Corydoras diphyes (Siluriformes: Callichthyidae) and *Otocinclus mimulus* (Siluriformes: Loricariidae), two new species of catfishes from Paraguay, a case of mimetic association

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Corydoras diphyes and *O. mimulus*, new species, are found in association in tributaries to the Río Monday, a right bank tributary of the Río Paraná, and are conspicuously similar to each other in color pattern. *Otocinclus mimulus* has been confused with *O. flexilis* up till now. *Otocinclus mimulus* mimics *O. diphyes*. The mimesis is unusual because the two species occupy different microhabitats and it is hypothesized to operate with a primarily visual predator moving between the microhabitats, tentatively identified as the cichlid *Crenicichla lepidota*. The mimetic association expressed by *C. diphyes* and *O. mimulus* extends to other species pairs of the same genera in southern South America with similarly impressive agreement in coloration, but the operating mechanism is not known in these pairs. In a cladistic analysis of *Otocinclus* using morphological characters, *O. mimulus* is included in a clade consisting also of *O. flexilis* and *O. affinis*. Addition of mimetic similarity results in a single most parsimonious tree with *O. mimulus*, *O. flexilis*, *O. affinis* and *O. xakriaba* forming a monophyletic group.

Introduction

In 1998, one of us (SOK) sampled several localities in the vicinity of Ciudad del Este and observed the frequent co-occurrence of a species of the callichthyid catfish genus *Corydoras* La Cepède and a species of the loricariid catfish genus *Otocinclus* Cope. The species were of about the same size and had about the same color pattern. Both species turned out to be undescribed and the closer analysis of the putative mimicry yielded conclusions of a more general nature. The purpose of this paper is to describe the new taxa and to discuss their mimetic association.

Otocinclus is a genus of small hypoptopomatine loricariid catfishes living in groups or schools. They are diurnal and generally found in smaller-sized streams or along the margins of larger rivers, clinging to substrates using the mouth as a sucker, and feeding from algae or aufwuchs on roots, stones, macrophytes, and broad-leaved grasses. *Otocinclus* species are small-sized; the largest species reach about 45 mm SL (Schaefer, 1997). The genus is distributed east of the Andes,

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throughout the lowlands from Venezuela to northern Argentina, but is generally absent from the Amazon and Orinoco lowlands (Schaefer, 1997). Schaefer (1997) revised the genus, providing descriptions, illustrations and diagnoses for all species, as well as a phylogenetic analysis. He reported 13 species in total, and three species from Paraguay, viz., *O. flexilis* Cope, 1894, *O. vestitus* Cope, 1894, and *O. vittatus* Regan, 1904. Britto & Moreira (2002) most recently added *O. tapirape* from central Brazil, and analysed it using a modification of Schaefer's character matrix.

Material representing the new *Otocinclus* species described below was identified by Schaefer (1997) as the widespread species *O. flexilis*, but comparison with *O. flexilis* from Uruguay and southern Brazil does not confirm that identification.

The family Callichthyidae, or armored catfishes, includes about 160 species in 8 genera (Reis, 1998b). Callichthyids have a heavy body armor, but lack suction devices. The callichthyid genus *Corydoras* includes approximately 142 species (Reis, 1998a), which makes it by far the most species-rich genus of Neotropical fishes. *Corydoras* species are all small-sized, ranging from 25 to 120 mm maximum standard length. Species of *Corydoras* are distributed east of the Andes to the Atlantic coast, from Trinidad to the La Plata drainage in northern Argentina (Strauss, 1985; Reis, 1998b). They are generally found in smaller-sized streams, along the margins of larger rivers, in marshes and ponds. Most of the species are bottom-dwellers, foraging in sand, gravel or detritus. They are often seen in shoals (pers. obs.). Unlike most catfishes, which are nocturnal, *Corydoras* species are active during day-time (Nijssen & Isbrücker, 1980, 1986; Strauss, 1985). Six species have been reported from Paraguay (Nijssen & Isbrücker, 1979).

There are numerous records of non-arbitrary resemblance between different species of animals, as well as between plants and animals (e.g., Eigenmann & Allen, 1942; Wickler, 1968; Gilbert, 1983; Pough, 1988; Thompson, 1994; Goldschmidt, 1996). External resemblance between different fish species is frequently observed in syntopic fish assemblages in tropical freshwaters. A limited number of obvious cases of mimesis have been described from South America. Sazima (1977, 1983) described cases of scale-eating fishes (Characidae) and Sands (1994) described mimesis in *Corydoras*. In this paper we examine the available information on two catfish species to test for the probability of a real, coevolved mimetic resemblance.

Material and methods

Measurements were taken with digital calipers recording to 0.01 mm precision, rounded to the nearest 0.1 mm. Measurements were normally taken on the left side of the fish. Landmarks were chosen according to previous studies of *Otocinclus* (Schaefer, 1997) and *Corydoras* (Strauss, 1985; Nijssen & Isbrücker, 1986; Reis, 1998b), and the terminology should be self-explanatory. All measurements were taken point to point. Standard length (SL) is taken from the tip of the snout to the base of the caudal fin. Caudal peduncle length is taken from immediately posterior to the base of the last anal-fin ray to the middle of the caudal-fin base.

All meristic features were counted on the left side of the fish, except for canal-bearing plates in the median series, which were counted on both left and right sides in *Otocinclus*. Premaxillary and mandibular teeth were counted on one side (usually the left side) in *Otocinclus*.

In *Otocinclus* lateral plates were counted in the lateral median series, from the first plate posterior to the pterotic to the base of the caudal fin. Canal-bearing plates were counted separately. The plates of the posterior part of the median series are duplicated in, e. g., *O. mimulus* and *O. flexilis*, so that two plates occupy the position normally occupied by one plate. Such duplicated plates were counted as one plate. In *Corydoras* dorsal scutes were counted from the first scute posterior to the head to the base of the caudal fin. Ventral scutes were counted from the first scute posterior to the coracoid to the base of the caudal fin. Pre-adipose scutes were counted except for the adipose spine (which is a modified mid-dorsal scute according to Nijssen & Isbrücker, 1980).

Vertebrae were counted on radiographs and are reported as abdominal, precaudal and total vertebrae. Vertebrae of the Weberian complex are excluded from vertebral counts. Color characters were observed on specimens preserved in ethanol. Internal characters were observed from radiographs and from specimens cleared and stained (C&S) with alcian blue and alizarin red following the method described by Taylor & Van Dyke (1985).

Fig. 1. *Otocinclus mimulus*, Paraguay; Estancia María Belén; **a,** holotype, MNHNP uncat (ex NRM 43480), 34.1 mm SL; showing a continuous midlateral stripe; **b,** paratype, NRM 43557, 33.7 mm SL; showing a row of blotches along middle of side.

Statistics were calculated using SYSTAT version 10 (SPSS, 2000). Phylogenetic analysis of *Otocinclus* was performed with PAUP* 4.0 (Swofford, 2002), using the character matrix of Schaefer (1997) with the addition of corresponding data for *O. mimulus*. The branch-and-bound exhaustive search algorithm was used to find the most parsimonious trees. CI = consistency index, RI = retention index, RC = rescaled consistency index.

Material is deposited in: MCP, Laboratório de Ictiología, Museu de Ciências, Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre; MHNG, Muséum d'Histoire Naturelle, Genève; MNHNP, Museo Nacional de Historia Natural del Paraguay, San Lorenzo; NRM, Swedish Museum of Natural History, Stockholm. Holotypes and part of paratype material currently catalogued at NRM will eventually be deposited at MNHNP.

Otocinclus mimulus, new species
(Fig. 1)

Holotype. MNHNP uncat. (ex NRM 43480), 34.1 mm SL; Paraguay: Departamento Caaguazú: río Paraná drainage, small stream (arroyo) at Estancia María Belén, 8 km fom Colonel Patricio Colman; 25°40'13"S 55°5'52"W; 24 Feb 1998; S. O. Kullander, M. Medina & W. Gill M.

Paratypes. 49 specimens, 16.5-49.8 mm SL. All from Paraguay, río Paraná drainage. Departamento Caaguazú: MHNG 2531.072, 7, 16.5-32.7 mm SL; río Güyrauguá, small tributary 3 km E of D. Juan M. Frutos; 7 Nov 1990; C. Dlouhy et al. – MHNG 2353.027, 1, 49.8 mm SL; río Güyrauguá, small tributary 3 km E of D. Juan M. Frutos; 16 Apr 1985; F. Baud et al. – NRM 41800, 3, 32.7-37.1 mm SL; a few km E of Juan M. Frutos, Arroyo Zanja Pé; 25°22'24"S 55°47'44"W; 12 Mar 1998; E. Åhlander et al. – NRM 41924, 9, 34.7-42.7 mm SL; riverbed/swamp crossing at about 7 km on road Caaguazú-Repatriación; 25°30'17"S 56°0'8"W; 15 Mar 1998; E. Åhlander et al. – NRM 42102, 3, 29.2-33.7 mm SL; arroyo crossing road Colonia Sommerfeld-Repatriación; 25°34'58"S

55°49'2"W; 14 Mar 1998; E. Åhlander et al. – NRM 42278, 5, 30.1-37.4 mm SL; left side tributary of the río Güyrauguá where crossing Ruta 2 at Hotel Las Palmas and small pool; 25°23'23"S 55°47'41"W; 15 Mar 1998; E. Åhlander et al. – NRM 42332, 13, 30.1-36.9 mm SL, 2 measured: 33.8-36.9 mm SL; NRM 43557, 1, 33.7 mm SL; NRM 43558, 1, 37.1 mm SL; NRM 43478, 1 C&S, 42.0 mm SL; NRM 43479, 1 C&S, 36.2 mm SL; small stream (arroyo) at Estancia María Belén 8 km from Colonel Patricio Colman; 25°40'13"S 55°5'52"W; 24 Feb 1998; S. O. Kullander et al. – NRM 42466, 5, 29.4-33.6 mm SL; Arroyo Acapyta where crossing small road SW of Santa Rita (about 18 km W of Ruta 6); 25°38'59"S 55°8'22"W; 16 Mar 1998; E. Åhlander et al. (PAR-98-51). – NRM 45142, 1, 33.1 mm SL; NRM 46725, 1, not measured (tissue); left side tributary of río Güyrauguá where crossing Ruta 2 at Hotel Las Palmas; 25°23'28"S 55°47'42"W; 10 Nov 1999; E. Åhlander et al.

Diagnosis. *Otocinclus mimulus* is distinguished from all other *Otocinclus* species except for *O. affinis, O. xakriaba* and *O. flexilis* by presence of an iris diverticulum, and from all except *O. affinis* and *O. xakriaba* by elevated, enlarged odontodes at posterior supraoccipital tip. Distinguished from *O. xakriaba* by having more scales in lateral series (24-25 vs. 21-23), and lateral line canals only on first 4-6 anterior plates in median series (vs. on 4-9 anterior and 4-14 posterior canal-bearing plates, leaving gap of 1-11 plates without lateral line canals). Lateral trunk coloration variable, including either row of 4-6 distinct dark blotches or distinct dark stripe extending from pterotic posterior process to base of caudal fin, or diffuse mixture of those two color patterns. Coloration and variability in coloration distinguishes *O. mimulus* from *O. affinis,* which always has a continuous, notably narrow, well-defined midlateral stripe, and *O. flexilis,* which possesses 2-5 dark blotches along middle of side, never appearing as continuous well-defined stripe. Distinguished from *O. flexilis* by 14-18 (commonly 15-16) vs. commonly 11-14 premaxillary teeth and 12-16 (commonly 14) vs. commonly 11-12 mandibular teeth, and caudal vertebrae 15-17, modally 17, vs. 15. Triangular pigment mark at anterior dorsal-fin base occasionally faint or absent vs. persistent in *O. flexilis* and *O. affinis*, absent in *O. xakriaba.*

Description. Based on 30 specimens, 29.2-42.7 mm SL. See Figure 1 for general aspect. Proportional measurements are summarized in Table 1.

