

# Distributional patterns of freshwater Decapoda (Crustacea: Malacostraca) in southern South America: a panbiogeographic approach

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**Abstract.** A panbiogeographic analysis based on the track compatibility method was the starting point for analysing historical biogeographic patterns among freshwater Decapoda (Crustacea: Malacostraca) in southern South America. Based on distributional data of three groups, namely Parastacidae (Astacidea), Aeglidae (Anomura) and Trichodactylidae (Brachyura), eight areas of endemism were defined. The panbiogeographic analysis led to recognition of one generalized track, with a northern part including north western

Argentina, Paraguay, Paraná and Uruguay Rivers and southern Brazil; and a southern part, including central and southern Chile, the endorheic Subandean region, and extra-andean Patagonia. The direction of the track shows the past southward expansion of the tropical freshwater fauna.

**Key words.** Crustacea, Parastacidae, Aeglidae, Trichodactylidae, panbiogeography, South America.

## INTRODUCTION

Southern South America possess an amazing diversity of freshwater limnotopes including, among others, the second largest South American fluvial system (the Paraná–Plata drainage basin), the lacustrine Chilean region and the endorheic Subandean region. Although many advances in the limnology of the region have been undertaken (see Drago, 1990 for a review of Argentine limnology), historical biogeographic studies are scarce and restricted to partial treatments, e.g., Illies (1969), Ringuet (1975), Cione (1986), Feldmann (1986), José de Paggi (1990).

This paper represents a historical biogeographic analysis of the study area, based on distributional patterns of several freshwater Decapoda (Crustacea: Malacostraca), applying a panbiogeographic track compatibility method (Craw, 1988, 1989). This analysis represents a contribution for understanding the freshwater Decapoda distribution, and is preliminary to a general study of freshwater Decapoda evolution in southern South America.

## MATERIALS AND METHODS

Specimens from the following collections were examined, as follows.

**FIML** Fundación e Instituto Miguel Lillo, San Miguel de Tucumán, Argentina.

**MACN** Museo Argentino de Ciencias Naturales

‘Bernardino Rivadavia’, Buenos Aires, Argentina.

**MHNM** Museo Nacional de Historia Natural, Montevideo, Uruguay.

**MHNS** Museo Nacional de Historia Natural, Santiago, Chile.

**MLP** Museo de La Plata, La Plata, Argentina.

Distributional data for this study were also obtained from literature (Müller, 1876; Schmitt, 1942a, b; Ringuet, 1948a, b, 1949a, b, c, 1959, 1960; Haig, 1955; Williamson & Martínez Fontes, 1955; López, 1959, 1960, 1965; Bahamonde & López, 1961, 1963; de Mello, 1969; Riek, 1971; Burns, 1972; Buckup & Rossi, 1977, 1980; Hebling & Rodrigues, 1977; Hobbs, Hobbs & Daniel, 1977; Jara, 1977, 1980, 1982, 1986, 1989; Hobbs III, 1978; Lopretto, 1978, 1979, 1980, 1981; Jara & López, 1981). Species only known from the type locality and not related to other species were omitted. Subspecies of *Aegla neuquensis* Schmitt and *A. abtao* Schmitt were treated separately.

Drago (1990) divided Argentina into limnological regions, based on volume of lotic and lentic waters, and on the development of those environments. For this study, we plotted species ranges on maps of southern South America and analysed where they overlap, determining areas of endemism.

Panbiogeographic principles were originally developed by Croizat (1958, 1981). Croizat’s method was, basically, to plot distributions of organisms on maps and connect

their disjunct distribution areas with lines called 'individual tracks'. Individual tracks for unrelated groups of organisms were then superimposed and if they coincided the resulting summary lines were considered 'generalized tracks'. Generalized tracks indicate the pre-existence of ancestral biotas, that subsequently become fragmented by tectonic and/or climatic changes. Subsequent theoretical developments are found in Page (1987), Craw (1988, 1989), Grehan (1988, 1989) and Henderson (1989).

The track compatibility method applied here, developed by Craw (1988), basically consists of constructing a matrix (areas  $\times$  tracks), where each entry is 1 or 0 depending on whether the track is present or absent, and using a compatibility analysis program to find the largest cliques of compatible tracks. The largest clique is mapped and considered a generalized track. For more details and other applications of this method see Craw (1988, 1989), Morrone & Crisci (1990), Morrone (1992) and Crisci & Morrone (1992). Based on the distributional data a matrix of eight areas  $\times$  twenty-five tracks was constructed (Table 1). This matrix was analysed with program CLIQUE of PHYLIP (Felsenstein, 1986).

After an individual track is constructed its direction may be determined using a phylogenetic criterion, directing the track from the areas where the most plesiomorphic taxa are found to the areas where the most apomorphic are found. For this study, only the phylogenetic analysis of a group of species of *Aegla* was available (Schuldt *et al.*, 1988). These data were re-analysed, applying the implicit enumeration option of Hennig86 (Farris, 1988) for calculating cladograms. Then, areas of endemism were superimposed to the species, thus resulting in an orientated track.

## RESULTS

### Areas of endemism

By plotting ranges of all the species analysed here, we were able to delimit eight areas of endemism (Fig. 1): (a) central Chile; (b) southern Chile; (c) endorheic Subandean region; (d) extra-andean Patagonia; (e) north western Argentina; (f) Paraguay-Paraná Rivers; (g) Uruguay River; (h) southern Brazil.

### Individual tracks

The family Parastacidae comprises two South American genera: *Samastacus* Riek and *Parastacus* Huxley (Riek, 1971; Hobbs Jr, 1974; Buckup & Rossi, 1980). *Samastacus* comprises *S. spinifrons* (Philippi) (Fig. 2) and *S. araucanius* (Faxon). The individual track of the former connects central and southern Chile (Fig. 3); the latter is only known from the type locality. *Parastacus* has a disjunct distribution pattern; *P. pugnax* (Poeppig) is found in central and southern Chile (Fig. 4), while the other five species are distributed in north eastern Argentina, Uruguay and southern Brazil. *Parastacus defossus* Faxon, *P. brasiliensis* (von Martens), *P. varicosus* Faxon, and *P. saffordi* Faxon range from southern Brazil to southern Uruguay (Figs 5, 6). The

individual track of *P. pilimanus* (von Martens) is similar to the species mentioned above (Fig. 6).

The Aegliidae comprise two genera: the fossil *Haumuri-aegla* Feldmann, from marine rocks in New Zealand, and the South American *Aegla* Leach (Feldmann, 1986). *Aegla* (Fig. 7) has thirty-eight species (Martin & Abele, 1988), which basically show the same disjunct pattern as *Parastacus*. *Aegla abtao riolimayana* Schmitt extends from Neuquén province (Argentina) to Chiloé island (Chile) (Fig. 8). Lopretto (1979) considered *A. a. riolimayana* closely related to *A. n. neuquensis* Schmitt; their track joins southern Chile and extra-andean Patagonia (Fig. 8). Furthermore, *A. scamosa* Ringuelet and *A. montana* Ringuelet, from central west Argentina, are related to *A. a. riolimayana* and *A. n. neuquensis* (Lopretto, 1979). Schuldt *et al.* (1988) added *A. a. abtao* to the group. The individual track of this group is shown in Fig. 8.

