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A new species of freshwater anomuran crab of the genus *Aegla* Leach, 1821 (Crustacea: Decapoda: Aeglidae) from the Nahuelbuta Coastal Range, Chile

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Abstract.—*Aegla occidentalis,* a new species of the family Aeglidae, is described from the Tucapel River basin, on the western slope of the Nahuelbuta Coastal Range, in Chile. Morphologically, the new species closely resembles *A. laevis* (Latreille) from Central Chile but differs in having the apex of the carpal lobe of the chelipeds topped by two to four blunt scales mixed with a group of short, stout setae, the dorsum of the palmar crest slightly, if at all, concave, and the distal half of the subligulate rostrum not distorted. The morphological similarity between *A. occidentalis* and *A. laevis* contrasts with the high degree of genetic divergence between these two taxa, based on mtDNA sequence analysis. Our molecular results show *A. occidentalis* and *Aegla bahamondei* Jara to be sister species, with a 1.4%–1.6% average pairwise sequence divergence, compared with 5.9%–7.4% between *A. occidentalis* and *A. laevis.*

The anomuran freshwater crabs of the genus *Aegla* Leach, 1821 are found in rivers and lakes of southern South America (Schmitt 1942), displaying a vast array of minute morphological differences in the shape and ornamentation of carapace and appendages (Bond-Buckup & Buckup 1994). However, the group is constrained to a rather conservative general morphotype that renders the discrimination of most species difficult (Schmitt 1942). By necessity, all known species of *Aegla* have until now been discriminated and diagnosed on the basis of discrete combinations of morphological characters, and therefore the existence of cryptic or sibling species (sensu Mayr & Ashlock 1991) cannot be ruled out. Molecular techniques can potentially reveal levels of genetic differentiation among populations of *Aegla* hidden within morphologically similar populations (Hillis 1987). Such was the case when ~2.6 kb from the mitochondrial genes 12S, 16S, COI and COII were sequenced for most of the *Aegla* species occurring in the continental territory of Chile to reconstruct their phylogenetic relationships (Pérez-Losada et al. 2002).

Some of the specimens collected in the River Tucapel, Province of Arauco, on the western slope of Nahuelbuta Coastal Range, and provisionally assigned by Jara (1996) to *Aegla araucaniensis* Jara, 1980, were subsequently linked to *A. bahamondei* Jara, 1982 by molecular analysis (Pérez-Losada et al. 2002). In this study, the specimens of River Tucapel are described as a new species. The type material and other reference specimens were deposited in the Crustacean Collection of the Instituto de Zoología of the Universidad Austral de Chile (IZUA-C), Valdivia, Chile. The size of specimens was recorded as carapace

length (CL), measured between the tip of rostrum and posterior margin of the carapace.

Aegla occidentalis, new species
Figs. 1, 2

Aegla "not yet identified".—Jara, 1982: 235 (see Remarks).

Aegla araucaniensis.—Jara, 1996:63, 194, 195, figs. 42, 43 (in part, see Remarks).

Aegla sp.—Pérez-Losada et al., 2002:305.

Material examined.—Holotype: ♂, CL 28.3 mm, River Tucapel, at Quelen Quelen, 100 m eastward from bridge at national roadway P-60-R, 7 km N of Cañete, 37°44′09″S, 73°22′49″W, 40 m above sea level, Arauco, VIII Región, Chile, 7 Dec 1974, colls. C. G. Jara, C. A. Moreno, and J. N. Arenas, IZUA C-66A. Allotype: ♀, CL 19.0, same data as holotype, IZUA C-66A. Paratypes: 2 ♂♂, CL 17.5, 21.7; ♀, CL 14.3, same data as holotype, IZUA C-66A.