Body moderately short, robust and depressed; head depressed. Dorsal profile of head from snout to origin of dorsal fin smoothly convex. Dorsal profile of trunk, from posterior end of dorsal fin base to caudal fin base, straight. Ventral profile of head and abdomen straight, transversely flat; from origin of anal fin to caudal peduncle concave. Snout rounded, rostrum convex. Body between origin of pectoral fin and origin of anal fin ovoid in cross-section; cross-section between origin of anal fin and base of caudal fin rectangular. Eyes moderately large; orbit diameter 17.5-21.3 % head length. Eyes positioned approximately midway between snout tip and pterotic posterior

Table 1. Morphometry of *Otocinclus mimulus.* Measurements are in per cent of SL, except SL (mm) and regression line (linear, Y=a+bX) parameters which are calculated from original measurement data in mm. Regressions are all significant at P<0.005 (ANOVA).

	N	min	max	mean	SD	a	b	r
SL (mm)	30	29.2	42.7	34.3	2.90			
Predorsal length	30	44.5	50.2	47.2	1.42	1.730	0.421	0.937
Pre-supraoccipital length	30	33.0	38.4	35.7	1.37	3.226	0.262	0.896
Head length	30	33.5	37.5	35.3	1.12	1.519	0.308	0.929
Prepectoral length	30	26.1	30.4	28.1	1.15	1.304	0.243	0.885
Preorbital length	30	13.5	16.7	15.2	0.79	1.103	0.119	0.806
Dorsal fin length	30	25.5	30.2	27.9	1.19	2.235	0.213	0.858
Pectoral fin length	30	22.3	26.5	24.1	1.22	1.369	0.201	0.825
Body depth	30	19.6	23.9	21.3	1.01	−2.033	0.273	0.925
Caudal peduncle length	30	37.1	43.5	39.7	1.62	−0.487	0.412	0.909
Caudal peduncle depth	30	11.5	13.3	12.4	0.47	−0.518	0.139	0.932
Orbit diameter	30	6.1	8.0	6.9	0.46	1.486	0.026	0.650
Interorbital width	30	15.2	17.9	16.4	0.76	0.026	0.163	0.874

process; distance between ventral orbit margin and ventral surface of head ≥50 % orbit diameter. Eyes not visible from ventral side. Iris diverticulum present. Greatest body depth at origin of dorsal fin.

Depressed dorsal fin reaching to vertical from middle of anal fin length; branched rays 6 (2), 7 (28). Pectoral fin reaching just beyond origin of pelvic fin; branched rays 4 (4), 5 (26). Pelvic fin reaching just beyond anus. Caudal fin with 15 (1), 16 (28), 17 (1) principal rays.

Body between head and base of caudal fin covered with plates bearing odontodes; plates arranged in lateral series; number of plates in median series 24 (28) or 25 (2); only first 4-6 plates in median series bearing lateral line canals; posterior plates tandemly duplicated, so that two plates occupy normal position of one plate.

Odontodes evenly distributed on head, body, and pectoral and caudal fins. Enlarged odontodes on anterior snout margin, posterior tip of supraoccipital, posterior distal portion of pectoral fins, and on keels along dorsal and ventral lateral trunk margins, progressively pronounced posteriorly. Males with a swirl of odontodes ventrally at base of caudal fin.

Mandibular teeth 12-16; premaxillary teeth 14-18 (Table 2). Maxillary barbels present.

Vertebrae 6+17=23 (23), 7+15=22 (1), 7+16=23 (6).

Coloration. Preserved specimens pale ochre, except for dark grey region posterior to pterotic-supracleithrum and origin of pectoral fin, extending vertically just beyond origin of pelvic fin. Top of head and snout densely pigmented with evenly distributed melanophores. Anterior tip of supraoccipital and adjoining parts of each frontal dark brown, creating a pattern of three round dots. Pterotic-supracleithrum close to supraoccipital dark brown. Dorsum of trunk with melanophores in irregular clusters, except for discrete dorsal clusters 1) posterior to dorsal fin base, 2) at caudal peduncle, and 3) midway between clusters 1 and 2.

Lateral sides of trunk, posterior to pterotic-supracleithrum, with surface and deep-lying melanophores arranged in 4-6 blotches, a continuous stripe, or diffuse mixtures of these two color patterns (Fig. 1). Pigment pattern occasionally varying between left and right side in same individual. Unbroken, uniform stripes in approximately 50 % of sample; remaining 50 % with blotches or broken stripes. 4-6 blotches, when clearly separated, arranged as follows:

4 blotches: 1) below middle of dorsal fin; 2) above origin of anal fin; 3) above posterior base of anal fin; 4) at least depth of caudal peduncle.

5 blotches: 1) below middle of dorsal fin; 2) above origin of anal fin, or above middle of anal fin; 3) above middle of anal fin, or above posterior base of anal fin; 4) above posterior end of first ray of adpressed anal fin; 5) at base of caudal fin.

6 blotches: 1) below middle of dorsal fin; 2) above origin of anal fin; 3) above middle of anal fin; 4) above posterior base of anal fin; 5) above posterior end of first ray of adpressed anal fin; 6) at base of caudal fin.

Ventral side more or less without melanophores, except for scattered melanophores along length of caudal peduncle and between snout tip and upper lip margin.

All fins with melanophores distally (unbranched rays), most pronounced on pectoral and dorsal fins, and dorsally on caudal fin. Dorsal fin with dark pigment bands or irregular dots; more or less pronounced pigmented triangular mark at anterior part of dorsal fin base, usually associated with cluster of pigments on adjacent dorsum; triangular mark frequently small or absent. Unbranched caudal fin rays occasionally with 4-5 dark blotches; rest of caudal fin with dark pigment forming bands or occasionally a repeated chevron pattern. Rest of fins with few, irregular dark dots.

Table 2. Frequency distribution of mandibular and premaxillary tooth counts for *Otocinclus mimulus, O. flexilis,* and *O. xakriaba*. (a) our count; (b) from Schaefer (1997: 89).

		mandibular teeth							
	N	9	10	11	12	13	14	15	16
O. mimulus	30				2	5	15	5	3
O. flexilis (a)	13		1	5	6	1			
O. flexilis (b)	25	1	4	9	7	1	3		
O. xakriaba	20			2	10	8			

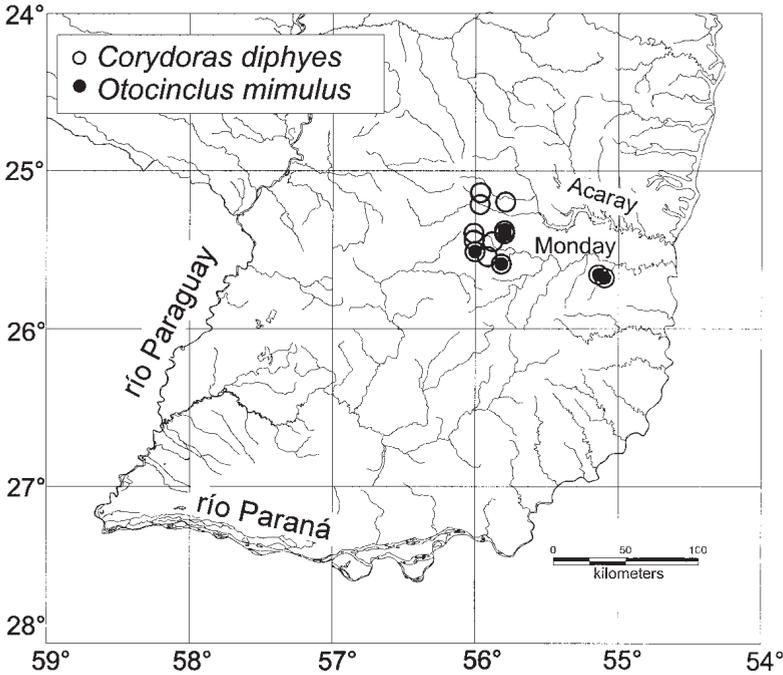|		premaxillary teeth								
	N	10	11	12	13	14	15	16	17	18
O. mimulus	30					5	9	10	5	1
O. flexilis (a)	13		3	3	5		2			
O. flexilis (b)	24	1	4	3	4	7	3	2		
O. xakriaba	20				3	8	4	4	1	

Fig. 2. Collecting sites of *Corydoras diphyes* and *Otocinclus mimulus* in southeastern Paraguay. A symbol may cover more than one collecting event.

Table 3. Frequency of *Otocinclus mimulus, Corydoras diphyes,* and other fishes at localities of *C. diphyes,* expressed as number of specimens. *Crenicichla* are *C. lepidota* except at locality 98-64 where represented by an undescribed *Crenicichla* species (asterisk). Localities 98-20-64 are from the high water period (February-March 1998), localities 99-51-56 from low water period (November 1999). Locality 98-50 and 99-51 represent the same collecting site visited twice. Time is recorded fishing time.

field no	O. mimulus	C. diphyes	Creni- cichla	total species	total specimens	time (min)
98-20	18	128		6	183	50
98-35	3	15	1	10	59	50
98-39		7		6	31	46
98-44	3	279		8	307	45
98-46		1		4	11	21
98-47	9	3		8	22	40
98-50	5	56	1	11	126	105
98-51	5	23		12	74	30
98-58		2	4	5	11	25
98-59A		12	1	9	71	22
98-62		18		10	36	50
98-64		1	1*	12	166	35
99-51	2	40		16	121	150
99-56		32	4	12	73	40

Distribution. *Otocinclus mimulus* is collected in tributaries of the río Monday, a right bank tributary of the río Paraná (Fig. 2).

Habitats. The type locality was a small stream with dark, slightly turbid water, flowing through a landscape of mixed low forest and pasture (Fig. 3). The collecting site was at the margin of an open field, but the stream flowed though dense low forest left along its bank and providing shadow. Collecting was made in a period of near continuous rainfall and the stream carried water to the bank margin. The bottom was soft, with abundant leaf litter and tree branches; the margins were vegetated with grass hanging in the water, and submerse plants in quiet portions. Besides *O. mimulus* and *Corydoras diphyes* only four other species were sampled here, viz., two species of *Astyanax* (Characidae), *Cichlasoma pusillum* (Cichlidae), and an undescribed hypoptopomatine (Loricariidae). Other habitats with either *C. diphyes* alone or both *C. diphyes* and *O. mimulus* present were similar, usually with sand bottom, bank vegetation entering the water or with marginal aquatic plants, dark, clear or slightly turbid water, and limited associated fau-

Fig. 3. Type locality of *Corydoras diphyes* and *Otocinclus mimulus*. Paraguay, Departamento Caaguazú, small stream at Estancia María Belén, near Colonel Patricio Colmán, 24 Feb 1998. *Otocinclus mimulus* was found in vegetation along bank, *C. diphyes* in middle of stream.

na, including mostly *Astyanax* species, other small characids and crenuchids, *Microlepidogaster maculipinnis* (Loricariidae), and *Phallothorynus victoriae* (Poeciliidae) as most significant in number of individuals.