*Aegla papudo* Schmitt is distributed in central Chile. Jara & López (1981) described *A. alacalufi* from Magallanes, and considered it to be related to *A. papudo*; the individual track of this pair is shown in Fig. 9. The track of *A. concepcionensis* Schmitt connects central and southern Chile, and *A. rostrata* Jara is found in the north eastern part of central Chile (Fig. 9). The group integrated by *A. manni* Jara, *A. maulensis* Bahamonde & López, and *A. araucaniensis* Jara (Jara, 1980) shows a track connecting central and southern Chile (Fig. 10). *Aegla laevis* (Latreille) is endemic to central Chile, and *A. denticulata* Nicolet is endemic to southern Chile (Fig. 10).

*Aegla platensis* Schmitt is widely ranged in southern Brazil, Argentinian and Uruguayan margins of La Plata River, northern Argentina and Paraguay (Fig. 11). *Aegla uruguayana* Schmitt extends from Uruguayan and Argentinian margins of La Plata River to central Argentina (Fig. 11). Schuldt *et al.* (1988) considered *A. uruguayana* and *A. neuquensis affinis* Schmitt, from northern Argentina (Fig. 11), to be in a monophyletic group with *A. n. neuquensis*, *A. abtao abtao*, *A. a. riolimayana*, *A. scamosa*, and *A. montana*. *Aegla singularis* Ringuelet, distributed in north eastern Argentina, is endemic to Uruguay River (Fig. 11). *Aegla parana* Schmitt (Fig. 12) unites southern Brazil and Uruguay River. *Aegla castro* Schmitt, *A. odebrechtii* Müller and *A. prado* Schmitt are endemic in southern Brazil and Uruguay River. *Aegla franca* Schmitt, with a disjunct distribution in southern Brazil and north western Argentina, is closely related to *A. sanlorenzo* Schmitt, *A. humahuaca* Schmitt and *A. jujuyana* Schmitt from north western Argentina (Lopretto, 1981); the individual track of this group connects north western Argentina to southern Brazil (Fig. 13).

The Trichodactylidae comprise the genera *Trichodactylus* Latreille (Fig. 14), *Sylviocarcinus* Milne Edwards (Fig. 15), *Dilocarcinus* Milne Edwards and *Poppiana* Bott (Bott, 1969). In southern South America, *Trichodactylus* has four species, *Sylviocarcinus* two and *Dilocarcinus* and *Poppiana* one. The individual track of *Trichodactylus borellianus* Nobili (Fig. 16) connects Paraguay-Paraná and Uruguay Rivers. *Trichodactylus fluviatilis* Latreille is distributed from southern Brazil to Argentina (Misiones province) (Fig. 16); *T. panoplus* (Martens) extends from

TABLE 1. Data matrix. 1, *S. spinifrons*; 2, *P. pugnax*; 3, *P. defossus*; 4, *P. varicosus*; 5, *P. saffordi*; 6, *P. pilimanus*; 7, *A. a. riolimayana*; 8, *A. a. riolimayana*/ *A. n. neuquensis*; 9, *A. a. riolimayana*/ *A. n. neuquensis*/ *A. a. abtao*/ *A. scamosal*/ *A. montana*; 10, *A. papudo*/ *A. alacalufi*; 11, *A. concepcionensis*; 12, *A. mannii*/ *A. maulensis*/ *A. araucaniensis*; 13, *A. platensis*; 14, *A. uruguayana*; 15, *A. uruguayana*/ *A. neuquensis affinis*/ *A. n. neuquensis*/ *A. a. riolimayana*/ *A. a. abtao*/ *A. scamosal*/ *A. montana*; 16, *A. parana*; 17, *A. franca*; 18, *A. sanlorenzol*/ *A. humahuacal*/ *A. franca*/ *A. jujuyana*; 19, *T. borellianus*; 20, *T. fluviatilis*; 21, *T. panoplus*; 22, *T. petropolitanus*; 23, *S. pictus*; 24, *D. pagei*; 25, *P. argentinianus*. Presence = 1, absence = 0.

	1										2									
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0
Central Chile	1	1	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0
Southern Chile	1	1	0	0	0	0	1	1	1	1	1	1	0	0	1	0	0	0	0	0
Endorheic Subandean region	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0
Extra-andean Patagonia	0	0	0	0	0	0	1	1	1	0	0	0	0	0	1	0	0	0	0	0
North western Argentina	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	1	0	0
Paraguay-Paraná Rivers	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	1	0	1
Uruguay River	0	0	1	1	1	1	0	0	0	0	0	0	1	1	1	1	1	1	1	1
Southern Brazil	0	0	1	1	1	1	0	0	0	0	0	0	1	0	1	1	0	0	1	1