Non-paratype material: 6 ♀♀, CL 16.2, 17.6, 18.2, 18.5, 18.6, 19.5; ♂, CL 15.5, same data as holotype, 19 Nov 1975, coll. C.G.Jara, IZUA C-156. ♀, CL 16.1; 5 ♂♂, CL 17.0, 17.9,18.5, 18.6, 25.5, same data as holotype, 18 Sep 1981, coll. C. G. Jara, IZUA C-429. 2 ♀♀, CL 18.0, 18.9; 4 ♂♂, CL 16.5, 17.4, 18.3, 19.8, same data as holotype but 100 m westward from bridge, 22 Feb 2000, colls. C. G. Jara, M. Pérez-Losada, and A. Riedemann, IZUA C-592. 3 ♀♀, CL 7.9, 19.8, 22.5; 2 ♂♂ CL 17.9, 22.8, River Caramávida, 37°41′16″S, 73°21′27″W, 05 Nov 1981, coll. C. G. Jara, IZUA C-242. 2 ♀♀, CL16.2, 16.9; 4 ♂♂ CL 18.9, 19.8, 21.0, 24.8, River Pocuno, 2 km north from Colonia Antiquina, under bridge of national roadway S-70, 38°02′07″S, 73°23′37″W, 11 Dec 1981, coll. C. G. Jara, IZUA C-428. 2 ♀♀, CL 18.1, 18.7; 4 ♂♂, CL 16.7, 18.8, 19.4, 20.2, Lake Lanalhue, 37°55′37″S, 73°15′18″W, 7 Nov 1974, colls. C. G. Jara, C. A. Moreno, and J. N. Arenas, IZUA C-65. 2 ♀♀, CL 13.6, 13.8; 4 ♂♂, CL 15.8, 15.8, 16.0, 20.8, Lake Lleu Lleu, at Puerto Choque, 38°11′43″S, 73°21′21″W, 8 Dec 1981, coll. R. Arriagada, IZUA C-260.

Diagnosis.—Body contour almond shaped; carapace surface grossly punctated; rostrum triangular to subligulate, short and low profiled, apex with scale surrounded by rosette of short stiff setae and minute acicular scales; orbital spine absent; branchial margins of carapace not expanded, smooth; anterolateral angle of second abdominal epimeron blunt, frequently with small scale hidden among short setae; carpal lobe subpyramidal tipped with row of 1–4 scales in a row mingled with short stiff setae; lobe on proximodorsal end of dactylus of chelae low and blunt; palmar crest subrectangular, slightly expanded and faintly concave, its margin subdenticulate; fourth thoracic sternum flat, unornamented, at most with semicircular swelling ending abruptly at frontal end.

Description of holotype.—Body (Fig. 1a) almond-shaped in contour; precervical portion clearly distinct from postcervical; carapace most protuberant and convex on gastric area. Carapace surface with coarsely, shallow punctae, with pappose setae. Rostrum subligulate, straight, at same level of front; margins, from orbital sinus to tip, with row of tiny scales; rostral carina extended from point equidistant to protogastric eminences to distal third of rostrum, and merging beyond that point into rostrum body (Fig. 1g). Space between carina and margins not noticeably troughed; carina summit with 2 irregular rows of tiny acute scales. Rostrum tip with small, acute, conical scale flanked by flat scales at base; scales interspersed with minute, stiff, pappose setae. Ventral surface of rostrum protruding as blunt keel, reaching deepest point between and behind ocular peduncles. Orbits broad, deeply U-shaped, without orbital spine or extraorbital sinus (Fig. 1a). In place of extraorbital sinus 2 minute scales protruding from slanted margin merging with anterolateral lobe of carapace; lobe tipped with a cuspidate scale, and posterior