Corydoras diphyes was sampled on 14 occasions in 1998-1999. *Otocinclus mimulus* was present in 7 of these samples. There is an indication that longer sampling time was more successful in obtaining *O. mimulus* (Table 3), probably as a side effect of more microhabitats being sampled. Some of the sites provided only difficult access, especially as the water levels in 1998 were very high, with frequent rain, fast flowing water and numerous obstacles along the flooded stream banks. In 1998 no special effort was made to obtain either species; but 1999 localities were screened purposefully for *O. mimulus* and *C. diphyes*.

Etymology. The species epithet, *mimulus*, is a Latin noun, diminutive of *mimus*, actor, given with reference to the mimicry in color pattern with *C. diphyes*.

Remarks. For comparative morphometrics between *O. mimulus, O. flexilis*, and *O. xakriaba*, see Tables 1, 4-5; no significant differences were found in proportional measurements between adult *O. mimulus* and *O. flexilis. Otocinclus xakriaba* is much smaller than the other two species, and comparisons of similar-sized material were not possible. *Otocinclus mimulus* has usually 23 vertebrae (6-7+16-17), to be contrasted with 6+15=21 (1) or 7+15=22 (12) in *O. flexilis*; otherwise the two species are similar in meristics. The lower lateral scale number (21 (5), 22 (9), 23 (6)), distinguishes *O. xakriaba* from both *O. flexilis* (23 (1), 24 (10), 25 (2)) and *O. mimulus* (24-25).

Otocinclus mimulus was included in the concept of *O. flexilis* by Schaefer (1997), as he referred to that species two samples, MHNG 2531.72 and MHNG 2353.27, from within the exclusive range of *O. mimulus*, and which we identify as *O. mimulus*. Our specimens of *O. flexilis* from Brazil, Uruguay, and Argentina lack the raised tuft of enlarged odontodes at the tip of the supraoccipital posterior process, conforming to Schaefer's (1997)

diagnosis of *O. flexilis.* All *O. mimulus* specimens examined by us have a raised tuft with enlarged odontodes at the tip of the supraoccipital posterior process. In Schaefer's (1997: 52) description of *O. flexilis* the values given for premaxillary and mandibular teeth do not match the values for tooth counts in his tables 7 and 8 (in Schaefer, 1997: 88, 89). In our comparison of teeth frequencies, Table 2, we use his table values for *O. flexilis.*

Otocinclus fimbriatus Cope, 1894, with same type locality as *O. flexilis* (rio Jacui, Rio Grande do Sul, Brazil) was synonymised with *O. flexilis* by Aquino (1996, 1997) and Schaefer (1997), based on comparison of type specimens. *Otocinclus flexilis* has priority by action of the first reviser, Regan

(1904: 267), not by page priority as argued by Schaefer (1997: 53). *Otocinclus arnoldi* Regan, 1909, is based on aquarium specimens said to be from ''La Plata''. The holotype was examined by Aquino (1996, 1997) and compared with Argentinian *O. flexilis* and syntypes of *O. flexilis* and *O. fimbriatus.* She concluded that they are the same species, with which Schaefer (1997) concurred.

Schaefer's (1997) phylogenetic analysis of the genus *Otocinclus* included 13 ingroup species, outgroup (*Microlepidogaster notatus, M. perforatus,* and the tribe Hypoptopomatini), and 27 characters (25 parsimony-informative), resulting in two most parsimonious trees (length 44, CI = 0.682, RI = 0.800) of which the strict consensus tree was

Table 4. Morphometry of *Otocinclus flexilis.* Measurements are in per cent of SL, except SL (mm) and regression line (linear, Y=a+bX) parameters which are calculated from original measurement data in mm. Regressions are all significant at P<0.005 (ANOVA).

	N	min	max	mean	SD	a	b	r
SL (mm)	13	28.2	44.3	32.9	4.36			
Pre-dorsal length	13	45.2	48.6	47.2	0.91	0.194	0.466	0.991
Pre-supraoccipital length	13	31.4	37.6	35.3	1.69	3.370	0.249	0.931
Head length	13	33.2	37.8	35.4	1.19	2.247	0.284	0.978
Pre-pectoral length	13	27.1	30.9	28.5	1.24	1.496	0.239	0.951
Pre-orbital length	13	13.3	16.7	15.3	0.90	1.758	0.099	0.877
Dorsal fin length	13	26.3	30.5	27.7	1.22	0.658	0.257	0.952
Pectoral fin length	13	21.8	26.2	23.7	1.44	0.790	0.213	0.901
Body depth	13	20.2	24.5	22.6	1.29	−1.716	0.278	0.963
Caudal peduncle length	13	35.0	40.7	38.1	1.65	−0.098	0.385	0.952
Caudal peduncle depth	13	11.4	13.1	12.1	0.47	0.087	0.118	0.960
Orbit diameter	13	6.8	8.2	7.5	0.39	0.810	0.050	0.947
Interorbital width	13	16.0	18.4	16.8	0.73	0.989	0.137	0.952

Table 5. Morphometry of *Otocinclus xakriaba.* Measurements are in per cent of SL, except SL (mm) and regression line (linear, Y=a+bX) parameters which are calculated from original measurement data in mm. Regressions are all significant at P<0.005 (ANOVA).

	N	min	max	mean	SD	a	b	r
SL (mm)	20	17.8	25.2	21.0	1.82			
Predorsal length	20	45.4	48.8	46.9	0.95	0.511	0.445	0.974
Pre-supraoccipital length	20	36.0	40.7	37.7	1.26	1.379	0.311	0.927
Head length	20	32.2	38.2	34.9	1.66	0.955	0.303	0.860
Prepectoral length	20	26.4	29.7	27.6	0.83	0.509	0.252	0.942
Preorbital length	20	15.3	17.4	16.3	0.63	0.395	0.144	0.898
Dorsal fin length	20	23.8	27.5	25.4	1.06	1.390	0.188	0.887
Pectoral fin length	20	23.4	26.6	24.6	0.98	0.655	0.215	0.898
Body depth	20	16.4	18.8	17.5	0.61	−0.027	0.177	0.930
Caudal peduncle length	20	36.1	42.7	39.3	1.69	2.657	0.266	0.872
Caudal peduncle depth	20	9.5	11.2	10.2	0.44	0.030	0.100	0.896
Orbit diameter	20	7.2	8.4	7.7	0.33	0.633	0.047	0.897
Interorbital width	20	14.4	17.4	15.4	0.66	0.502	0.129	0.868

published by Schaefer (1997: fig. 57). All characters were ordered except character 19, which was unordered; the ordering was not mentioned by Schaefer (1997) (S. A. Schaefer, pers. comm., 1999).

The tree divided *Otocinclus* into two clades. The *affinis* clade consists of *O. affinis* and *O. flexilis*, uniquely diagnosed by an expanded infrapharyngobranchial 4 process, tandemly duplicated posterior median plates, and a triangular pigment mark on the dorsal fin base. All other species belong to the *O. vestitus* clade, with *O. xakriaba* as a sistergroup to all other species of the *O. vestitus* clade. Britto & Moreira (2002) added *O. tapirape* to Schaefer's (1997) matrix and obtained the same topology except that *O. tapirape* appears in the as sister group to all *O. vestitus* clade species except *O. xakriaba*.

Isbrücker et al. (2001: 103) proposed the genus *Macrotocinclus* for *O. affinis* and *O. flexilis*, apparently only for the reason that they form a clade in Schaefer's (1997: fig. 57) tree. That same clade is shown below to include also *O. xakriaba* and *O. mimulus*. We believe it is premature to attempt formal breakup of *Otocinclus* based on parsimony analyses before trees have stabilized, and even so there may be no point to assign a name to every clade.

Two of Schaefer's (1997) characters are variable in *O. mimulus*. Character 23 may be expressed as either his state 1 (triangular mark present) or 0 (triangular mark absent), but we understand this pigmentation as present though variably expressed in *O. mimulus*, and code it as state 1 rather than as variable or polymorphic. Character 21 is polymorphic in *O. mimulus*, being expressed as either state 1 (a series of diffuse blotches) or state 0 (a lateral band) or intermediate conditions, but we consider the state in *O. mimulus* to be variable expressions of more or less contiguous or discrete blotches, i.e., Schaefer's state 1. In the *vestitus* clade, with a lateral band, the band is always uniform.

Adding *O. mimulus* to the matrix (Table 6), and retaining Schaefer's ordering, results in seven equally short trees. *Otocinclus mimulus* is placed within the *affinis* clade, and appears in a trichotomy with *O. affinis* and *O. flexilis* in the consensus tree (Fig. 4a). In one of the trees *O. xakriaba* is placed as a sistergroup to *O. mimulus, O. affinis,* and *O. flexilis*. In the other six trees *O. xakriaba* keeps its position in the *vestitus* clade as a sistergroup to all the other members of this clade, and in the consensus tree (Fig. 4a), *O. xakriaba* forms a branch in an unresolved trichotomy with the *O. affinis* and *O. vestitus* clades.

As discussed further below, *O. mimulus, O. flexilis, O. affinis,* and *O. xakriaba* are considered to be mimics of particular sympatric *Corydoras* spe-

Table 6. Matrix of characters used for phylogenetic analysis of three outgroup taxa and 15 species of *Otocinclus*, modified from Schaefer (1997) and Britto & Moreira (2002) by adding *O. mimulus* and mimetic association with *Corydoras* (character 28, absent=0, present=1). See Schaefer (1997) for extensive descriptions of characters.