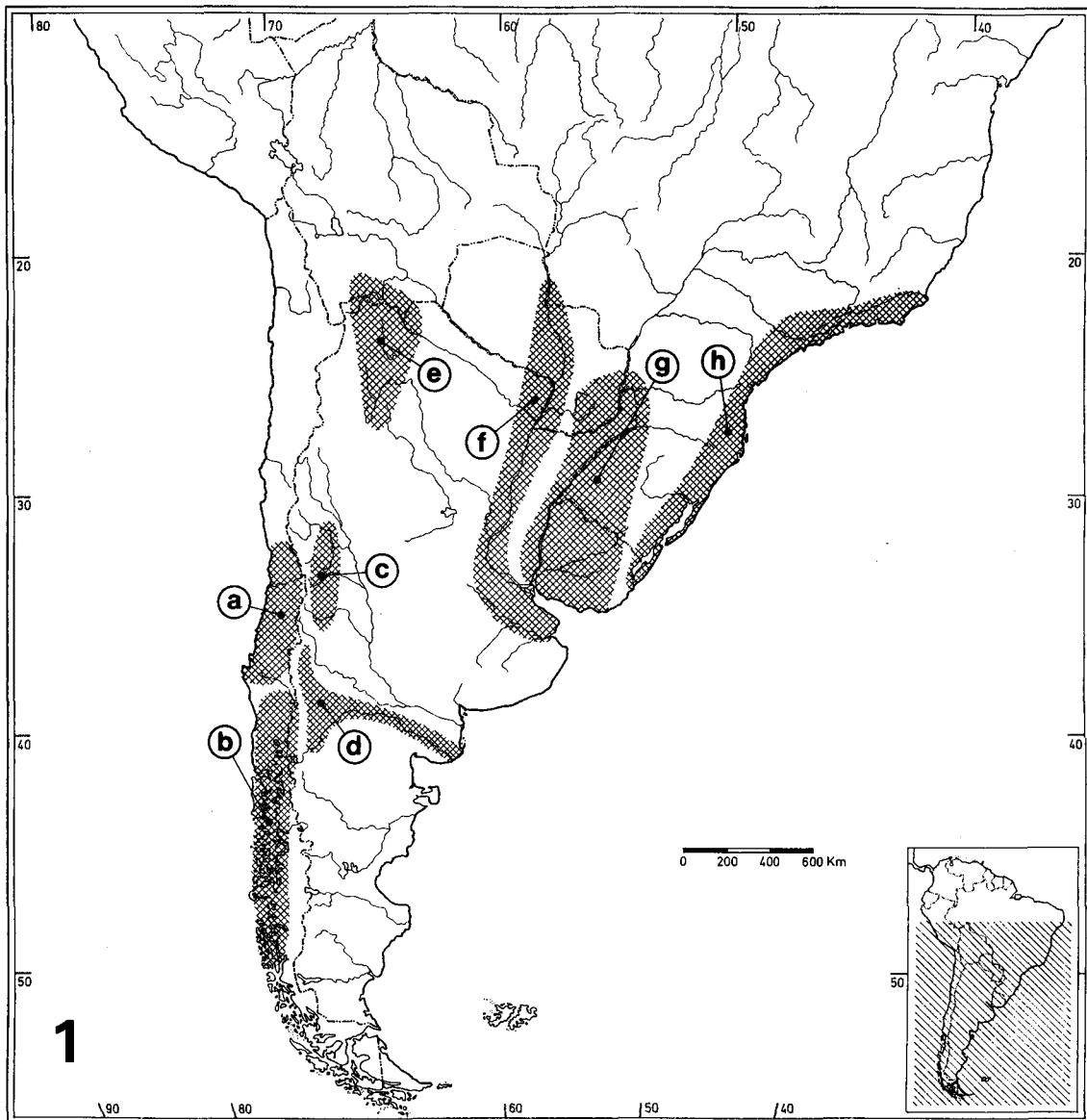
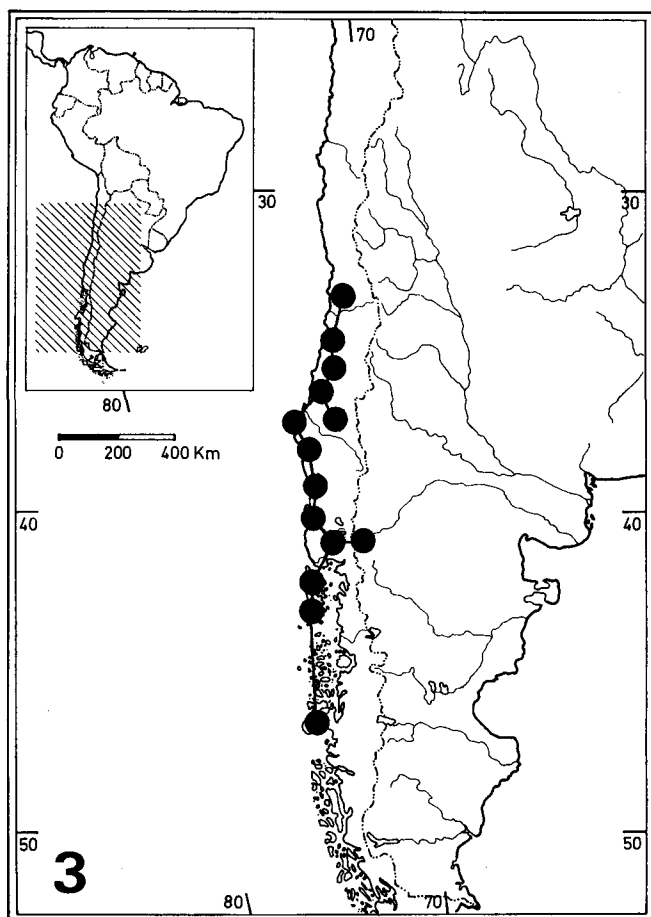
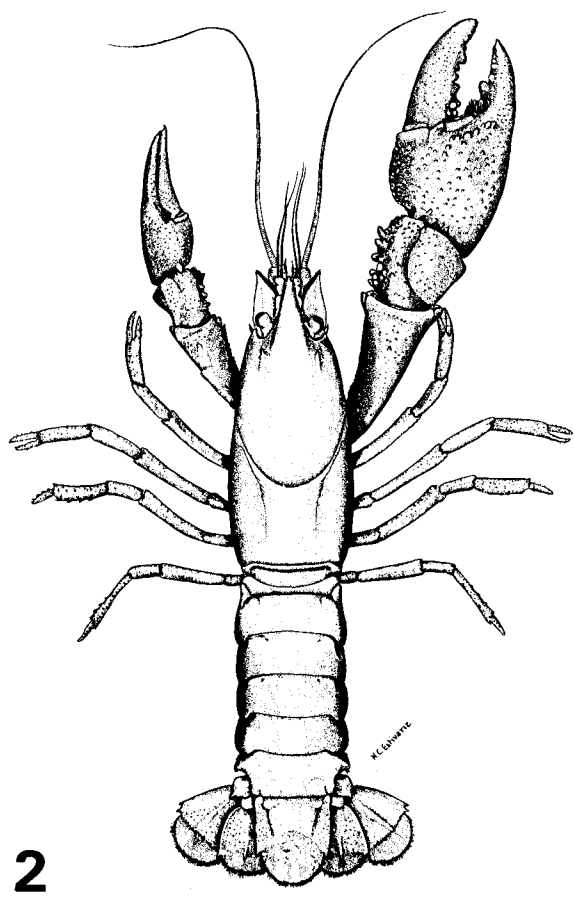


FIG. 1. Areas of endemicity. a, central Chile; b, southern Chile; c, endorheic Subandean region; d, extra-andean Patagonia; e, north western Argentina; f, Paraguay-Paraná Rivers; g, Uruguay River; h, southern Brazil.



FIGS 2 and 3. *Samastacus spinifrons*. Fig. 2, Male habitus. Fig. 3, Individual track.

southern Brazil to Uruguay and Buenos Aires province (Fig. 17); and *T. petropolitanus* (Göldi) has a similar pattern to *T. fluviatilis* (Fig. 17). *Sylviocarcinus cameranoi* Nobili is endemic on Paraguay–Paraná Rivers; the individual track of *S. pictus* (Milne Edwards) (Fig. 18) connects northwestern Argentina, Paraguay–Paraná Rivers, and Uruguay River. The track of *Dilocarcinus pagei* Stimpson (Fig. 19) connects north western Argentina, Paraguay–Paraná Rivers and Uruguay River. The track of *Poppiana argentinianus* (Rathburn) is similar to *D. pagei* (Fig. 20).

The only individual track that could be orientated was that corresponding to the group of *Aegla uruguayana*, *A. neuquensis affinis*, *A. n. neuquensis*, *A. abtao riolimayana*, *A. a. abtao*, *A. scamosa* and *A. montana*. Hennig86 produced three cladograms of fifteen steps (consistency index of 0.80 and retention index of 0.66). The direction of the track was determined according to the strict consensus tree (Fig. 21).

### Generalized track

Based on the data matrix (Table 1), eight cliques were obtained with PHYLIP. The combination of these cliques resulted in one generalized track that was mapped and,

based on the individual track of Fig. 21, orientated (Fig. 22). This generalized track has two parts as follows.