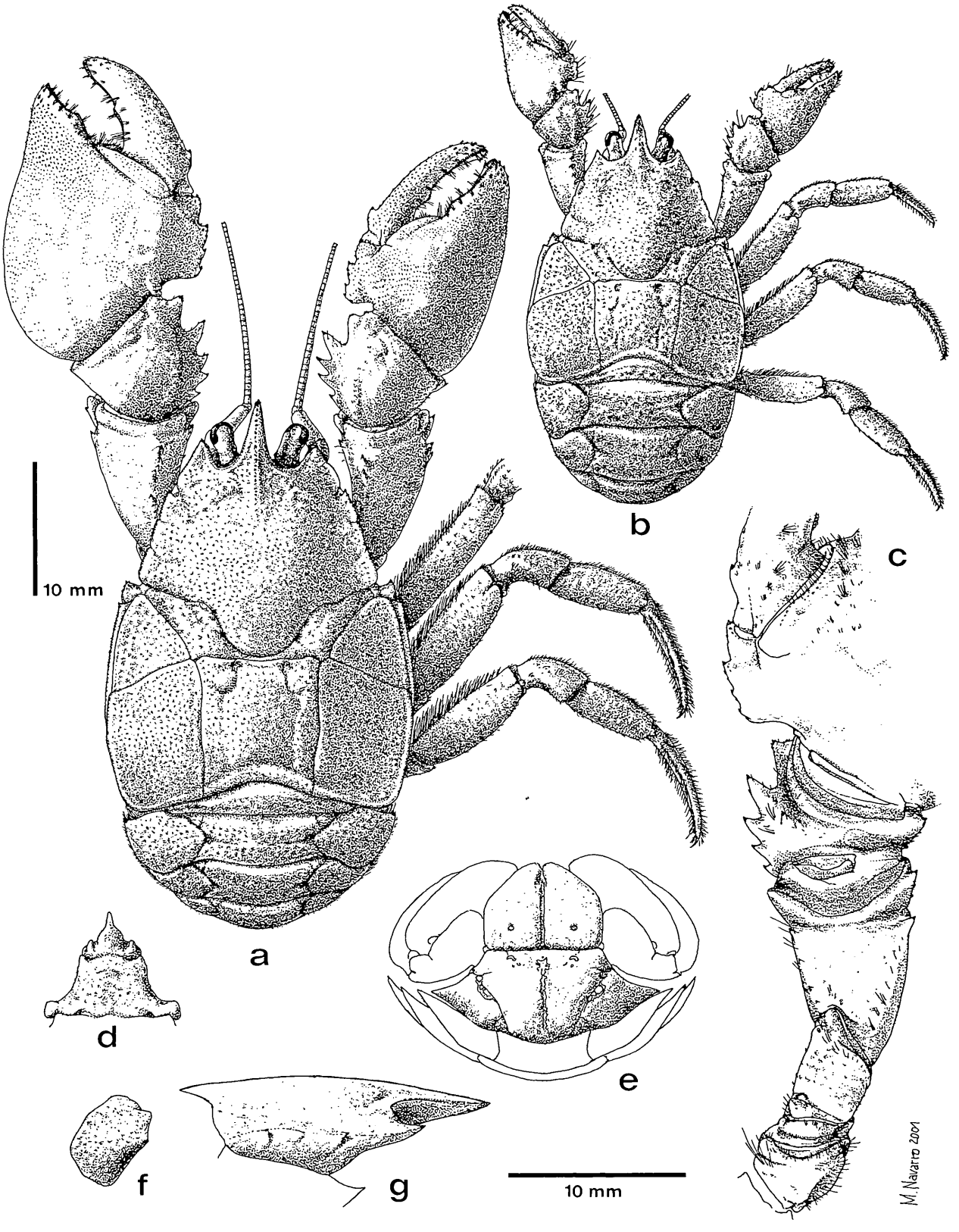

Fig. 1. *Aegla occidentalis*, new species. a, male holotype (IZUA C-66A), dorsal view; b, female allotype, dorsal view; c–g, male holotype; setae mostly omitted: c, left cheliped, ventral view; d, third and fourth sterna, ventral view; e, telson plate and sixth abdominal somite, dorsal view; f, second abdominal epimeron; g, pre-cervical portion of carapace, side view.