|	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
M. perforatus	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
M. notatus	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hypoptopomatini	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0
O. affinis	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	1	2	0	0	1	0	0	1	0	0	1	0	1
O. bororo	1	1	1	0	1	1	1	0	1	1	1	0	0	0	1	0	0	1	0	0	0	1	0	0	1	1	1	0
O. caxarari	1	1	1	0	1	1	1	0	1	1	1	0	0	0	1	0	1	0	1	0	0	1	0	0	1	1	0	0
O. flexilis	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	1	2	0	0	0	1	0	1	0	0	1	0	1
O. hasemani	1	1	1	0	0	1	1	0	1	1	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0
O. hoppei	1	1	1	0	1	1	1	0	1	1	1	0	0	0	1	0	1	0	0	0	0	1	0	1	1	1	0	0
O. huaorani	1	1	1	0	1	1	1	0	1	1	1	0	0	0	1	0	0	0	0	0	0	1	0	0	1	1	1	0
O. macrospilus	1	1	1	0	1	1	1	0	1	1	1	0	0	0	1	0	1	0	0	0	0	1	0	1	1	1	0	0
O. mariae	1	1	1	0	0	1	1	0	1	1	1	0	0	0	1	0	0	1	0	0	0	1	0	0	1	1	1	0
O. mura	1	1	1	0	1	1	1	0	1	0	1	0	0	0	0	0	0	1	2	0	0	1	0	0	1	1	1	0
O. vestitus	1	1	1	0	1	1	1	0	1	1	1	0	1	0	1	0	2	0	0	0	0	1	0	0	1	1	0	0
O. vittatus	1	1	1	0	1	1	1	0	1	1	1	0	0	0	1	0	1	0	0	0	0	1	0	0	1	1	0	0
O. xakriaba	1	1	1	1	0	1	1	0	2	1	0	1	0	1	1	0	0	0	2	1	1	0	0	0	0	0	1	1
O. tapirape	1	1	1	0	0	1	1	0	1	1	1	0	0	0	1	0	2	0	0	0	0	0	0	0	1	0	0	0
O. mimulus	1	0	1	1	0	1	1	0	1	0	0	0	0	0	0	1	2	0	0	1	1	0	1	0	0	1	0	1
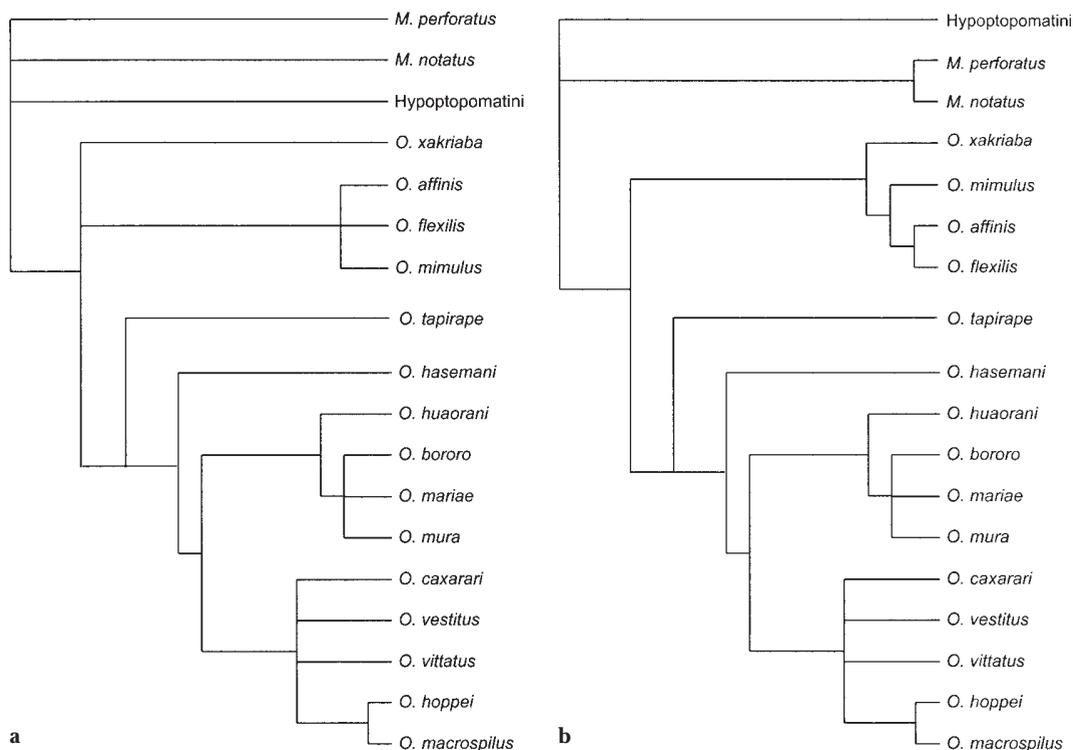
Fig. 4. a, Strict consensus tree of relationships among *Otocinclus* species, based on Schaefer (1997) and Britto & Moreira (2002), with addition of *O. mimulus*. Tree length 48 steps, CI = 0.6250, RI = 0.7907, RC = 0.4942. **b,** Single most parsimonious tree of relationships among *Otocinclus* species, as (**a**), but with mimetic relationship with *Corydoras* species added as character. Tree length 50 steps, CI = 0.6200, RI = 0.7889, RC = 0.4891.

cies (*C. diphyes*, *C. paleatus*, *C. nattereri* and *C. garbei,* respectively), and we added mimetic association with *Corydoras* species as a character to the matrix (character 28). With this expanded matrix, we obtained a single most parsimonious tree in which *O. mimulus, O. affinis, O. flexilis,* and *O. xakriaba* are included in the same exclusive clade (Fig. 4b).

Corydoras diphyes, new species
(Fig. 5)

Holotype. MNHNP uncat. (ex NRM 43483), 28.9 mm SL; Paraguay: Departamento Caaguazú: río Paraná drainage, small stream (arroyo) at Estancia María Belén, 8 km from Colonel Patricio Colman; 25°40'13"S 55°5'52"W; 24 Feb 1998; S. O. Kullander, M. Medina & W. Gill M.

Paratypes. 621 specimens, 21.3-44.8 mm SL. All from Paraguay, Departamento Caaguazú, río Paraná drainage. MHNG 2482.23, 2, 23.1-43.9 mm SL; río Güyraugua; 26 Oct 1988. – NRM 41798, 15, 31.4-38.0 mm SL, 5 measured: 32.9- 38.0 mm SL; a few km E of Juan M. Frutos, Arroyo Zanja Pé; 25°22'24"S 55°47'44"W; 12 Mar 1998; E. Åhlander et al. – NRM 41826, 1, 26.1 mm SL; Arroyo crossing at about 35 km on road Caaguazú–Yhú; 25°12'31"S 55°57'58"W; 20 Mar 1998; E. Åhlander et al. – NRM 41928, 3, 30.5-44.8 mm SL; river bed/swamp crossing at about 7 km on road Caaguazú-Repatriación; 25°30'17"S 56°0'8"W; 15 Mar 1998; E. Åhlander et al. – NRM 41930, 1, 41.3 mm SL; Arroyo crossing road Pueblo de Dios-Repatriación; 25°32'7"S, 55°55'0"W; 14 Mar 1998; E. Åhlander et al. – NRM 42062, 18, 26.5-36.7 mm SL; Arroyo crossing at about 40 km on road Caaguazú-Yhú; 25°8'2"S 55°57'51"W; 20 March 1998; E. Åhlander et al. – NRM 41765, 1, not measured (tissue); NRM 42094, 75, 22.3-31.0 mm SL; NRM 42095, 101, 22.5-34.0 mm SL, 5 measured: 28.7-

Fig. 5. *Corydoras diphyes*, Paraguay: Estancia María Belén; **a,** holotype, MNHNP uncat. (ex NRM 43483), 28.9 mm SL; showing colour pattern intermediate between blotched and striped morphs; **b,** paratype, NRM 43555, 27.6 mm SL; morph with distinct blotches; **c,** paratype, NRM 43556, 29.9 mm SL; morph with complete midlateral stripe.

34.0 mm; NRM 42096, 101, 22.4-33.1 mm SL; Arroyo crossing road Colonia Sommerfeld-Repatriación; 25°34'58"S 55°49'2"W; 14 Mar 1998; E. Åhlander et al. – NRM 42280, 31, 25.4-32.3 mm SL; NRM 42281, 25, 27.2-34.4 mm SL, 5 measured: 27.2-34.4 mm SL; Left side tributary of río Güyrauguá where crossing Ruta 2 at Hotel Las Palmas + small pool; 25°23'23"S 55°47'41"W; 15 Mar 1998; E. Åhlander et al. – NRM 42326, 2, 38.9-39.4 mm SL; Arroyo crossing at about 3 km on road Caaguazú–Yhú; 25°26'1"S 56°0'30"W; 19 Mar 1998; E. Åhlander et al. – NRM 42331, 128, 22.5-43.0 mm SL, 4 measured: 27.6-34.2 mm SL; NRM 43555, 1, 27.6 mm SL; NRM 43556, 1, 29.9 mm SL; NRM 43481, 30.7 mm SL (cleared and stained); NRM 43482, 30.8 mm SL cleared and stained); Small stream (arroyo) at Estancia María Belén, at 8 km Colonel Patricio Colman; 25°40'13"S 55°5'52"W; 24 Feb 1998; S. O. Kullander et al. – NRM 42472, 23, 21.3-28.1 mm SL, 5 measured: 21.3-28.1 mm SL; Arroyo Acapyta where crossing small road SW of Santa Rita (about 18 km W of Ruta 6); 25°38'59"S 55°8'22"W; 16 Mar 1998; E. Åhlander et al. – NRM 42929, 7, 32.5-33.5 mm SL; Arroyo Torovai (district of 3 de febrero); 25°11'34"S 55°47'18"W; 13 Mar 1998; E. Åhlander et al. – NRM 42930, 12, 25.1-41.2 mm SL; Arroyo crossing at about 8 km on road Caaguazú–Yhú; 25°23'21"S 56°0'34"W; 19 Mar 1998; E. Åhlander et al. – NRM 45117, 1, 33.5 mm SL; NRM 45118, 1, 32.9 mm SL; NRM 45259, 30, 28.4-41.9 mm SL; río Güyrauguá where crossing ruta 2 between Caaguazú and J M Frutos; 25°26'32"S 55°52'40"W; 12 Nov 1999; E. Åhlander et al. – NRM 45123, 1, 32.5 mm SL; NRM 45124, 1, 29.0 mm SL; NRM 45152, 37, 27.6.9-42.1 mm SL; NRM 46724, 1, not measured (tissue); left side tributary of río Güyrauguá where crossing Ruta 2 at Hotel Las Palmas; 25°23'28"S 55°47'42"W; 10 Nov 1999; E. Åhlander et al.

Diagnosis. A species of the *C. barbatus* group (Nijssen & Isbrücker, 1980), with relatively low scute numbers (dorsal/ventral row, 23-24/20-21, pre-adipose scutes 2-4, usually 3), distinguished from most species in that group by having a series of 4-6 distinct spots or a continuous mid-lateral band along the middle of the side instead of 2-3 large dark blotches, and dorsal and pectoral fins not elongated in either sex. Different from *C. nattereri*, the only *C. barbatus* group species with a continuous lateral band, in having distinct stripes in dorsal and caudal fins.

Description. Based on 28 specimens, 21.3-44.8 mm SL. See Figure 5 for general aspect. Proportional measurements are summarized in Table 7.

Body short, robust, moderately deep. Dorsal profile of head from snout to eye convex; from eye to origin of dorsal fin straight. Dorsal profile of trunk, from posterior end of dorsal fin base to base of caudal fin, like two concave curves midway separated by the adipose fin. Ventral profile of head and abdomen straight, transversely flat. Ventral profile from origin of anal fin to base of caudal fin straight, slanting dorsally. Snout long and compressed laterally, pointed; snout length 48.5-56.0 % of head length; snout width 72.0-89.0 % of snout length. Mouth ventral. Body ovoid

Table 7. Morphometry of *Corydoras diphyes* . Measurements are in per cent of SL, except SL (mm) and regression line (linear, Y=a+bX) parameters which are calculated from original measurement data in mm. Regressions are all significant at P<0.005 (ANOVA).

	N	min	max	mean	SD	a	b	r
SL (mm)	28	21.3	44.8	31.0	4.87			
Fontanel	28	40.5	48.1	44.4	2.14	0.235	0.037	0.957
Head length	28	29.2	33.8	31.5	1.14	1.419	0.268	0.976
Snout length	28	15.5	17.9	16.6	0.63	0.393	0.153	0.972
Caudal peduncle length	28	25.3	32.2	28.6	1.61	1.140	0.248	0.933
Caudal peduncle depth	28	13.4	15.7	14.5	0.56	0.759	0.120	0.974
Dorsal spine length	28	26.3	30.8	28.5	1.48	0.374	0.272	0.944
Pectoral spine length	28	24.9	32.0	28.6	1.73	−0.642	0.307	0.951
Body depth	28	31.9	37.9	34.4	1.32	−0.485	0.360	0.968
Body width	28	22.9	28.8	25.4	1.02	−0.600	0.274	0.962
Coracoid width	28	13.7	17.4	15.1	0.80	−0.613	0.171	0.952
Orbit diameter	28	7.8	11.3	9.6	0.67	1.365	0.051	0.957
Interorbital width	28	11.9	14.2	12.9	0.62	0.546	0.111	0.960

in cross-section. Eyes moderately large; orbit diameter 25.7-35.3 % of head length. Eyes horizontally positioned approximately midway between snout tip and origin of pectoral fin, and vertically positioned more than one orbit diameter above ventral surface of head. Eyes not visible from ventral side. Greatest body depth at origin of dorsal fin. Nuchal plate exposed right in front of dorsal fin and in contact with supraoccipital.

