

A systematic review of *Planaltina* (Teleostei: Characiformes: Characidae: Glandulocaudinae: Diapomini) with a description of two new species from the upper rio Paraná, Brazil*

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Abstract.—Two new species, *Planaltina glandipedis* and *Planaltina britskii*, glandulocaudine fishes of the family Characidae, tribe Diapomini, are described herein. They were collected from tributaries of the rio Grande and or the rio Tietê, both tributaries of the upper rio Paraná in the State of São Paulo, Brazil. The previously described species, *Planaltina myersi*, until now known almost exclusively from the holotype, is here redescribed from 47 specimens taken from tributaries of the rio Corumbá, a tributary of the upper rio Paraná. The two new species differ most prominently from the previously known species by possession of three somewhat elongate scales along the dorsal border of the male's caudal pouch opening. There is only one elongate scale in *P. myersi*. *Planaltina glandipedis* differs from *P. britskii* in having six or seven horizontal scale rows between the dorsal-fin origin and the lateral line versus five in the later species. The possible phylogenetic relationships among the three inseminating species within the tribe Diapomini, subfamily Glandulocaudinae, are discussed along with the putative phylogenetic relationships of the Diapomini to the newly recognized glandulocaudine outgroup containing the characid genera *Knodus* and a new genus related to *Attonitus*. Brief comments are presented concerning the geographical distribution and ecology of the species of *Planaltina*.

Resumo.—Duas novas espécies, *Planaltina glandipedis* e *Planaltina britskii*, peixes glandulocaudineos da família Characidae, tribo Diapomini, são aqui descritas. Elas foram coletadas em afluentes do rio Grande e/ou do rio Tietê, ambos tributários do rio Paraná no Estado de São Paulo, Brasil. A espécie apenas descrita, *Planaltina myersi*, conhecida até o presente apenas a partir do holótipo, é aqui redescrita com base em 47 exemplares originários do rio Corumbá, também tributário do rio Paraná. As duas espécies novas diferem marcadamente da espécie previamente conhecida pela presença de três escamas algo alongadas ao longo da margem dorsal da abertura da bolsa glandular dos machos. Há apenas uma escama alongada em *P. myersi*. *Planaltina glandipedis* difere de *P. britskii* pela presença de seis ou sete séries horizontais de escamas entre a

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origem da nadadeira dorsal e a linha lateral ao invés de cinco na última espécie. As possíveis relações filogenéticas entre as três espécies, todas inseminadoras dentro da tribo Diapomini, subfamília Glandulocaudinae, são discutidas juntamente com as relações filogenéticas tentativas de Diapomini com o grupo externo recentemente reconhecido de Glandulocaudinae constituído pelos gêneros *Knodus*, *Attonitus* e um novo gênero relacionado a *Attonitus* da família Characidae. Breves comentários são feitos sobre a distribuição geográfica e ecologia das espécies de *Planaltina*.

Relatively little is known about *Planaltina* Böhlke (1954:265) except from its original description based on *Planaltina myersi* described from a single damaged specimen collected through the use of dynamite. This specimen, the holotype, was collected from "Sarandi brook, Planaltina, Goyaz, Brazil," 21 September 1923 by Dr. Carl Ternetz. Böhlke (1954:265–267) was uncertain of the relationships of *Planaltina*, but considered it to possibly be among the "borderline" genera (between the Tetragonopterinae and Glandulocaudinae of Eigenmann) . . ." Böhlke referred to these genera as *Landonia*, *Argopleura*, *Acrobrycon*, and *Phenacobrycon*. Böhlke (1954) doubted the monophyly of the Glandulocaudinae and considered that these genera and the divergent members of the Glandulocaudinae may have arisen "at different times from different members of such generalized tetragonopterines as *Bryconamericus*." No additional specimens were examined until Weitzman & Fink (1985:106) listed additional specimens with locality data. Weitzman et al. in Weitzman & Fink (1985:113) published a critique of the concept of the monophyly of the Glandulocaudinae and concluded that there was insufficient evidence to confirm or reject the monophyly of the subfamily. Burns et al. (1995:135–143) provided information that *P. myersi* is an inseminating species with aquasperm. Weitzman & Menezes (1998:184) assigned this species to the Diapomini, which also included species of the characid genera *Acrobrycon* Eigenmann and *Diapoma* Cope, and, based on additional gross