to it with row of 12 (left) or 14 (right) minute, size-decreasing scales extending on lateroexternal margin. Protogastric eminences nodular, bearing 6 (left) or 8 (right) irregularly placed minute blunt scales. Epigastric eminences low, rounded, not well defined, bearing patch of minute scales, some arranged in semicircular row on frontal edge with remaining scales spreading backwards over somewhat triangular area. Hepatic area wide, margin slightly upturned and bearing row of minute scales; anterolateral angle of first right hepatic lobe tipped with acuminate scale larger than that on left side. Second and third lobes distinct, blunt. Epibranchial tooth pyramidal, well defined but not particularly elongated, tipped with small acuminate scale followed by row of 5 (right) or 7 (left) tiny scales on lateroexternal margin. Margin of anterior branchial areas thin, almost smooth, slightly expanded, bearing homogeneous band of tiny scales mingled with short stiff pappose setae. Posterior branchial margin non-recurved, somewhat thickened, with band of scales and setae extending to posterior carapace rim. Cardiac area subrectangular, slightly longer than wide. Areola rectangular (length/width ratio = 1.5), not noticeably protuberant. Sternal surface of carapace not ornamented. Central portion of fourth thoracic sternum slightly protuberant (Fig. 1d), bearing patch of long stiff simple setae on frontal edge. Dorsum of abdominal somites covered by short stiff pappose setae especially dense on epimera. Anterolateral angle of second abdominal epimeron as short acuminate tubercle ending in scale concealed by short stiff pappose setae (Fig. 1f). Lateroventral angle of third and fourth epimera also tipped with acute scale. Telson subpentagonal, slightly wider than long, clearly divided by mesial joint (Fig. 1e).

Chelae massive, unequal in size, left larger. Basis-ischium ventromesial edge smooth, slightly nodulated, bearing tiny conical scale on subdistal knob. Merus dorsal edge blunt, bearing row of tubercular denticles tipped with acuminate scale; distodorsal margin smooth, bearing scattered minute scales and short stiff pappose setae more numerous and closely packed on middorsal low profiled tubercle; ventrolateral inner margin slightly sinuous, bearing row of 3 minute scales, and pronounced acuminate conical tubercle distally; ventrolateral outer margin smooth, with 1 (left) or 2 (right) spiniform tubercles distally; with another small acuminate tubercle distally and close to article margin. Carpus markedly convex, globose, almost smooth, bearing scattered minute scales irregularly distributed, larger and more prominent on distal margin; carpal ridge slightly protuberant, and nodulated, bearing few minute scales; tubercles (1 left, 2 right), each with 3 scales in oblique row on apex; dorsomesial margin of carpus with 4 large proximally size-decreasing conical tubercles in a row; tubercles thick, tipped with moderately acute scales; frontmost tubercle on left carpus with accessory scale some distance behind apical one, and separated from low-profiled carpal lobe by wide sinus (Fig. 1c). Carpal lobe broad-based, subtriangular in outline, flattened, tipped with row of 3 or 4 short coalescent scales interspersed with short stiff pappose setae. Ventral face of carpus (Fig. 1c) clean, smooth, bearing 1 short stout acuminate tubercle on central area surrounded by few long stiff simple setae; right carpus with second acuminate tubercle close to base of third tubercle of dorsomesial carpal margin; corresponding site on left carpus with slightly protuberant swelling. Ventral margin of carpus with minute scale on carpus-propodus articular knob. Propodus inflated, markedly convex (particularly left); dorsal surface covered by minute lens-like scales variously arranged, and becoming more dense and protruding on fixed finger. Palmar crest as moderately expanded laminar ridge, with margin irregularly serrated; palmar crest neatly separated from distalmost pyramidal palmar lobe by shallow groove; distal margin of palmar lobe blunt, scaly. Left chela cutting edge of molar process with double row of imbricate

short transversal corneous scales. Dactylus with slender molar process; dorsal margin with low broad-based corneous tipped tubercle close to articular furrow.