Dorsal fin with 7 (5) or 8 (23) branched rays. Unbranched dorsal ray spinous, rigid, a little shorter than first 1-2 branched rays. Anal fin with 2 unbranched rays; anal fin reaching to base of caudal fin. Pectoral fin unbranched ray rigid, pointing distally; inner edge weakly serrated (Fig. 6); branched rays 6 (1), 7 (16) or 8 (11). Pectoral fin slightly longer than dorsal fin. Pelvic fin origin just anterior to anus, reaching to origin of anal fin. Adipose fin present, positioned midway between posterior base of dorsal fin and base of caudal fin. Caudal fin deeply emarginate.

Lateral scutes in dorsal row 23 (24) or 24 (4), in ventral row 20 (6) or 21 (22); 4th dorsal scute broader that the rest. Only first two scutes posterior to pterotic-supracleithrum with lateral line-line canals. Pre-adipose scutes 2 (2), 3 (24) or 4 (2).

Odontodes evenly distributed on head, body and fins. Concentration of odontodes on posterior margin of each plate and on unbranched fin rays. Maxillary (rictal) barbels 2 pairs, longest nearly reaching gill-opening/reaching below middle to posterior half of eye, and long mental barbels, one in each lobe of lower lip.

Vertebrae 9+9=18 (1), 10+8=18 (1), 10+9=19 (8).

Coloration. Color in preserved specimens pale ochre. Dorsum of head and snout densely pigmented with evenly distributed melanophores. Dorsal sides with melanophores in irregular clusters, except for dorsal clusters 1) at origin of dorsal fin, 2) at end of dorsal fin base, and 3) at base of adipose fin. Clusters 1-3 often contiguous ventrally by a dark, irregular, often interrupted band. Sides posterior to pterotic-supracleithrum, with dark horizontal markings arranged in 4-6 blotches, or an irregular stripe, or diffuse mixtures of blotches and stripe. Stripe and blotch pattern sometimes varying between left and right side in the same individual. Unbroken, uniform stripe along middle of side in approximately 50 % of specimens, remainder with blotches or interrupted stripes (Fig. 5). Blotches, when clearly separated, arranged as follows:
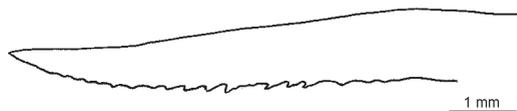

Fig. 6. *Corydoras diphyes*, holotype, MNHNP uncat., 28.9 mm SL; serration on inner edge of pectoral fin.

4 blotches: 1) below middle of dorsal fin; 2) midway between dorsal and adipose fin, or below origin of adipose fin; 3) below middle of adipose fin, or below posterior base of adipose fin; 4) at base of caudal fin.

5 blotches: 1) below middle of dorsal fin; 2) below posterior base of dorsal fin; 3) midway between dorsal and adipose, or below origin of adipose fin; 4) below origin of adipose fin, or below middle of the adipose fin; 5) at base of caudal fin.

6 blotches: 1) below middle of dorsal fin; 2) below posterior base of dorsal fin; 3) midway between dorsal and adipose fin; 4) below origin of adipose fin; 5) below middle of adipose fin; 6) at base of caudal fin.

Ventral side whitish except for scattered melanophores along length of caudal peduncle. Dorsal and pectoral fins (unbranched rays) and adipose spine with melanophores distally. Dorsal fin with 2-3 dark bands or irregular dot rows across soft rays. Caudal fin with 3-4 more or less distinct vertical or chevron-shaped dark cross bars. Pectoral, pelvic, and anal fin without dark spots or bands.

Distribution. *Corydoras diphyes* is restricted in distribution to tributaries of the río Monday and río Acaray, right bank tributaries of the río Paraná (Fig. 2).

Habitats. See under *Otocinclus mimulus*.

Etymology. *Diphyes*, Greek adjective meaning of double nature, in reference to the unique variation in color patterns expressed in this species, striped and blotchy.

Remarks. The genus *Corydoras* includes more than 140 species, and comparisons could not be made with all of them; remarks will be made only on other Paraguayan species and a number of similar species in the Paraguay, Paraná, and São Francisco drainages and south-eastern coastal Brazil with a series of blotches along the side and which require special consideration. The lat-

ter comprise species assigned to the *C. barbatus* group by Nijssen & Isbrücker (1980). We are unaware of any synapomorphies for this group.

Six *Corydoras* species have been reported from Paraguay so far, viz. *C. undulatus*, *C. aeneus*, *C. hastatus*, *C. aurofrenatus*, *C. macropterus*, and *C. ellisae* (Nijssen & Isbrücker, 1979). Our collections also contain *C. polystictus* from the río Aguaray-Guazú (NRM 15925) and Ayolas (NRM 42014).

Corydoras aeneus has immaculate fins and lacks blotches and punctuations on the sides. *Corydoras hastatus* is a very small species with a conspicuous black stripe along the side, contrasting with light body color. *Corydoras undulatus* varies in color pattern, but typically features an irregular pattern with numerous light spots enclosed by blackish lines. *Corydoras polystictus* is overall light with numerous small brown spots on head and sides.

Corydoras diphyes is distinguished from *C. aurofrenatus* in having fewer dorsal lateral scutes (23-24 vs. 24-26), and different color pattern. In *C. aurofrenatus* there are two large dark blotches on the side, one below the adipose fin, and one immediately behind the head, and never any stripe or series of contiguous blotches. *Corydoras aurofrenatus* has no dark markings on the head, but has 3-4 dark stripes across the dorsal fin, and numerous (up to 8) narrow stripes across the caudal fin. Unlike all other Paraguayan *Corydoras* species, the caudal fin lobes are long, and the dorsal lobe significantly longer than the ventral lobe. The holotype of *C. aurofrenatus*, from near Arroyo Trementina, in the río Aquidabán drainage, was apparently in a poor state of preservation at the time of description. It is described as colorless on the sides, but with several narrow cross bars in the caudal fin, which are well evident in the photograph (Eigenmann et al., 1907: 38, fig. 4). Specimens from the arroyo Laguna Penayo, in the río Aquidabán drainage near Concepción (NRM 23529) have very faint body markings and agree with the diagnosis of *C. aurofrenatus.* NRM specimens from elsewhere in Paraguay have faint to boldly expressed blotches on the side, representing a graded series between the *C. aurofrenatus* condition and a pattern resembling or even stronger than that in a specimen from Sapucay [Sapucaí, 25°40'S 56°55'W], figured by Ellis (1913: pl. 28 fig. 1) as *C. flaveolus* Ihering, 1910. Ellis's material of *C. flaveolus* was made type series of *C. ellisae* by Gosline (1940), who did not compare *C. aurofrenatus* and *C. ellisae*. There are no obvious morphometric or meristic differences between lighter and darker colored *C. aurofrenatus*, and all specimens share the distinctive caudal fin color pattern and caudal fin shape. The intensity of dark pigmentation may be habitat related. Lighter colored samples are from open, sandy shores, and darker colored samples are from shaded forest streams. We thus synonymize *C. ellisae* with *C. aurofrenatus*.

Corydoras diphyes is distinguished from *C. bertoni* by shorter dorsal and pectoral spines (pectoral spine shorter than head vs. pectoral spine equal in length to head) and different lateral body coloration (*C. bertoni* is described having light sides with numerous, irregular dark, vertical spots).

The holotype of *C. bertoni*, with locality Puerto Bertoni (on the río Paraná little south of the mouth of the río Monday, at 25°39'S 54°35'W), is the only specimen of the species so far recorded and was reported missing in 1997 (Eschmeyer, 1998). Nijssen & Isbrücker (1980) treated it as a synonym of *C. macropterus*, possibly inspired by the first sentence in the description, "unusually slender with large fins". According to the original description, *C. bertoni* would have 23/21 lateral scutes, similar to *C. diphyes* (23-24/20-21, modally 23/21 in C. *diphyes*), but pigmented pectoral, pelvic and anal fins unlike *C. diphyes:* "Sides light, with numerous, irregular, dark, vertical spots; dorsal with two oblique bands; caudal with three cross bands; anal with a vertical band across anterior third; upper surfaces of pectoral and ventral faintly marked." Although Puerto Bertoni, located on the bank of the río Paraná, is not distant from known localities of *C. diphyes*, it is notably below the lower falls of Paraná tributaries in the region. Collections sent by A. de Winkelried Bertoni to FMNH and ANSP (about 1917?) include only single specimens of widespread floodplain species (NEODAT search 2001-02-07), and no further *Corydoras* specimens than the holotype of *C. bertoni*. There are no recent collections of *Corydoras* from near Puerto Bertoni.

Corydoras macropterus was described on the basis of aquarium material from Paranaguá on the coast of the state of Paraná. In comparison with *C. macropterus* as reported by Regan (1913), *C. diphyes* has longer head (29.2-33.8 % SL vs. 27.4), greater body depth (31.9-37.9 % SL vs. 30.1), shorter dorsal and pectoral fins (dorsal fin reaching the origin of the adipose fin vs. to the tip of adipose fin [female] or base of caudal fin [male]),

averaging fewer dorsal and ventral lateral scutes (23-24/20-21 vs. 24-25/21-22), and different coloration, *C. macropterus* possessing three oblique vertical blotches on the side.

Corydoras carlae from the río Iguazú drainage in Argentina is similar to *C.* sp. aff. *ehrhardti* and *C. ehrhardti* in general aspect and color pattern, apparently with two major, but indistinct blotches along the middle of the side, but appears to be more slender (Nijssen & Isbrücker, 1983: fig. 5). It has 24/21 lateral scutes (Nijssen & Isbrücker, 1983), similar to 23-24/20-21 in *C. diphyes.*

Corydoras carlae is known only from the holotype and a paratype. The type locality given by Nijssen & Isbrücker (1983) would be a tributary of the río Iguazú on road 101 between Puerto Iguazú and Bernardino de Irigoyen [=Bernardo de Irigoyen], 50 km from Puerto Iguazú. Road 101 runs along the water divide between the río Iguazú and the río Urugua-í, mostly crossing tributaries of the Iguazú, and the type locality appears to be in the Arroyo Yacuy near the border of the Iguazú National Park. Nevertheless, and without having additional material of *C. carlae*, Miquelarena et al. (1997) placed the type locality in the Arroyo Urugua-í drainage. Severo & Azevedo (1994) reported *C. paleatus* from several localities in the Brazilian Iguaçu drainage and illustrated it with a fish with very long dorsal and pectoral fins. Garavello et al. (1997) listed both *C. paleatus* and *C.* sp. from the Iguaçu. They considered the former a possible introduction. Their description of the color pattern of the unidentified *Corydoras* species agrees with that of *C. paleatus, C. carlae*, and *C. macropterus. Corydoras macropterus, C. ehrhardti* and *C. paleatus* have been sampled repeatedly in the Iguaçu drainage (R. Reis, pers. comm., MCP collection).

Corydoras steindachneri, also from Paranaguá, is very similar to *C. carlae* and *C. ehrhardti. Corydoras diphyes* is distinguished from *C. steindachneri* as described from two specimens by Isbrücker & Nijssen (1973) by body proportions, e.g., a longer head (29.2-33.8 vs. 27.5-28.4 % SL), greater body depth (31.9-37.9 vs. 30.3-32.2 % SL), broader coracoid (42.9-57.4 vs. 31.8-37.8 % head length), and different coloration on both fins and body (*C. steindachneri* has two large, rounded, midlateral blotches).