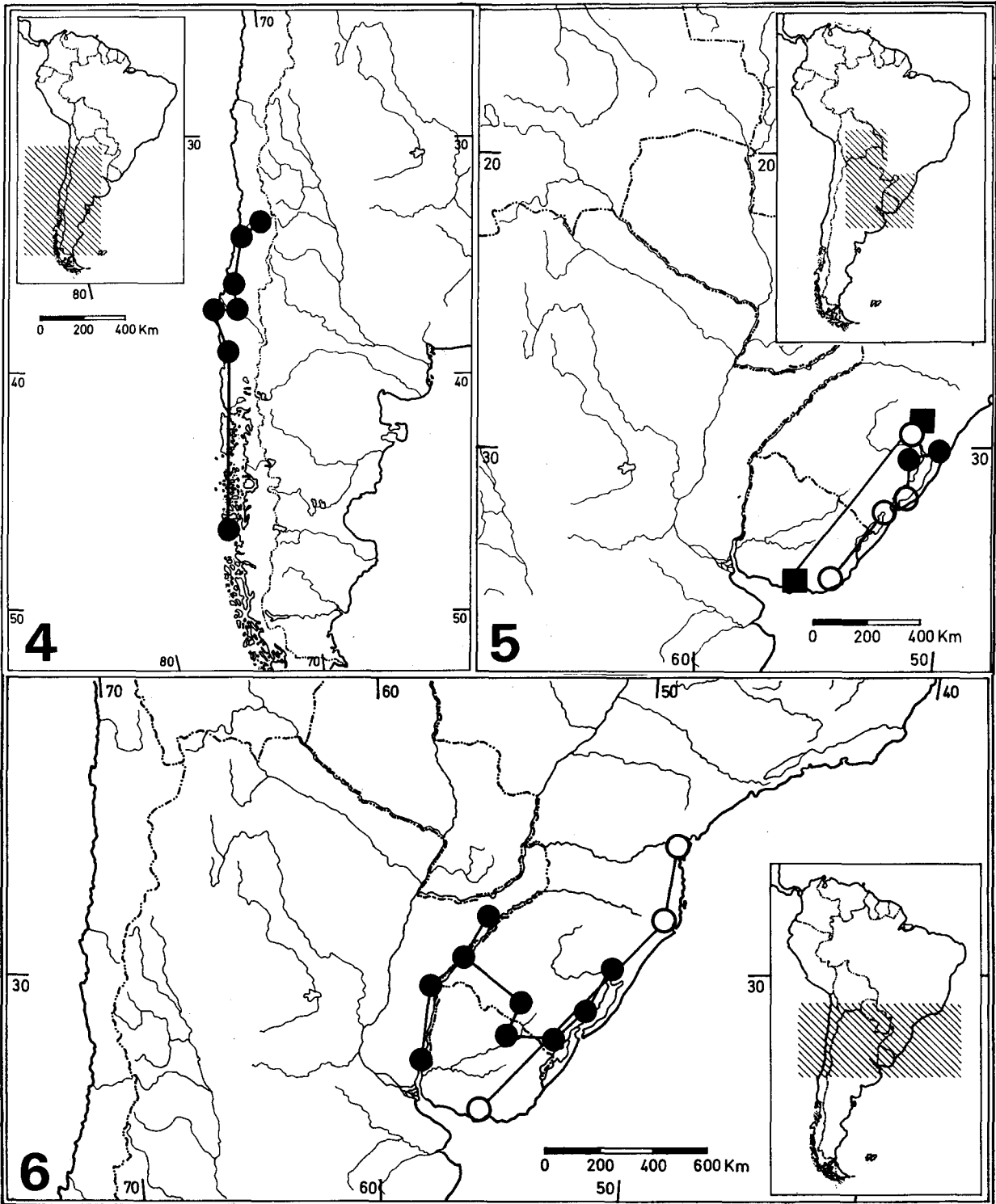
(1) *Northern*. Includes north western Argentina, Paraguay, Paraná and Uruguay Rivers and southern Brazil. Taxa belonging in this part are presented in Table 2.

(2) *Southern*. Basically the lacustrine region of central and southern Chile, endorheic Subandean region, and extra-andean Patagonia. Taxa belonging in this part are presented in Table 3.

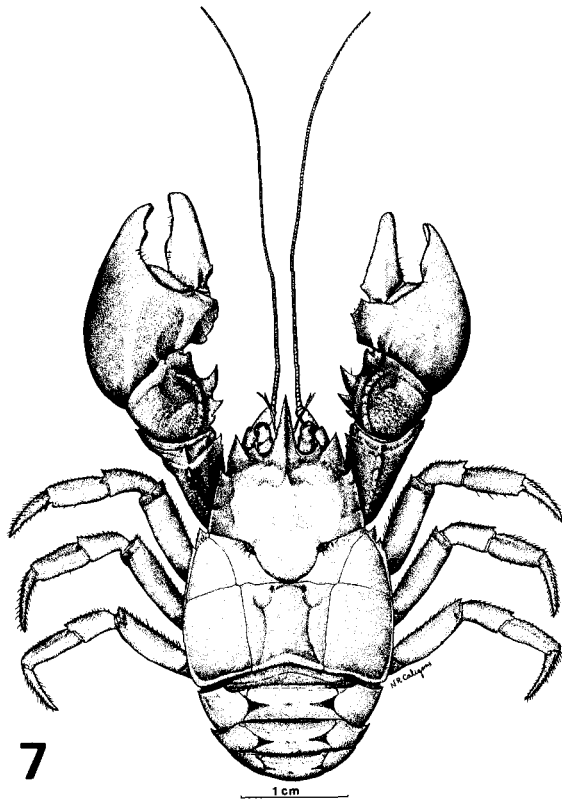
### DISCUSSION

This analysis allows us to speculate on the existence of an ancient tropical freshwater biota that in the past extended further south. Ringuélet (1961) has postulated the past extension of the tropical conditions, serving the Paraná River as a route of diffusion for tropical elements. Available data from other groups of the freshwater fauna confirm this, e.g. sponges (Ezcurra de Drago, pers. comm.), rotifers (José de Paggi, 1990), molluscs (Castellanos & Landoni, 1990; Castellanos & Miquel, 1991) and fish (Ringuélet, 1975; Cione, 1986).