Dactylus of second, third, and fourth pereiopods long, slender, with elongate, markedly recurved corneous tip, especially at fourth; ventral margin of dactylus with 2–4 needle-like corneous spines in longitudinal row behind tip; distodorsal angle of carpus and merus with 1 or 2 tiny, acute scales concealed by dense band of short stiff pappose setae; frontodorsal margin of carpus and propodus with dense band of short stiff pappose setae; same margin of merus with dense row of long soft plumose setae.

Description of allotype.—Differs from holotype in having rostral carina flanked by troughs on middle third of rostrum. Carapace (Fig. 1b) worn out, blackened by deposition of organic matter. Chelae less massive, unequal in size, left larger. Dorsomesial margin of carpus of chelipeds with only 3 conical tubercles. Ventral face of carpus of right cheliped with 2 coalescent blunt tubercles, 1 on left cheliped. Lobe on proximodorsal end of dactylus of chelae slightly prominent. Ventral margin of dactylus of left second pereiopod with row of 5 slender acuminate scales behind tip, and row of 3 scales in the remaining dactyli.

Morphometrics.—Descriptive morphometrics of the type series specimens (see Bond-Buckup & Buckup 1994) are recorded in Table 1.

Variations.—Typically lacking extraorbital sinus, but in two of the smallest paratypes both orbits have thickened margin bearing one small tubercle delimiting a very narrow extraorbital sinus.

Apex of carpal lobe of chelipeds typically with row of two to four scales mixed with short stiff pappose setae. In the smallest paratype, both carpal lobes are monocuspidate.

Anterolateral angle of second abdominal epimeron; it typically protrudes as small tubercle tipped with acuminate scale surrounded by short stiff pappose setae. However, the largest male paratype has blunt angles bearing an almost imperceptible scale hidden by setae.

Table 1.—Morphometric ratios of the type series specimens of *Aegla occidentalis,* new species. CL, carapace length, between tip of rostrum and median point on rear margin of carapace; RL, rostral length, between tip of rostrum and median point between proximal end of orbits; AL, areola length, between frontal and caudal midpoints; AW, areola width, between midpoint of lateral grooves of areola; PCL, precervical length, between tip of rostrum and midpoint of cervical groove; FW, frontal width, between tips of anterolateral angles of carapace.

Ratios	N	Range	Mean	Mean confidence limits ($P \leq 0.05$)
CL/RL	5	5.5–5.6	5.5	5.2–5.8
AL/AW	5	1.3–1.5	1.4	1.2–1.6
PCL/FW	5	2.1–2.2	2.1	1.9–2.4

Ventromesial margin of merus of chelipeds with ornamentation varying from completely lacking, as in the smallest female paratypes, to a row of small tubercles, some of which are tipped with a small scale, as in the smallest male paratype.

Ornamentation of fourth thoracic sternum, in both male paratypes, with frontal margin sharp, and convex, forming a rim that is not apparent in the remaining type specimens.

The morphological variation among nonparatype specimens of *A. occidentalis* is summarized in Table 2. In addition, among the specimens from Lake Lanalhue and Lake Lleu Lleu, the rostral carina varies from a sharp elevated ridge, stretched along the whole rostrum, to a ridge restricted to the proximal third or half of the rostrum; beyond that it appears flat and apically recurved. The same specimens have a faintly marked ridge, with variable intensity, along the midline of the gastric area behind the protogastric eminences. This ridge is also present in the specimens of River Caramávida and River Pocuno but only sporadically among the specimens of River Tucapel.

Distribution.—Known from the River Paicaví drainage system, which includes the

Table 2.—Variation of morphotypic characters in *A. occidentalis*, new species. Relative frequencies (%) refer to the number of specimens from each locality examined as non-paratype material, irrespective of sex. River Tucapel (n = 19), River Caramávida (n = 5), Lake Lanalhue (n = 6), River Pocuno (n = 6), and Lake LleuLleu (n = 6).