Corydoras ehrhardti from the Jaraguá mountains near Joinville (*C. meridionalis* von Ihering, 1911 from Colonia Hansa is a synonym according to Nijssen & Isbrücker, 1980) features tree large
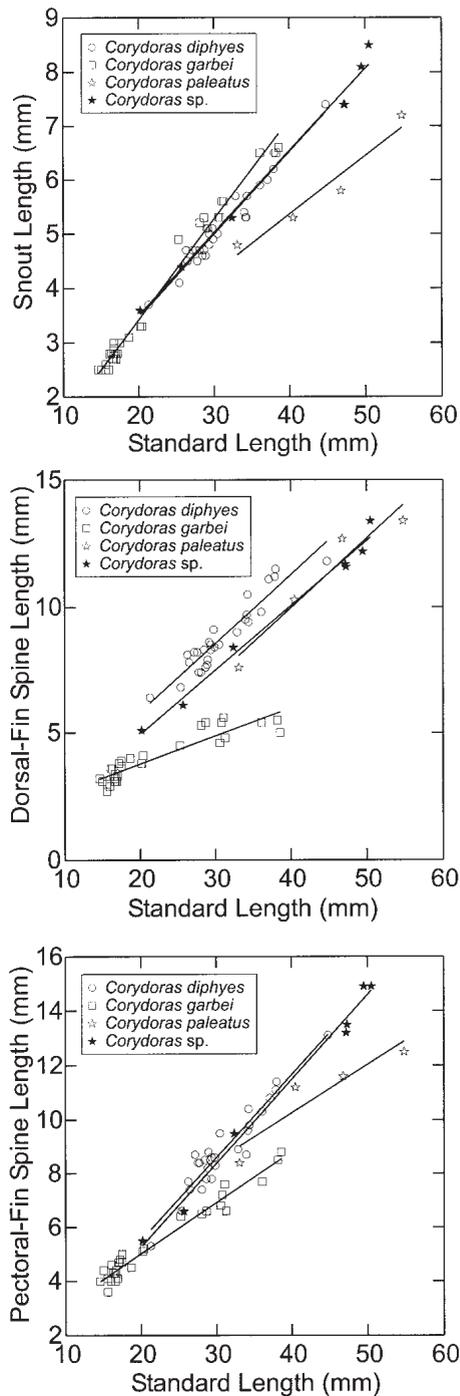

Fig. 7. Snout length, dorsal spine length and pectoral spine length plotted against standard length, showing major morphometric differences between *Corydoras diphyes, C. garbei* (Tables 8-9), *C.* sp. aff. *ehrhardti.* (Table 10), and *C. paleatus* (Table 11).

dark blotches, one at the dorsal fin base, one anteriorly on the side and one posteriorly on the side between the adipose fin and anal fin.

Corydoras diphyes is distinguished from *C. paleatus* by having a longer snout and shorter pectoral fin (Fig. 7). In *C. paleatus* the pectoral spine exceeds the length of the head. In *C. paleatus* all fins are intensely pigmented, including dark blotches on pectoral, pelvic and anal fin, and along the middle of the side runs a series of large blackish, more or less confluent blotches.

Corydoras sp. aff. *ehrhardti* from eastern Uruguay and Rio Grande do Sul is characterized by two dark blotches, one anteriorly and one posteriorly on the side, similar to *C. ehrhardti*. Males of

this species have elongated first two branched dorsal fin rays. This species seems to be identified as *C. paleatus* in current literature (e.g., Sands, 1990).

Corydoras nattereri deviates from *C. diphyes,* as well as all other species listed in this comparison, by a color pattern essentially consisting of a dark blotch close to the dorsal fin base and a well-delimited stripe along the middle of the sides, and fins without dark spots or stripes.

Corydoras diphyes is distinguished from similar-sized *C. garbei* by having a shorter and more narrow snout, longer dorsal and pectoral fins, a different relation between length of dorsal and pectoral fins (Fig. 7; Tables 7-11), different serra-

Table 8. Morphometry of *Corydoras garbei*, juveniles. Measurements are in per cent of SL, except SL (mm) and regression line (linear, Y=a+bX) parameters which are calculated from original measurement data in mm. Regressions are all significant at P<0.005 (ANOVA).

	N	min	max	mean	SD	a	b	r
SL (mm)	20	14.6	20.4	16.9	1.48			
Fontanel	20	43.6	48.7	46.2	1.44	0.113	0.040	0.939
Head length	20	29.9	34.3	32.5	1.15	−0.441	0.351	0.941
Snout length	20	15.6	18.0	16.7	0.59	0.235	0.153	0.921
Caudal peduncle length	20	26.3	32.1	29.7	1.71	1.331	0.218	0.767
Caudal peduncle depth	20	12.8	15.0	14.0	0.56	0.178	0.129	0.895
Dorsal spine length	20	17.3	22.4	20.1	1.58	0.030	0.199	0.749
Pectoral spine length	20	23.1	29.3	26.2	1.68	0.855	0.211	0.760
Body depth	20	28.3	31.5	30.3	1.03	0.865	0.252	0.922
Body width	20	25.6	28.1	26.8	0.80	0.626	0.231	0.943
Coracoid width	20	12.7	16.3	14.9	0.92	−0.530	0.181	0.873
Orbit diameter	20	10.2	12.3	11.0	0.57	0.840	0.060	0.842
Interorbital width	20	10.9	14.0	12.3	0.73	1.088	0.059	0.716

Table 9. Morphometry of *Corydoras garbei,* adults. Measurements are in per cent of SL, except SL (mm) and regression line (linear, Y=a+bX) parameters which are calculated from original measurement data in mm. Regressions are all significant at P<0.005 (ANOVA), except for dorsal spine length.

	N	min	max	mean	SD	a	b	r
SL (mm)	10	25.3	38.6	31.9	4.40			
Fontanel	10	39.5	43.9	41.7	1.41	0.119	0.038	0.973
Head length	10	30.6	33.2	31.9	0.95	0.933	0.289	0.976
Snout length	10	17.0	19.4	17.9	0.75	1.294	0.138	0.974
Caudal peduncle length	10	24.3	28.9	26.5	1.47	2.419	0.188	0.931
Caudal peduncle depth	10	14.4	17.1	15.5	0.81	1.146	0.119	0.937
Dorsal spine length	10	13.0	18.9	16.4	2.07			
Pectoral spine length	10	21.1	25.3	22.9	1.29	1.521	0.180	0.925
Body depth	10	31.0	35.2	33.1	1.19	1.146	0.295	0.971
Body width	10	24.6	28.5	26.7	1.07	1.725	0.212	0.966
Coracoid width	10	14.8	17.2	16.2	0.74	0.983	0.131	0.941
Orbit diameter	10	7.9	10.7	9.2	0.83	1.804	0.034	0.867
Interorbital width	10	13.2	16.2	14.8	1.05	1.768	0.091	0.858

tion on the inner edge of the pectoral fin, and three instead of usually two pre-adipose scutes (*C. garbei*: 1 (1), 2 (27), 3 (2)). *Corydoras garbei* (Fig. 8a) has a distinct dark stripe across the dorsal fin, and stripes on the caudal fin straight or only slightly curved instead of chevron-shaped, and a trunk color pattern consisting of distinct large blotches both on the dorsum and the sides, and not arranged primarily in a lateral row as in *C. diphyes*.

Discussion

Mimetic association. We interpret the co-existence and similarity of *Corydoras diphyes* and *Otocinclus mimulus* as a likely case of coevolved mimicry. Our interpretation of this mimetic association demands consideration of constraints expressed by theories of mimicry and coevolution.

Cryptic coloration and mimicry, combined with behavioral characters, are antipredation tactics (Wickler, 1968; Lowe-McConnell, 1987). Cryptic coloration (camouflage, mimesis) serves to protect the individual by resembling the substrate or the background. Thus, being camouflaged is a way of avoiding giving signals to a predator. As cryptic coloration – to make the

Table 10. Morphometry of *Corydoras* sp. aff. *ehrhardti*. Measurements are in per cent of SL, except SL (mm) and regression line (linear, Y=a+bX) parameters which are calculated from original measurement data in mm. Regressions are all significant at P<0.005 (ANOVA).

	N	min	max	mean	SD	a	b	r
SL (mm)	7	20.2	50.5	39.0	12.6			
Fontanel	7	4.1	5.0	4.4	0.28	0.212	0.038	0.992
Head length	7	30.1	33.5	31.5	1.20	0.899	0.289	0.998
Snout length	7	15.6	17.8	16.5	0.78	0.453	0.152	0.994
Caudal peduncle length	7	25.2	27.7	26.3	1.05	0.891	0.237	0.998
Caudal peduncle depth	7	13.3	14.8	14.0	0.58	0.284	0.132	0.990
Dorsal spine length	7	23.7	26.5	25.1	0.94	−0.194	0.256	0.993
Pectoral spine length	7	25.7	30.1	28.3	1.52	−0.972	0.311	0.995
Body depth	7	33.7	37.4	36.1	1.28	−0.203	0.368	0.997
Body width	7	26.4	28.2	27.3	0.65	0.381	0.262	0.999
Coracoid width	7	15.0	17.5	16.1	0.93	0.616	0.143	0.988
Orbit diameter	7	8.3	11.9	9.7	1.54	1.364	0.057	0.990
Interorbital width	7	12.5	14.8	13.4	0.82	0.441	0.122	0.983

Table 11. Morphometry of *Corydoras paleatus*. Measurements are in per cent of SL, except SL (mm).