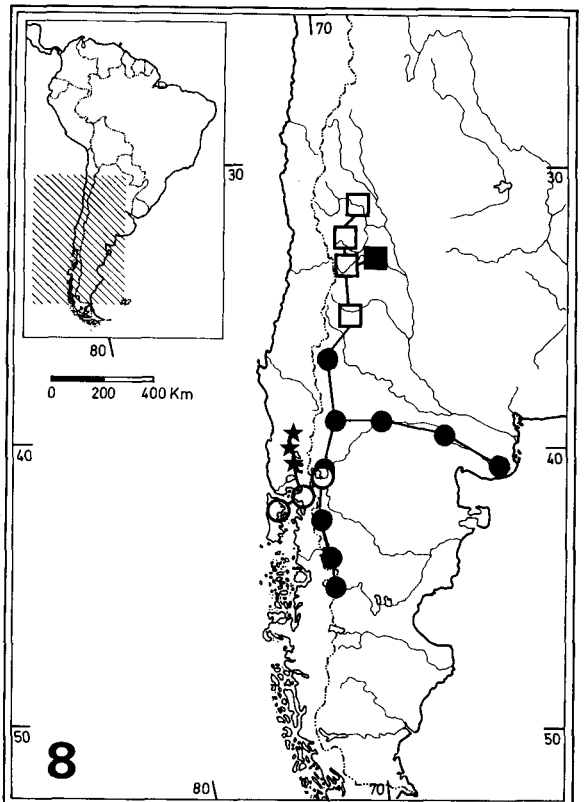
Phylogenetic relationships of *Aegla* species have intrigued biologists for a long time. Due to its similar distribution to *Parastacus*, Ortmann (1902) considered that



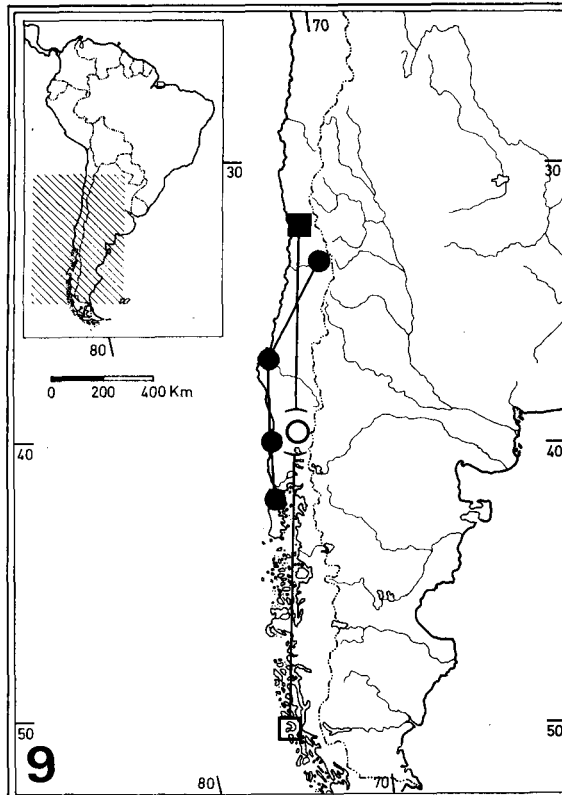
FIGS 4–6. *Parastacus* spp., individual tracks. Fig. 4, *P. pugnax*. Fig. 5, (●), *P. brasiliensis*; (○), *P. varicosus*; (■), *P. defossus*. Fig. 6, (●), *P. pilimanus*; (○), *P. saffordi*.



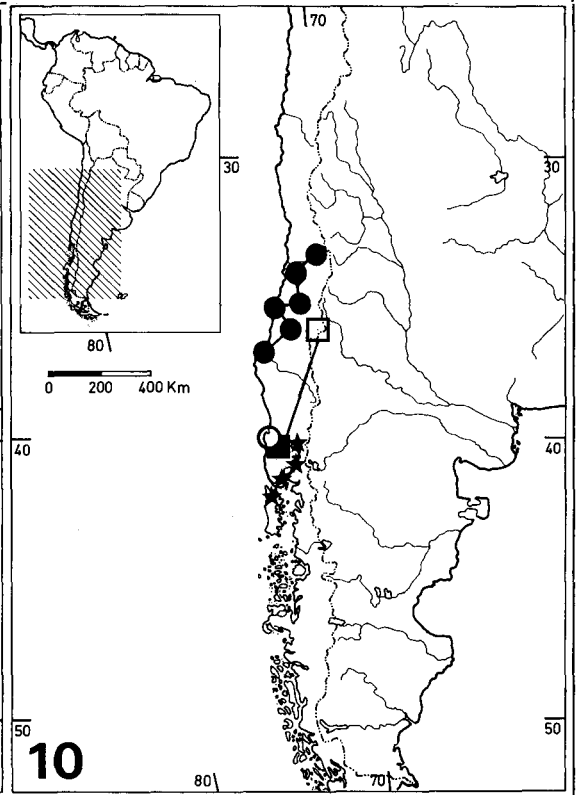
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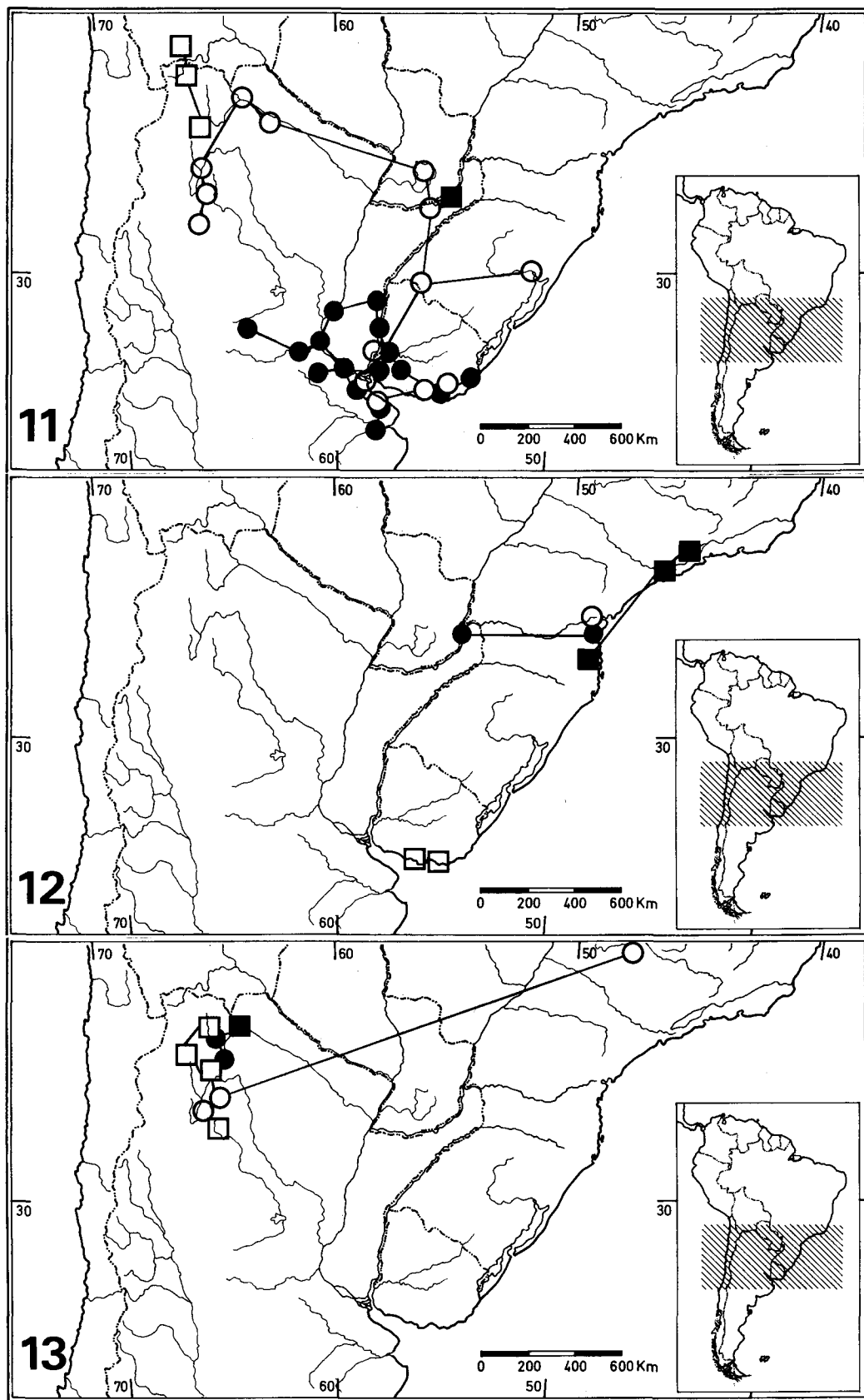