	Localities				
	Tucapel	Caramávida	Lanalhue	Pocuno	LleuLleu
Shape of rostrum:					
Triangular	36.8	80.0	33.3	33.3	33.3
Subligulate	63.2	20.0	66.7	66.7	66.7
Troughs both sides of rostrum:					
Well marked	52.6	60.0	50.0	50.0	50.0
Faintly marked	47.4	40.0	50.0	50.0	50.0
Orbits:					
Without spine/tubercle	47.4	60.0	16.7	83.3	50.0
With spine/tubercle	52.6	40.0	83.3	16.7	50.0
Apex of carpal lobe of chelipeds:					
With two or more scales	73.7	60.0	83.3	83.3	66.7
With one scale	26.3	40.0	16.7	16.7	33.3
Frontalmost tubercle of dorso-medial margin of carpus of chelipeds:					
Monocuspid	94.7	80.0	83.3	100.0	100.0
Bicuspid	5.3	20.0	16.7	0.0	0.0
Anterolateral angle second abdominal epimeron:					
Armed with scale	63.2	60.0	33.3	50.0	83.3
Unarmed	36.8	40.0	66.7	50.0	16.7
Angle of third abdominal epimeron:					
With acuminate scale	15.8	0.0	50.0	0.0	0.0
Blunt	84.2	100.0	50.0	100.0	100.0
Angle of fourth abdominal epimeron:					
With acuminate scale	89.5	100.0	83.3	66.7	66.7
Blunt	10.5	0.0	16.7	33.3	33.3

River Tucapel, the River Caramávida and Lake Lanalhue, and from the River Lleu Lleu drainage system, which includes the River Pocuno and Lake Lleu Lleu (Fig. 2). Both systems drain contiguous sections of the western slope of the Nahuelbuta Costal Cordillera, between 37°40′S and 38°15′S.

Notes on natural history.—The general description of the biotope where *A. occidentalis,* new species, lives was published by Jara (1982) with the description of *A. bahamondei,* a species with which the former coexists.

The females of *A. occidentalis* collected in the River Caramávida (IZUA C-242) were ovigerous. Their eggs contained embryos in advanced state of development, probably close to hatching. Also, five of the six females from River Tucapel (IZUA C-156) had fresh, empty egg-shells, indicating that the juveniles hatched only a few days before collection. Therefore, it is likely that recruitment in populations of *A. occidentalis* occurs in springtime (September to November), as in other species of *Aegla* (see Bahamonde & López 1961, López 1965, Rodrigues & Hebling 1978).

Etymology.—The specific name is from the Latin *occidentalis*, western, in allusion to the geographic distribution of the new species, which is apparently restricted to a section of the drainage system of the western slope of the Nahuelbuta Coastal Cordillera.

