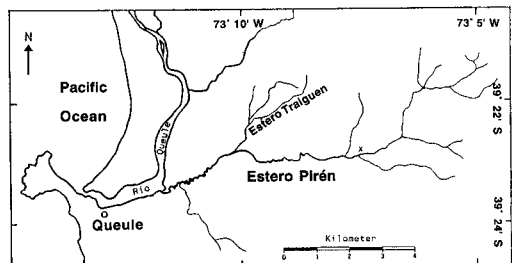


Fig. 6. Location of Estero Pirén. X shows the location of the sampling site.

## POPULATION DYNAMICS IN THE ESTERO PIRÉN

*Methods*

Quantitative samples of the stream sediments were taken in approximately monthly intervals during most of the period from July 1984 to June 1986 at site X in Fig. 6 using a modified Hess-sampler according to JACOBI (1978). With the sampler, a projection of the streambed surface area of 683.5 cm<sup>2</sup> was sampled (mesh Ø 300 µm) and used for the calculations of individuals/m<sup>2</sup>. Four samples were taken on each date and the values from each sample added. All mayfly specimens were scanned for the occurrence of *Symbiocladius* counted and measured and the results plotted in size-frequency histograms.

*Results and discussion*

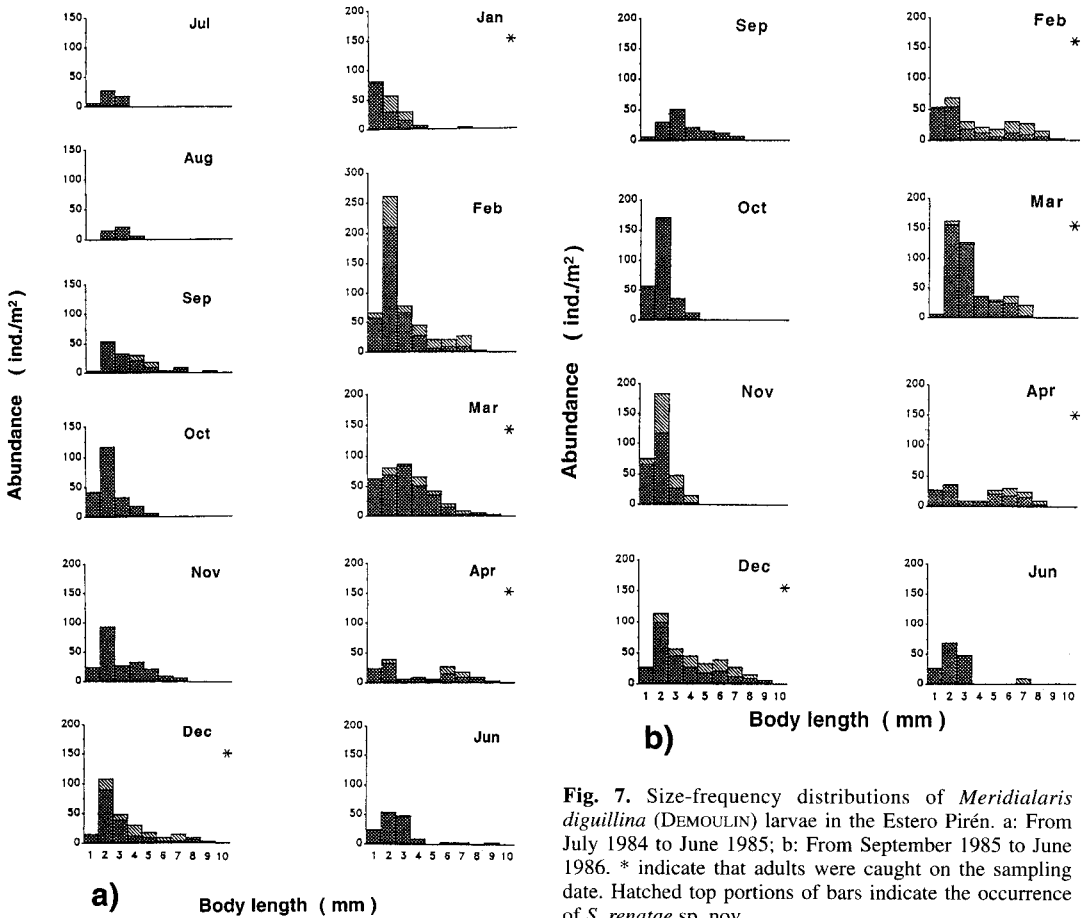
The mayfly fauna in the Estero Pirén is composed of the following species: *Chiloporter peñai* DEMOULIN (Ameletopsidae), *Murphyella needhami* LESTAGE (Coloburiscidae), *Meridialaris chiloeense* DEMOULIN (Leptophlebiidae), *Meridialaris diguillina* DEMOULIN (Leptophlebiidae), *Hapsiphlebia anastomosis* (DEMOULIN) (Leptophlebiidae), *Demoulinellus coloratus* PESCADOR & PETERS (Leptophlebiidae), at least 2 species of *Nousia* NAVÁS (Leptophlebiidae) and at least 2 species of Baetidae. Although the congeneric species *Meridialaris chiloeense* is much more abundant than *Meridialaris diguillina* in the Estero Pirén throughout the year, only on one sampling date a few small *Meridialaris chiloeense* larvae were found to be attacked by *S. renatae* sp. nov. The preferred host in the Estero Pirén is *Meridialaris diguillina*. In Fig. 7 the size-frequency distributions of *M. diguillina* larvae and the portions of larvae attacked by *S. renatae* sp. nov. during the study period are given.