|	NRM 36856	NRM 39325	NRM 39309	NRM 39305	mean	SD
SL (mm)	33.1	40.5	46.8	54.8	43.8	9.23
Fontanel	4.1	3.9	3.9	3.7	3.9	0.17
Head length	30.2	28.9	28.4	27.7	28.8	1.04
Snout length	14.5	13.1	12.4	13.1	13.3	0.88
Caudal peduncle length	29.3	27.7	27.4	26.6	27.7	1.13
Caudal peduncle depth	14.8	12.6	12.2	10.6	12.5	1.74
Dorsal spine length	23.0	25.4	27.1	24.5	25.0	1.75
Pectoral spine length	25.4	27.7	24.8	22.8	25.2	1.99
Body depth	37.5	36.5	33.1	33.8	35.2	2.11
Body width	26.0	26.4	25.6	27.4	26.4	0.75
Coracoid width	16.3	15.3	14.7	17.2	15.9	1.07
Orbit diameter	9.7	9.1	8.8	8.0	8.9	0.69
Interorbital width	15.4	13.6	13.0	11.7	13.4	1.54
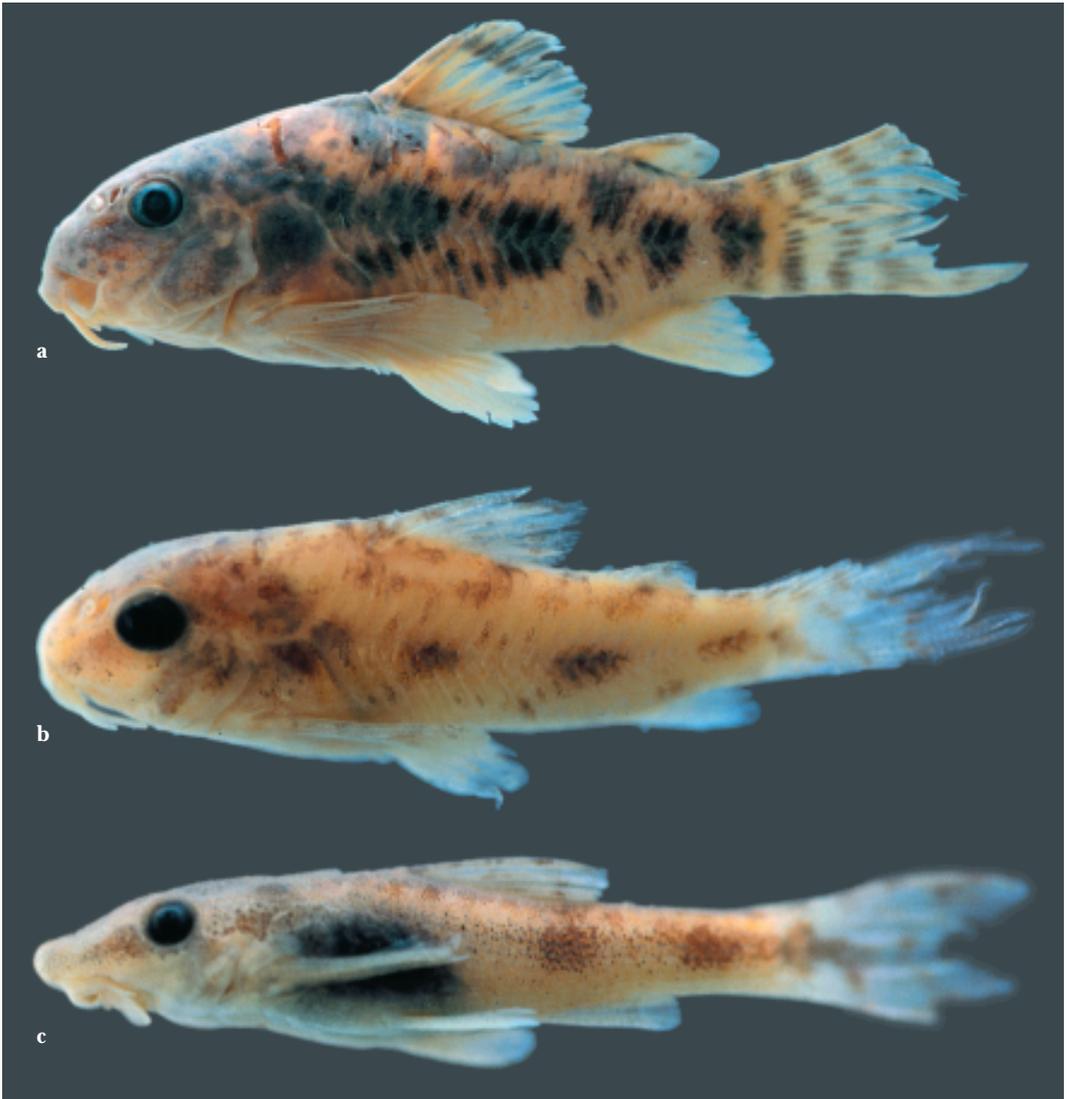
Fig. 8. a, *Corydoras garbei,* MCP 16993, adult, 29.6 mm SL; Brazil: Bahia: Rio São Francisco drainage, Guanambi; **b,** *C. garbei,* MCP 16916, juvenile, 16.7 mm SL; Brazil: Minas Gerais, Monte Azul, Rio São Francisco drainage, Arroio Salinas 51 km WSW of Monte Azul; **c,** *Otocinclus xakriaba,* MCP 16905, adult, 17.9 mm SL; same locality as Fig. 8b.

animal less conspicuous – must blend with the background or environment, the animal must either match the substrate, search for a matching background or change its coloration. The latter two alternatives are called cryptic behavior and can be observed among different groups of animals when changing habitats, e.g., in correspondence with seasonal changes, or when threatened by a potential predator (Wickler, 1968). It has been observed, for example among several spe-

cies of *Corydoras,* that the fishes, after an initial evasive reaction to threat, lay still. This freezing behavior has been suggested as a component of crypsis in *Corydoras* (Sands, 1994). The antipredator effect of both cryptic coloration and freezing behavior has, however, been contested with the reason that most species do not use either of these options and still continue to exist (Eigenmann & Allen, 1942; Wickler, 1968).

Mimicry, which involves a model, a mimic

and a signal-receiver (e.g., a predator), is usually separated into Batesian and Müllerian mimicry (Wickler, 1968). Mimicry can be recognized in that a signal of interest (originally from a model) to the signal-receiver is imitated by a mimic. Mimetic characters are functional only in the presence of definite behavior patterns and a complex of mimetic characters usually incorporates behavior patterns that are more ancient than the anatomical features (Wickler, 1968).

In Batesian mimicry a palatable mimic imitates an unpalatable model in order to deceive a predator. The Batesian mimic benefits at the expense of both model and predator. The model must be more common than the mimic, since the presence of a mimic weakens the deterrent effect due to occasional experimental attacks by predators (Wickler, 1968; Huheey, 1988). Model fitness decreases with increasing mimic-frequency, and selection favors divergence from the color pattern shared with the mimic. Fitness of the mimic also decreases with increasing mimic-frequency. The result may be a coevolu!ionary chase between model and mimic, as natural selection favors the model diverging from the color pattern of the mimic and the mimic following the changes of the model (Thompson, 1994). Populations involved in Batesian mimicry often produce stable polymorphism, rarely more than two morphs (Huheey, 1988; Thompson, 1994).

In Müllerian mimicry two (or more) more or less inedible species have similar appearance. Closely related species may also be Müllerian mimics because of their parallel evolution. With similar appearance, a predator will only have to learn one type of warning signals, which reduces predation on each species (Wickler, 1968; Huheey, 1988). The advantage increases with increasing density. Resemblance need not necessarily to be as exact as in Batesian mimicry – reminding the predator is enough, since both mimic and model are unpalatable (Huheey, 1988), but different looking phenotypes could suffer lower fitness, because predators might not recognize and avoid rare patterns (Thompson, 1994). In Müllerian mimicry natural selection favors fixation of the most common model and almost all Müllerian mimicry complexes are locally monomorphic (Huheey, 1988; Thompson, 1994). If one species is rarer than the other, the more abundant species is likely to be the model. Sexual dimorphism is not supposed to occur or to be conspicuous.

Similarity and relationship. Several causal and functional aspects of acquired resemblance have been identified and discussed at length (e.g., Wickler, 1968; Brower, 1988; Sands, 1994; Thompson, 1994). Except where closely related species are concerned, far-reaching resemblance among syntopic species is supposed to have a co-evolutionary explanation. Shared external appearance between syntopic species could actually be undesirable as it could confuse intraspecific recognition and courtship (Wickler, 1968; Sands, 1994). Thus, the resemblance must convey an obvious gain for at least one of the species.

Co-evolved mimetic resemblance can easily be confused with simple ancestral resemblance. Thus, small characoid fishes of similar shape and simple color pattern often occur in mixed shoals. This similarity may have a functional significance for formation of mixed-species shoals, but is plesiomorphic in terms of acquisition of the characters marking the resemblance.

The basic test of evolutionarily acquired shared external appearance among interacting syntopic species is that they are not closely related phylogenetically. Any statement of acquired similarity in such species must therefore be backed by a phylogenetic analysis showing that the character was not already present in a common ancestor.

Both the Callichthyidae and the Loricariidae are corroborated as monophyletic groups (de Pinna, 1998), and *C. diphyes* and *O. mimulus* are not similar due to symplesiomorphy. The similarity between *O. mimulus* and *C. diphyes* can thus be labeled as either (1) plesiomorphic characters shared with other loricariids and callichthyids, or (2) independently derived autapomorphies of the species or the clades in which they are contained, or (3) co-evolved resemblance. The actual resemblance includes both prerequisite and interactive components. Prerequisites include agreement in size and a basic pigmentation that can be modified. Interactive components include autapomorphies of both species, and seem here to be restricted to color pattern. Thus, similarity in coloration can be treated as a derived character, at least for the *Otocinclus* species (cf. Wickler, 1968; Gilbert, 1983; Thompson, 1994).

Similarity and camouflage. One possible explanation of similarity between sympatric species is that the shared colors and similar color patterns serve as camouflage, equally appropriate for both

species but independently evolved. Similarity in color pattern thus also has to be evaluated comparing with other species in the same habitat and with related species of the systematic groups concerned.

Independently evolved coloration within the *C. diphyes* - *O. mimulus* species pair is less probable for two reasons. First, other species, including those with a cryptic body coloration sharing the same environment, do not have a similar color pattern, not even other Loricariidae or Callichthyidae. Second, the coloration is unusual within the genera, especially in *Otocinclus*. If there are genetic constraints concerning the coloration exhibited by the species pairs, there is reason to assume that species of the same genus would look more alike than species from different families (Thompson, 1994).

Conspicuous characters in models. In the theories of Batesian and Müllerian mimicry as well as in the examples given, the models are more or less unpalatable. They signal this unpalatability to a signal receiver usually by being conspicuously colored or by having conspicuous morphological characters. In doing this they avoid mistakes made by a predator (e.g., Wickler, 1968; Gilbert, 1983; Pough, 1988; Huheey, 1988; Thompson, 1994). The early theories of mimicry are based on observations made on diurnal butterflies, which are generally brightly colored (Wickler, 1968; Gilbert, 1983). There are numerous examples supporting this, but there also exist examples of mimicry where the model is not necessarily conspicuous by having bright colors.

Evolution of mimicry. Mimicry is a coevolutionary process (Gilbert, 1983; Thompson, 1994). Both Batesian and Müllerian mimicry genetically involve a two-stage process, where major genes of the mimic produce a fairly close resemblance to the model in the first step. Smaller effects, local or individual, to increase the resemblance are secondarily accomplished by modifier genes (Thompson, 1994). Coevolution resulting in a mimetic association is possible only when the species involved co-exist during a long period of time, with stable ecological conditions and show definite behavior patterns (Wickler, 1968; Thompson, 1994).

***Corydoras* as model in Batesian mimicry.** The first issue to consider is what form of mimicry operates between *C. diphyes* and *O. mimulus* –

Batesian or Müllerian. The relative unpalatability and frequencies of model and mimic are important ecological conditions in Batesian and Müllerian mimicry (Gilbert, 1983; Huheey, 1988; Thompson, 1994).

Size. *Corydoras diphyes* and *O. mimulus* are similar in size. The size range of available C. *diphyes* is 21-45 mm, and that of *O. mimulus* 29-43 m SL, except one extraordinary large specimen of *O. mimulus*, 49.8 mm. Thus the two species are similar in size and their color markings are of similar magnitude. The *Corydoras* species is much more deep-bodied but this may be irrelevant since the most conspicuous markings are along the middle of the side only.

Palatability. All *Corydoras* species have a bony armor and a strong and sharp spine in the dorsal fin and each pectoral fin. When handled the spines are raised and locked in a position away from the body. Structures like body armor and stout spines (combined with behavioral devices – see below) are typical antipredation devices. A triangle of erect spines increases the effective size, making a small fish available only to larger piscivores (Lowe-McConnell, 1987). The pungent dorsal and pectoral fin spines and the bony body armor make *C. diphyes* less suitable as prey than *O. mimulus* or other *Otocinclus* species that lack strong armor or spines as well as other obviously repellent traits.