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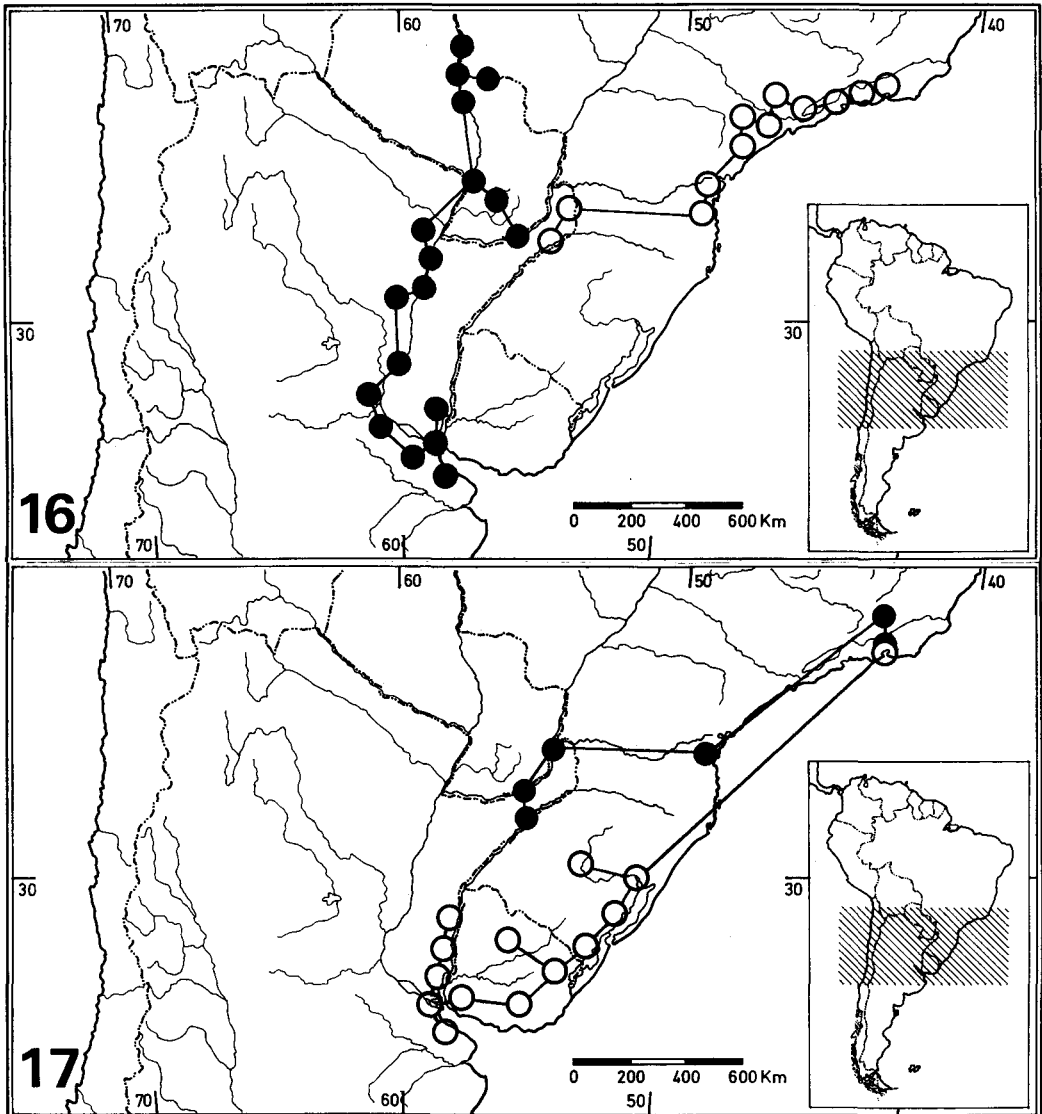
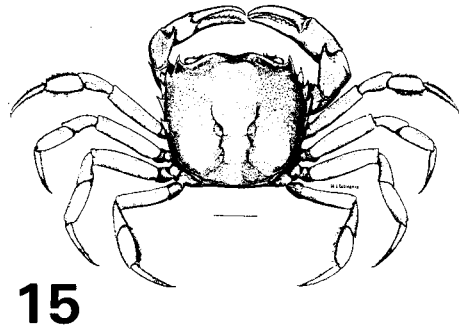
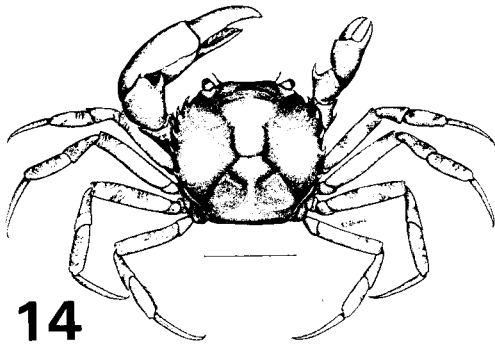


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FIGS 7-10. *Aegla* spp. Fig. 7, *A. platensis*, male habitus. Figs 8-10, individual tracks. Fig. 8, (●), *A. n. neuquensis*; (○), *A. abtao riolimayana*; (■), *A. montana*; (□), *A. scamosa*; (★), *A. a. abtao*. Fig. 9, (●), *A. conceptionensis*; (○), *A. rostrata*; (■), *A. papudo*; (□), *A. alacalufi*. Fig. 10, (●), *A. laevis*; (○), *A. manni*; (■), *A. araucaniensis*; (□), *A. maulensis*; (★), *A. denticulata*.