*M. diguillina* appears to have a winter generation of small larvae that show little growth until November or December. Adults from these larvae emerge from December to February. Already before all the larvae of this generation have matured and emerged in February, small larvae of the next generation appear. In this situation the large larvae remaining from the older generation show a particularly high rate of attack by *S. renatae*. The following generation develops rapidly with emergence occurring at least from the end of March to the beginning of May. In April, a similar situation is encountered as in February, with two genera-

tions occurring simultaneously, while the older generation shows a high rate of attack by *S. renatae*. All larvae larger than 4 mm found in June of both years were attacked by *S. renatae*. The small larvae that appear in April form the winter generation. Thereby *M. diguillina* is a bivoltine species with a winter and a summer generation. Both generations are poorly synchronized so that overlapping generations occur twice (January/February and April) during the year. This poor synchronization of development appears to be a common feature of mayflies in the southern hemisphere (WINTERBOURN, 1974, 1978; TOWNS, 1983; CAMPBELL, 1986).

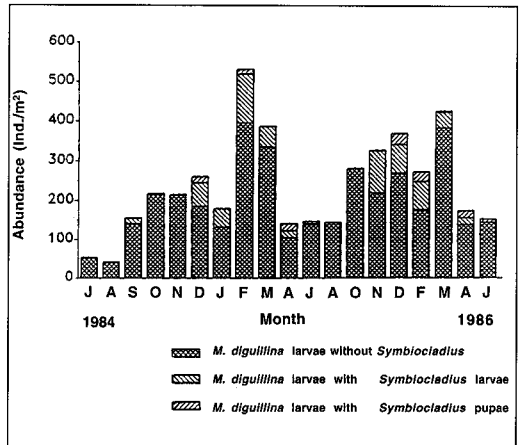
The small *M. diguillina* larvae of the winter generation exhibited little or no occurrence of *Symbiocladius* between June through October (Fig. 7). In November (1985) or December (1984) a strong increase in the rate of attack by *Symbiocladius*-larvae could be observed. Between the months of November and April an attack rate of 10-34% was recorded. In general a distinct increase of attack rate could be detected with the increase of host larval size. In both years a decrease in attack rate was observed from February to March (Fig. 8). The attack rate increased in April (from 13% to 27% in 1985, and from 10% to 21% in 1986), however not in absolute terms. The attacked larvae are inhibited in their development while the other larvae mature and emerge. A significant increase in the number of pupae could be observed in April of both years. In the Estero Pirén, *S. renatae* appears to have a developmental cycle that corresponds with the growth period of *M. diguillina* larvae. *M. diguillina* larvae are attacked in late spring when they begin to grow. *S. renatae* larvae can develop rapidly and some are able to pupate after only one month. The data suggests that more than one generation per year occurs. By June only a few *Symbiocladius*-pupa can be found.

First instar larvae of *Symbiocladius* species are thought to be the only free-living, host-seeking aquatic stage. Once established on a suitable mayfly nymph, the parasite creates a break in the host integument, most often in the posterolateral regions of the thorax, to feed on hemolymph and associated tissues (CODREANU, 1939). Smaller instar *S. renatae* sp. nov. were found in various positions on the host abdomen, but most often curved horizontally across the



**Fig. 7.** Size-frequency distributions of *Meridialaris diguillina* (DEMOULIN) larvae in the Estero Pirén. a: From July 1984 to June 1985; b: From September 1985 to June 1986. \* indicate that adults were caught on the sampling date. Hatched top portions of bars indicate the occurrence of *S. renatae* sp. nov.

latter under the fore wing pads, with the head adjacent to the lateral host thorax. The prepupal larva firmly attaches itself to the host with silk, stretching from alongside the host thorax under parts of one wing pad to the dorsal abdomen, with the parasite's head pointing to posterior. While some younger larvae were examined with relatively incomplete shelters - possibly due to reconstruction during larval relocation on the host - pupae (and their associated larval exuviae) were always completely enclosed in a membranous sheath, which is often very thin and hyaline, but may be somewhat opaque or partially covered with detritus. For more information on *Symbiocladius* biology, and on the parasite's effects on physiology and life history of the host, refer to CODREANU (1939), and SOLDÁN (1979).



**Fig. 8.** Occurrence of *Symbiocladius renatae* sp. nov. on the larvae of *Meridialaris diguillina* (DEMOULIN) in the Estero Pirén from July 1984 to June 1986.

## ACKNOWLEDGMENTS

For facilitating work on Dr. Roback's specimens we are indebted to Drs David Grimaldi and Julian Stark (American Museum of Natural History, New York), and to Drs Donald Azuma and Jon Gelhaus (Academy of Natural Sciences of Philadelphia, Pennsylvania). Drs Manuel Pescador and William Peters (Florida A&M University, Tallahassee) kindly supplied additional South American data. Information on Australian *Symbiocladius* associations became available thanks to these colleagues: Dr. Peter Cranston (CSIRO Division of Entomology, Canberra), Dr. Tomáš Soldán (Czech Academy of Sciences, České Budejovice), Drs Ian Campbell and Sabine Schreiber (Monash University, Clayton, Victoria), and Drs Richard Marchant and Catriona McPhee (Museum of Victoria, Abbotsford). Dr. Friedrich Reiss (Zoologische Staatssammlung, München) provided invaluable help, with his enormous knowledge and expertise on the Chironomidae, and beyond. Special thanks go to Dr. Hugo Campos (Instituto de Zoología, UACH, Chile) who granted the senior author full use of the institution, to Dr. Elena Clasing (Instituto de Biología Marina, UACH, Chile) for logistical field work support and to Gilbert Challet (Orange County Vector Control District, Garden Grove, California) and Dr. Georg Haszprunar (Zoologische Staatssammlung, München) for allowing the junior author to use their respective institutions during this study.

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