anatomical, histological, and sperm ultrastructural evidence, concluded that the Glandulocaudinae are probably monophyletic. Weitzman & Menezes (1998) also illustrated the osteology of the caudal region and associated caudal organ of *P. myersi*.

We provide a new definition of *Planaltina*, redescribe *P. myersi* based on 47 specimens and discuss its putative relationships with the two new species described herein. We also briefly discuss the possible phylogenetic relationships of the Diapomini to the Glandulocaudinae and to some of the characid species currently in the genera *Attonitus* Vari & Ortega, *Knodus* Eigenmann and a species of a new genus Weitzman et al. (2004). Species of *Attonitus*, the new genus and *Knodus* lack caudal organs as described for adult glandulocaudine males, but some species of *Knodus* and the three species of *Attonitus*, and the species of the new genus were recently found to be inseminating, Weitzman et al. (2004), and at least some of these have one or more of the synapomorphies of the primary and/or secondary sexual systems of glandulocaudines that were used by Weitzman & Menezes (1998) to diagnose that subfamily. Furthermore, sexually active males of one of the new species described here, *P. glandipedis*, has numerous club cells at or near the surface of the skin of the pelvic fins and the anterior part of the anal fin whereas the species of *Attonitus* and the new genus possibly related to *Attonitus* are found to have club cells at or near the surface of the skin in the anterior part of the anal fin. These cells have been shown to secrete in a holocrine man-

ner in the species of the new genus. See Weitzman et al. (2004) for a more detailed discussion of the taxonomic distribution of these apparent glandulo-caudine and glandulo-caudine outgroup synapomorphies. Those authors also discuss the possible phylogenetic relationships of species of the glandulo-caudine tribes with the outgroup characid species currently in *Knodus*, the new genus, and *Attonitus* as well as their apparent relatives not belonging to the Glandulo-caudinae. The putative monophyletic relationships among the glandulo-caudine tribes recognized by Weitzman & Menezes (1998) must again come into question and be reinvestigated in light of the newly recognized outgroup species for the putative glandulo-caudine genera and tribes.

Methods and Materials

Counts and measurements and methods of taking and presenting data follow Menezes & Weitzman (1990:382–383) unless otherwise stated. For the most part, statistical comparisons were calculated using SigmaStat 2.0 for Windows 95. Meristic and morphometric data of males and females were treated separately in order to probe possible differences between the sexes, but secondary sexual differences were detected only in morphometric data. Morphometric data were transformed into ratios of standard length, or head length when they were subunits of that length, and are presented separately for males and females in the tables and regression graphs.

Although we summarize the statistical procedures used herein, see Weitzman & Malabarba (1999:2–4) and Weitzman & Palmer (1997:213–214) for more complete comments about their use. In making pairwise statistical comparisons of counts, all population samples except those few with non-variable counts were found to be at least somewhat skewed about the mean. In running simple *t*-tests, all paired samples failed to pass the normality test and some failed to pass an equal variance test. Thus

all pairwise comparisons of counts were made using Mann-Whitney rank sum tests, but also in all cases the results of simple *t*-tests were compared and although not testing the same statistical parameters, both were used to evaluate differences among the species. In most cases both kinds of tests were found to indicate the same overall statistical results regarding a statistical test of null hypotheses of character similarities. However, in a few cases the *t*-test and the Mann-Whitney rank sum test provided opposing results. In these cases the statistical results were of marginal significance for both kinds of tests, and we opted to disregard the resulting hypotheses of differences, especially considering the population sample size limitations.