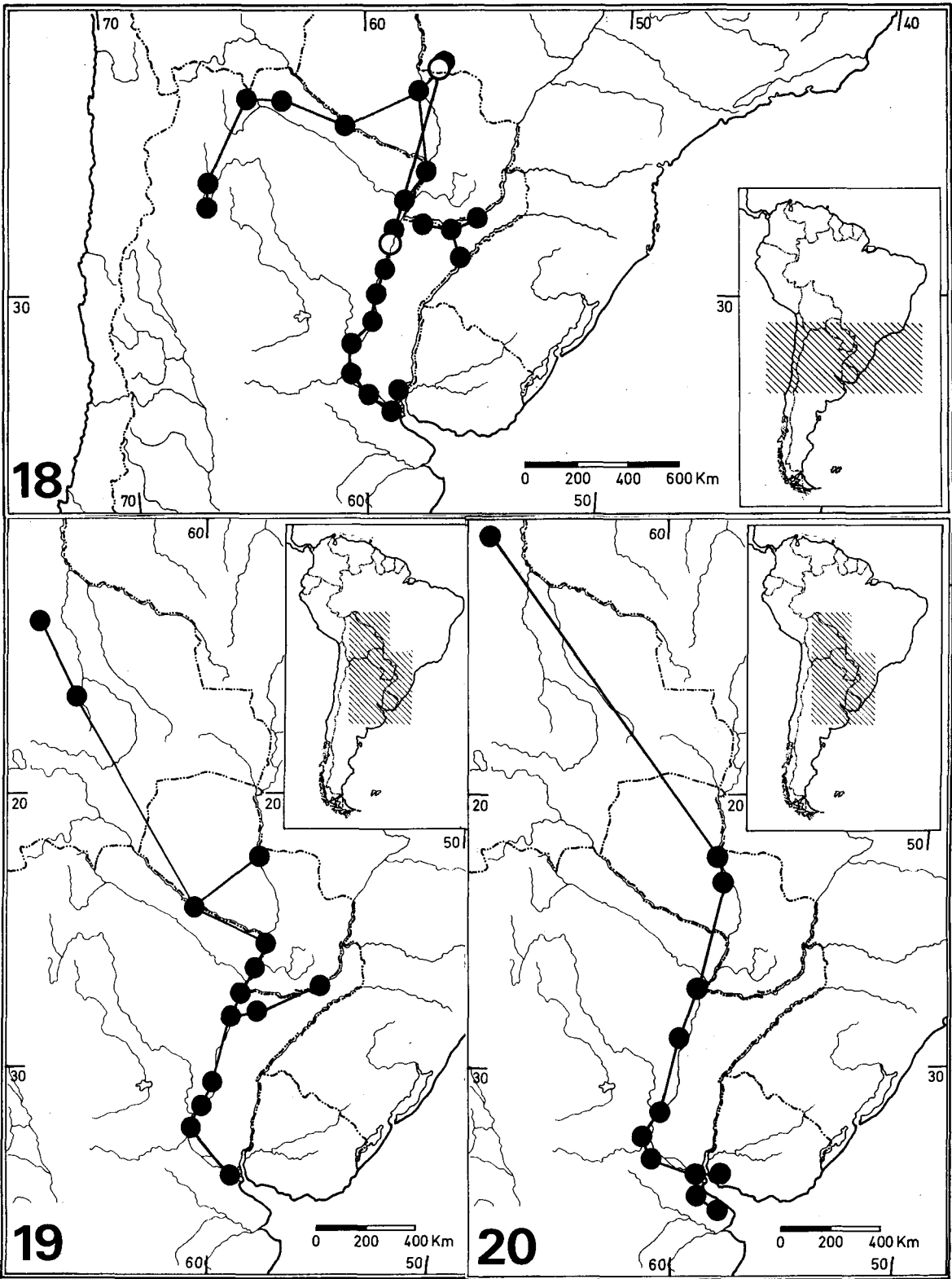


FIGS 11–13. *Aegla* spp., individual tracks. Fig 11, (●), *A. uruguayana*; (○), *A. platensis*; (■), *A. singularis*; (□), *A. neuquensis affinis*. Fig. 12, (●), *A. parana*; (○), *A. castro*; (■), *A. odebrechtii*; (□), *A. prado*. Fig. 13, (●), *A. jujuyana*; (○), *A. franca*; (■), *A. sanlorenzo*; (□), *A. humahuaca*.



FIGS 14–17. Trichodactylidae. Fig. 14, *Trichodactylus panoplus*, male habitus. Fig. 15, *Sylviocarcinus pictus*, male habitus. Figs 16 and 17, individual tracks. Fig. 16, (●), *Trichodactylus borellianus*; (○), *T. fluviatilis*. Fig. 17, (●), *T. petropolitanus*; (○), *T. panoplus*.





FIGS 18–20. Trichodactylidae, individual tracks. Fig. 18, (●), *Sylviocarcinus pictus*; (○), *S. cameranoi*. Fig. 19, *Dilocarcinus pagei*. Fig. 20, *Poppiana argentinianus*.

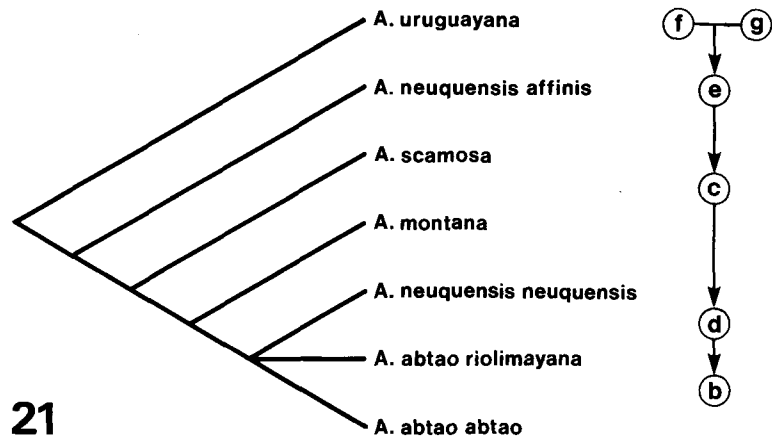


FIG. 21. Consensus tree of the three cladograms obtained for a group of species of *Aegla* (detail of characters in Schuldt *et al.*, 1989). b-g, areas of endemism as in Fig. 1.