A small fish that predominantly has to escape and hide from its predators by seeking shelter, would suffer less fitness by having erect spines on the dorsal and pectoral fins. This suggests another kind of behavior to escape or discourage predators in *Corydoras*. The coloration probably derives from crypsis (cf. above), offering protection when living close to the bottom. Fish with cryptic coloration must lie still to match the background, e.g., the bottom (freezing behavior). If spotted anyway, being unpalatable is an important selective advantage. If an individual is unpalatable to its predators, that individual will gain from being recognized when spotted, e.g., by having aberrant coloration. Conspicuous appearance would in that case originate from originally cryptic coloration, a condition that is thought not to be uncommon (Guilford, 1988).

Corydoras diphyes and *O. mimulus* thus fulfill requirements of differences in palatability under the Batesian mimicry model, but also have dis-

tinctive if cryptic color signals by which a predator can recognize them.

Relative frequency. Most theories about Batesian mimicry postulate the model to be more common than the mimic, at least initially (Huheey, 1988). Otherwise the predator would have little or no option of realizing a potential of learning to avoid a particular species. The collecting methods we used (seines and small nets), do not allow for calculating exact frequencies, but *Corydoras* specimens are much more common in the samples (Table 3). Both *O. mimulus* and *C. diphyes* vary in color patterns. About 50 % of the specimens in both species had a continuous stripe, the rest had blotches or broken stripes. Polymorphism is known from Batesian mimicry, but is rarely expressed by more than two morphs (Huheey, 1988; Thompson, 1994). The existence of polymorphism in *O. mimulus* and *C. diphyes* supports a hypothesis of Batesian mimicry.

Predator and microhabitat segregation. For the mimesis to work, a signal-receiver is required. The habitats of *C. diphyes* and *O. mimulus* are generally species poor, and none of the localities featured the otherwise common predatory fishes of the genera *Hoplias* or *Hoplerythrinus*. Occasional localities featured small catfish predators, such as *Rhamdia quelen*, *Hepapterus mustelinus*, or other fishes capable of eating small fish. The most significant predator, however, may be *Crenicichla lepidota*, which is widespread in the Paraguay and Paraná basins, and also occurring along the coast of Uruguay and southern Brazil (Kullander, 1982). We favor this species as a component of the *Corydoras-Otocinclus* mimesis because it is a diurnal, visually oriented species, with elaborate jaw mechanics suitable for manipulating potentially unpalatable prey, and is expected to be able to react on the spines of *Corydoras* by ejecting the prey.

A significant aspect of the hypothesized mimesis of *Otocinclus mimulus* and *Corydoras diphyes* is that the two species occupy different microhabitats. This means that *O. mimulus* pursues its mimicry advantage without interaction with the model, and must imply that the selection driving the mimicry rests entirely on a predator that must move between the different microhabitats. We call this kind of mimicry 'decoupled', referring to the lack of direct association between the model and mimic. In most cases of

mimicry the model and mimic interact directly, commonly by swimming in the same schools or frequenting the same microhabitat.

Most fish predators in the area that we sampled, including bottom-dwelling catfishes and potential mid-water acestrorhynchids (not captured), use only some of the microhabitats available. The cichlids are diurnal, visually oriented fishes, and are capable of moving between microhabitats. The mouth size of the *Crenicichla* species is proportionally suited to holding an adult *Otocinclus* or *Corydoras*. We therefore hypothesize that the *Crenicichla* found in sympatry with *O. mimulus* and *C. diphyes* represents a predator compatible with the decoupled mimicry model.

We are not able to test this hypothesis directly, because very few specimens of *Crenicichla* were collected with *O. mimulus* or *C. diphyes* (Table 3). The largest specimen is 88.5 mm SL, which is subadult size, but an adult *O. mimulus* can be pressed through the mouth. In none of our Paraguayan localities did we find large numbers of *Crenicichla lepidota*. In 79 samples, only three contain more than 9 specimens. A second species of *Crenicichla* also occurs in the Acaray and Monday rivers. This is an undescribed species similar to *C. niederleinii*, and mostly found in or near rapids, i.e., in a habitat where neither *O. mimulus* nor *C. diphyes* were collected, and it was collected with *C. diphyes* at one site only.

Species-pairs of *Otocinclus* and *Corydoras*. In addition to *O. mimulus* and *C. diphyes,* there are also other syntopic pairs of *Otocinclus* and *Corydoras* described from southern South America, which potentially represent mimicry pairs. These include *O. flexilis* co-occurring with *C. paleatus* in Uruguay and Argentina, and sharing a pattern of elongate blotches and distinctly marked fins; *O. affinis* and *C. nattereri* (Sands, 1990), principally from the río Paraná drainage in the state of São Paulo and the state of Rio de Janeiro in Brazil, sharing a simple pattern with a horizontal stripe along the middle of the side.

In our comparative material of *O. xakriaba* and *C. garbei*, from the rio São Francisco basin in Brazil, we notice one large sample of both species, consisting of juvenile *C. garbei* (MCP 16916; Fig. 8b) and adult *O. xakriaba* (MCP 16905; Fig. 8c). These specimens are conspicuously similar in general color, color pattern and shape. Adult *C. garbei*, however, have a unique distinct color pattern different from that of juveniles and from

O. xakriaba. We hypothesize that in this species pair, *O. xakriaba* may be mimicking only the juvenile *C. garbei*, what may explain the small size of *O. xakriaba*, which is the smallest species in the genus. Adult *C. garbei* have a significantly shorter dorsal and pectoral spine than other *Corydoras* species in our morphometric comparison (Fig. 7), but juvenile *C. garbei* have spine lengths comparable to that expected from juveniles of other species (Fig. 7), suggesting that the antipredatory role of the spines may be insufficient in large *C. garbei* to support a mimicry association, and that the spine length in *C. garbei* may be driving the evolution of *O. xakriaba* to small adult size.

Within the species-pairs, species are similar both in size and coloration, i.e., in visual appearance, but pairs differ significantly from each other. At present 15 species of *Otocinclus* are recognized (Table 6*). Otocinclus mimulus, O. xakriaba* and *O. flexilis* are the only members of the genus with blotches as main elements of the coloration, all of them distributed in southeastern South America. *Otocinclus affinis* has a narrow midlateral stripe by which it resembles the sympatric *C. nattereri* more than any other *Otocinclus* species. The basic coloration of the other ten *Otocinclus* species consists of a continuous, more or less broad stripe from head to caudal fin.

The color of all the species included in the *Otocinclus-Corydoras* species-pairs is pale ochre with brown medium-sized blotches and/or stripes, and the color pattern includes elements with phylogenetic signal. The coloration probably derives from crypsis, at least in *Corydoras* (as discussed above), giving protection by camouflage for species living close to sandy or muddy bottoms and modifications may be largely driven by mimicry factors. This again suggests that mimicry behavior may act as a key innovation in phylogenetic lineages and become incorporated in the evolutionary strategy of the species. The colors are shared with some other sympatric species, but the color pattern and high degree of similarity within the species-pairs are not seen in any other species.

Phylogenetic analysis. This transformation in the mimic, resulting in a coloration that deviates from other closely related species, as well as most species in its own genus, is a derived character state (Gilbert, 1983; Thompson, 1994). The correlated behavior, however, may be plesiomorphic. Also behavioral characters, when possible to code numerically and thus included in a data matrix, should be used in phylogeny reconstruction (de Pinna, 1997). By including mimicry as a character in the analysis of *Otocinclus*, we obtained a better resolved tree than without, and obtained monophyly of the mimicry group, with mimicry as a synapomorphy (Fig. 4b), and corresponding to a southern geographic distribution and mostly blotchy color pattern in distinction from the majority of *Otocinclus* species, which are found chiefly in northern South America, and have a contrasting broad midlateral stripe.

The inter-relationships among species of *Corydoras* are not resolved. Recently doubts have been raised about the monophyly of the genus *Corydoras* (Reis, 1998a) and analysis of some synapomorphies have resulted in a hypothesis of some *Corydoras*-groups being more related to, e.g., *Brochis* Cope, 1871, than to other *Corydoras* species (Britto, 1997). A test of the mimicry association will be obvious from a phylogenetic analysis of the *Corydoras* species hypothesized to be associated with particular *Otocinclus* species.

Comparative material. *Corydoras garbei*. MCP 16993, 30, 10 measured: 25.3-38.2 mm SL; Brazil: Bahia: Guanambi: rio São Francisco drainage: rio Pau da Colher, on the road between Guanambi and Mutas; 14°12'48"S 42°49'30"W; 18 Jul 1993, R. E. Reis et al. – MCP 16916, 74, 20 measured: 14.6-20.4 mm SL; Brazil: Minas: Monte Azul: rio São Francisco drainage, Arroio Salinas 51 km WSW of Monte Azul, on road to Jaiba; 15°12'53"S 43°15'49"W; 19 Jul 1993, R. E. Reis et al. – NRM 45408, 4, 25.2-28.7 mm SL; Brazil: Minas Gerais: Januáro/Itacarambi: rio Peruacu, left bank tributary to the rio São Francisco; 24-30 Nov 1990, D. F. Moraes et al.

C. paleatus. NRM 36856, 1, 33.1 mm SL; NRM 39309, 1, 46.8 mm SL; Uruguay: Rocha: Arroyo de la Rocha drainage: Arroyo Las Conchas on road Velásquez-Rocha (Ruta No 15), close to Rocha; 14 Nov 1997, S. O. Kullander & F. Cantera. – NRM 39305, 1, 54.8 mm SL; NRM 39325, 1, 40.5 mm SL; Uruguay: Canelones: Arroyo Pando drainage: Arroyo Tropa Vieja, 3 km from Salinas at bridge at road 87; 19 Nov 1997, S. O. Kullander & F. Cantera.

C. sp. aff. *ehrhardti*. NRM 27857, 6, 20.2-50.5 mm SL; Brazil: Rio Grande do Sul: Capão da Canoa, 'rio Cornélios', channel linking lagoa dos Quadros and lagoa Itapeva, at Vila Cornélios; 1 Oct 1989, S. O. Kullander et al. – NRM 36663, 1, 32.4 mm SL; Uruguay: Florida: arroyo Valentines, about 10 km from Valentines; 21 Nov 1997, S. O. Kullander & F. Cantera.

Otocinclus flexilis. MCP 9644, 21, 27.1-36.1 mm SL; Brazil: Rio Grande do Sul: rio Uruguay drainage, rio Santa Maria, at km 246 along BR-293, from Dom Pedrito to Santana do Livramento; 26 Oct 1982, C. A. S. Lucena & L. R. Malabarba. – NRM 9338, 3, 28.2-33.9 mm SL;

Argentina; 1891, Kullberg. – NRM 39307, 1, 44.3 mm SL; NRM 39315, 9, 28.8-36.3 mm SL; Uruguay: Canelones: arroyo Pando drainage, arroyo Tropa Vieja, 3 km from Salinas at bridge at road 87; 34°45'1"S 55°50'46"W; 19 Nov 1997, S. O. Kullander & F. Cantera. – NRM 43137, 2, 26.5-28.1 mm SL; Paraguay: Departamento Itapúa: río Paraná drainage: arroyo Tacuary at road 1 bridge; 27°12'23"S 56°10'3"W; 20 Feb 1998, S. O. Kullander et al.

O. xakriaba. MCP 16905, 70, 20 measured: 17.8-25.2 mm SL; Brazil: Minas Gerais: Monte Azul: rio São Francisco drainage, arroio Salinas 51 km WSW of Monte Azul, on road to Jaiba; 15°12'53"S 43°15'49"W; 19 Jul 1993, R. E. Reis et al.

Acknowledgements

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