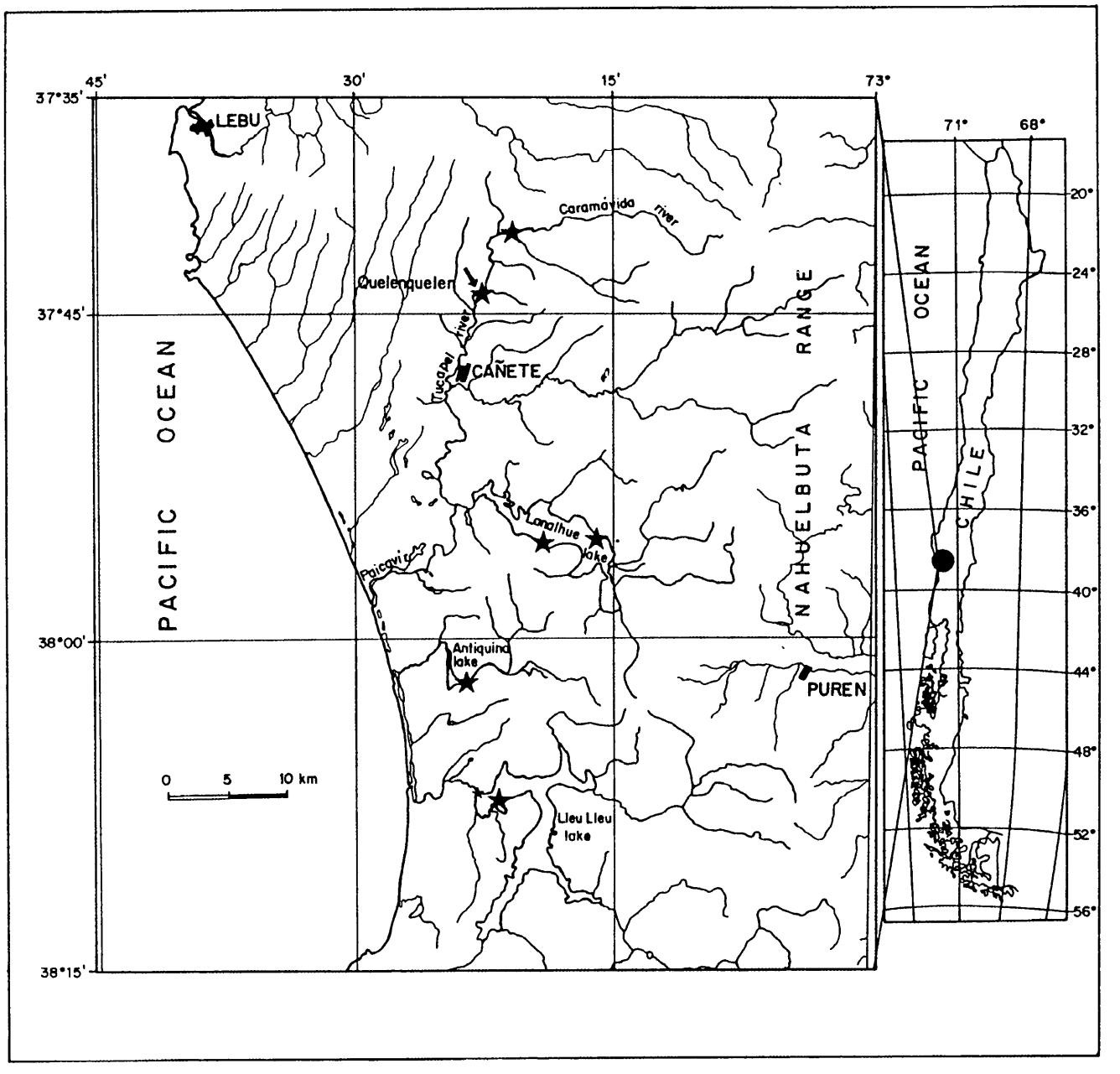

Fig. 2. Collection localities (stars) of *Aegla occidentalis,* new species, in the Tucapel and Pocuno river systems. Arrow indicates type locality.

Comparisons.—Aegla occidentalis, new species, closely resembles *A. laevis* (Latreille, 1818), and *A. araucaniensis.* The new species shares with those two species the almond-shaped body contour, the relatively short precervical section and narrow front, the absence of orbital spine, the elevated gastric area, the broad areola, the unornamented branchial margins, the scale ending rostral apex surrounded by rosette of short stiff pappose setae and minute acicular scales, the subligulate rostrum, the subrectangular denticulate palmar crest, and the tubercular lobe on the dorsum of the dactylus of the chelae. Furthermore, with *A. laevis* it shares the blunt slightly protruding epigastric eminences, the non-recurved posterior branchial margin, and the low profiled carpal lobe.