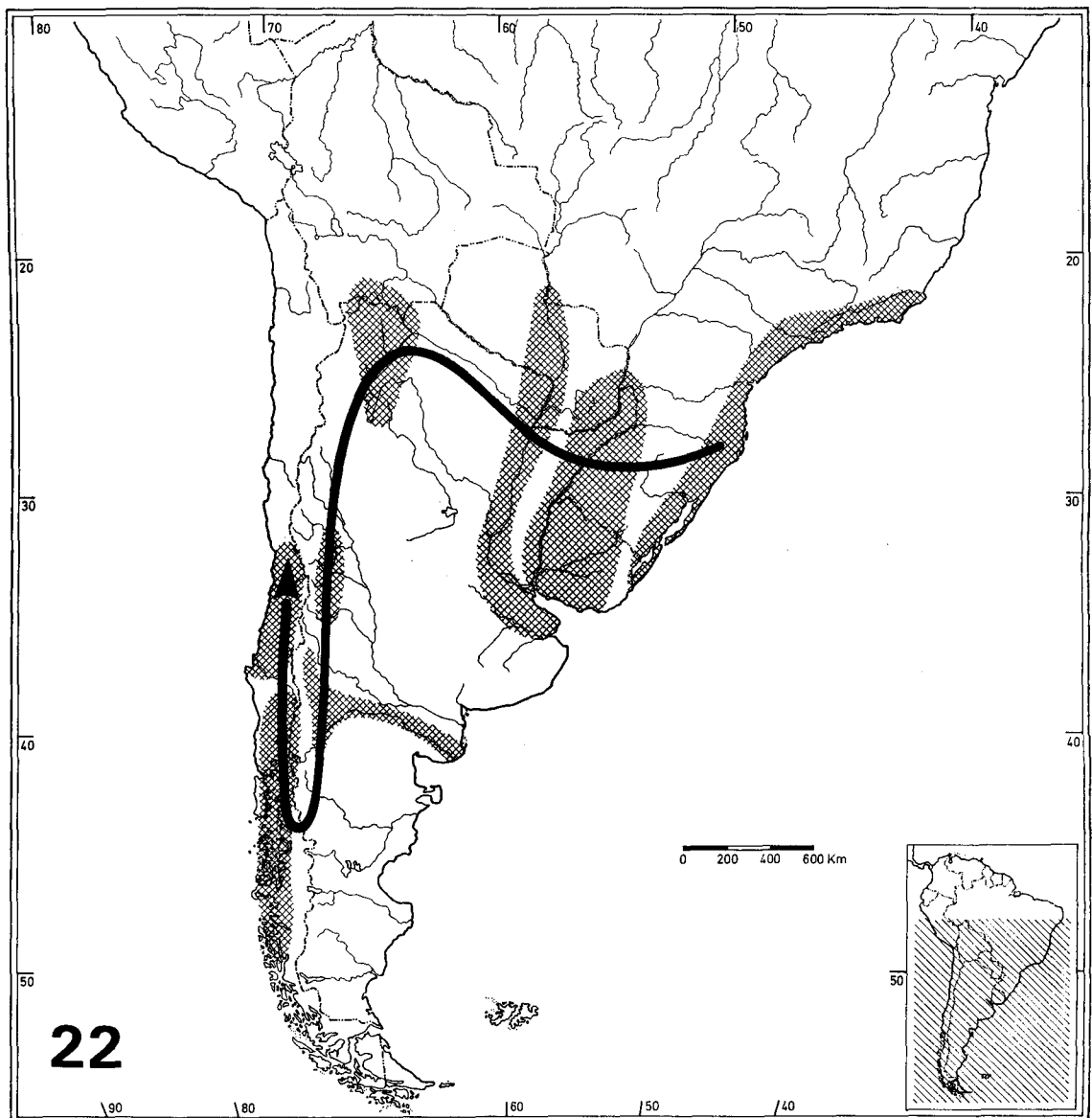


FIG. 22. Generalized track connecting the areas of endemism; the arrow indicates the direction.

TABLE 2. Taxa of the northern part of the generalized track.

North western Argentina	Paraguay–Paraná Rivers	Uruguay River	Southern Brazil
		<i>Parastacus defossus</i>	<i>P. defossus</i>
		<i>P. varicosus</i>	<i>P. varicosus</i>
		<i>P. saffordi</i>	<i>P. saffordi</i>
		<i>P. pilimanus</i>	<i>P. pilimanus</i>
<i>Aegla platensis</i>	<i>A. platensis</i>	<i>A. platensis</i>	<i>A. platensis</i>
	<i>A. uruguayana</i>	<i>A. uruguayana</i>	
		<i>A. singularis</i>	
<i>A. neuquensis affinis</i>			
		<i>A. parana</i>	<i>A. parana</i>
			<i>A. castro</i>
			<i>A. odebrechtii</i>
<i>A. franca/</i>		<i>A. prado</i>	
<i>A. sanlorenzo/</i>		<i>A. franca</i>	
<i>A. jujuyana</i>			
	<i>Trichodactylus borellianus</i>	<i>T. borellianus</i>	
		<i>T. fluviatilis</i>	<i>T. fluviatilis</i>
	<i>T. panoplus</i>	<i>T. panoplus</i>	<i>T. panoplus</i>
	<i>Sylviocarcinus cameranoi</i>		
<i>S. pictus</i>	<i>S. pictus</i>	<i>S. pictus</i>	
<i>Dilocarcinus pagei</i>	<i>D. pagei</i>	<i>D. pagei</i>	
<i>Poppiana argentinianus</i>	<i>P. argentinianus</i>	<i>P. argentinianus</i>	

TABLE 3. Taxa of the southern part of the generalized track.

Central Chile	Southern Chile	Extra-andean Patagonia	Endorheic Subandean region
<i>Samastacus spinifrons</i>	<i>S. spinifrons</i>		
<i>Parastacus pugnax</i>	<i>P. pugnax</i>		
	<i>Aegla abtao</i>	<i>A. a. riolimayana/ A. n. neuquensis</i>	<i>A. scamosa/ A. montana</i>
	<i>riolimayana/ A. a. abtao</i>		
<i>A. papudo</i>	<i>A. alacalufi</i>		
<i>A. concepcionensis</i>	<i>A. concepcionensis</i>		
<i>A. rostrata</i>			
<i>A. maulensis</i>	<i>A. manni/ A. araucaniensis</i>		
<i>A. laevis</i>	<i>A. denticulata</i>		

*Aegla* species from the Pacific embraced the more primitive forms of the genus. Schmitt (1942b) hypothesized that the *Aegla* from the Atlantic side of the continent were more primitive, because they were relatively less ornamented, and species in the Pacific drainage were more derived. Feldmann (1986) considered both conclusions to be speculative, but based on fossil evidence supported Ortmann's hypothesis. Ringuet (1949c) proposed five species groups for *Aegla*, giving in each case the sequence from 'ancestral' to 'recent' species. Although subsequent studies (Lopretto, 1978, 1979, 1980, 1981) changed the composition of these groups, it is interesting to note that they reflect the same pattern, where most plesiomorphic species from the

northern part are connected to more apomorphic species from the southern part. Our results show the same sequence, apparently in agreement with Schmitt's (1942b) and Ringuet's (1949c) points of view.

This study has generated many questions.

(1) In relation to the delimited areas of endemism, how general are they relative to other freshwater taxa?

(2) Are taxa that belong in the ancestral biota delineated by the general track derived from one or more sources? For example, have Trichodactylidae come from the same source as Parastacidae and *Aegla*?

(3) When comparing the relative richness of the different areas, why is the northern part of the general track richer

than the southern part? Does this represent a latitudinal trend in biological diversity? Why is the Paraguay-Paraná system richer than Uruguay River, inversely to the situation of another taxa (e.g. fish)?

(4) How can we explain certain anomalies that still remain, e.g. the absence of Trichodactylidae in the southern part of the generalized track? Or another curiosity: why are Parastacidae restricted to the first portion of the northern part and the last portion of the southern part of the track?

Hopefully, these questions will stimulate a greater number of studies on biogeography of the freshwater biota from southern South America. If biogeographic studies are to progress, there is a need for more intensive collecting. It would be interesting to discover if biogeographic patterns outlined here are similar to those of other freshwater taxa from the region. On the other hand, phylogenetic analyses of *Parastacus*, Trichodactylidae and particularly *Aegla*, as well as other taxa belonging in the freshwater biota, are greatly needed. Studies of this kind will enable a vicariance cladistic analysis of the areas involved, in order to complete the historical biogeography of the freshwater fauna of southern South America.

## ACKNOWLEDGMENTS

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