Aegla occidentalis differs from the other almond-shaped species by having the dorsal surface of the carapace grossly punctated, a feature most evident in specimens with old, darkened carapaces, and by having the anterolateral angle of the second abdominal epimeron rounded and frequently without

an apical scale (see Table 2). The palmar crest in *A. occidentalis,* although subrectangular, is slightly to moderately expanded, with the margin weakly serrate, and faintly concave on the dorsum. In that respect it differs from *A. araucaniensis,* in which the palmar crest is clearly expanded, markedly indented, and dorsally concave especially at its posterior end; and from *A. laevis,* which has a less expanded but similarly concave posterior ending palmar crest. The morphological differences between *A. occidentalis* and the above mentioned species are subtle, and subject to considerable variation but still enough to distinguish the species. From *A. bahamondei* it differs in lacking acute, apically elongate, conical rostrum; denticulate branchial margin; protuberant protogastric eminences; anterolateral angle of second abdominal epimeron spiniform; fourth thoracic sternum with median acute, conical, tubercle; and spine-like dactylar lobe of chelae (Jara 1982).

Genetically, *A. occidentalis* shows clear differences from all other Chilean species analyzed by Pérez-Losada et al. (2002). According to those authors, the interspecific degree of average pairwise genetic divergence estimated from the corrected genetic distances ranges from 1.3%–9.9%. The pair *A. occidentalis–A. bahamondei* has the lowest divergence, 1.4% to 1.6%, a value similar to that observed for other pairs (e.g., *A. cholchol* Jara & Palacios, 1999–*A. rostrata* Jara, 1977 = 1.3% to 1.5%), and higher than that observed in pairs of subspecies (e.g., *A. denticulata lacustris* Jara, 1989–*A. denticulata denticulata* Nicolet, 1849 = 0.3% to 0.4%), or in populations of a single species (e.g., *A. affinis* Schmitt, 1942 = 0.2%). Thus, these data suggest that the genetic differences observed between *A. occidentalis* and *A. bahamondei* are indicative of species distinctness within the Aeglidae.

Remarks.—The discovery of the new species *A. occidentalis* was facilitated by the application of molecular techniques in the study of phylogenetic relationships among the Chilean species of *Aegla* (Pérez-Losada et al. 2002), which provided a high-resolution approach to assess taxonomic limits. The existence of similar morphologies in two or more species may be due to close phylogenetic relationship (descendents from a common recent ancestor), or to morphological convergence. Convergence may result from the independent evolution of the same specialized (adaptive) features in response to similar selective pressures, or to retention of a generalized ancestral morphotype (Moore & Willmer 1997). In the present case, the comparison of *A. occidentalis* with other species of *Aegla* indicates that the morphotype of the new species is markedly similar to that of *A. laevis* and *A. araucaniensis.* The genetic divergence and phylogenetic analysis (Pérez-Losada et al. 2002) of four mitochondrial genes from 16 Chilean aeglids suggest that the species most closely related to *A. occidentalis* is *A. bahamondei,* a species from which the former clearly differs in morphology (Jara 1982), and the two occupy the same biotope. The high degree of genetic divergence between *A. occidentalis* and *A. araucaniensis* (3.5%–3.7%) and between *A. occidentalis* and *A. laevis* (5.9%–7.4%), and their clearly separated phylogenetic positions in the maximum likelihood and maximum parsimony trees (see Pérez-Losada et al. 2002), suggest the possibility of morphological convergence rather than the sharing of a generalized ancestral morphotype. In contrast, the inferred close relationship between *A. occidentalis* and *A. bahamondei,* and the fact that they share the same biotope with no appreciable differences in density (C. G. Jara, pers. obs.), suggest an evolutionary and geographic scenario that allowed for the allopatric speciation of both taxa, and for their subsequent concurrence in the same river basin.

The specimens of *Aegla* "not yet identified" mentioned by Jara (1982) have proven to represent the new species *A. occidentalis.* As previously mentioned, part of the material of *A. araucaniensis* reported by

Jara (1996), contains specimens of *A. occidentalis*.

Conservation.—From a conservation perspective, *A. occidentalis* qualifies as "Vulnerable" (VU) according to the criteria included in the IUCN (2001) Red List Categories, because, with only five recognized localities, its populations are likely fragmented and restricted in distribution due to severe perturbations in the river basins of the western slope of the Coastal Cordillera by intense logging activities (criterion D2).

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