We utilized Tukey box plots for visual comparison of count distributions of the three species. In these plots the mean is represented by a thick vertical bar, the median by a thin vertical line that is often the same as one of the vertical lateral borders of the boxes. Therefore, the numerical value of the median is given in the legend. The 25th and 75th percentiles are represented by the lateral borders of the boxes and indicate the respective values at which 25% of the samples fall below and 25% fall above the lateral borders of the boxes. Error bars represent the 10th and 90th percentile points, and the circles represent the 5th and 95th percentiles. Extremes, not shown in the plots, are given in the text.

Regarding analyses for differences in sexual dimorphism in body ratios we executed a series of tests and present a few graphs using regression analyses. We used linear regression analysis, even though the statistics derived from it may rarely be a fully accurate representation of the more or less curvilinear mean growth lines expressed by the data. Nevertheless linear regression graphs provide useful comparative visual presentations of the relative morphological parameters of the population samples being compared as well as reasonable population growth patterns. In using the lin-

ear regression model for comparing body ratios of population samples, statistical tests of a null hypothesis of character similarities for ratios of body measurements follow Weitzman & Palmer (1997:213–214) and employed linear multiple regression analyses using dummy (indicator) variables. See Glantz & Slinker (1990:69–72) for an explanation. Also, analyses of covariance (ANCOVA) using BIOM-PC, version 2, Exeter Publishing Ltd. were performed. Such tests were done using base 10 log transformed data. However, it was found that in the cases discussed here the results of such tests did not need publication because in those cases used to search for population sample differences, the regression graphs, the mean regression lines, and 95% confidence intervals demonstrated clear statistical differences in ratios of body measurements. Even though statistical tests were done using base 10 log transformed data, neither the regression graphs, their accompanying regression equations, nor the r^2 values presented here are derived from base 10 log transformed data because presentation of non-transformed data in graphs is more visually accessible to the reader. In regression analyses a series of diagnostic tests using SigmaStat Version 2.0 were run to determine the suitability of the data for the linear regression model. In all cases the normality tests and the constant variance tests were passed.

For histological analyses, tissues were removed from specimens initially fixed in 10% formalin and subsequently transferred to 70% ethanol. Tissues containing bony elements were first decalcified. Some tissues were then dehydrated in an ethanol series, embedded in paraffin, sectioned at 5–10 μm , and stained with modified Masson's trichrome (Schreibman 1964:219). Other tissues were dehydrated in an ethanol series to 95% ethanol and infiltrated with and embedded in glycol methacrylate. Sections were cut at 2.0–3.5 μm and stained with toluidine blue and periodic acid-Schiff reagent (PAS)/hematoxylin (Quintero-Hunter

et al. 1991:170). Measurements of testis areas were taken from mid sagittal sections as described by Burns et al. (1995:132).

For counts recorded in the descriptions, those of the holotype are provided first followed in parentheses by the mean of the population sample, (or median when the data are nonparametric), range, and the total number of specimens counted.

The terminations of the dorsal and anal fins are morphologically different and are treated as follows. The posterior branched ray of the dorsal fin has a single pterygiophore at its base, i.e., the ray is not split to its base and is counted as 1, but when it is rarely split to its base, then its last two rays are counted as 1 because there is only 1 pterygiophore at the base of these rays. In the anal fin the most posterior pterygiophore has its ray almost invariably split to its base and these two rays are counted as one.

The word pouch is used for that sac-like area internal to the modified caudal-fin scale or scales, called pouch scales, of the usually adult, sexually active males of glandulocaudine characids. The pouch opening to the surrounding water occurs along the posteroventral border of the scale or scales. In almost all case in males the pouch opening is provided with modified secretory cells presumably producing a pheromone. In diptomins both sexes have pouch scales. See Weitzman & Fink (1985) and Weitzman & Menezes (1998) for further explanation.

Specimens examined for this research are deposited in the Museu de Zoologia, Universidade de São Paulo (MZUSP); Museu Nacional, Universidade Federal do Rio de Janeiro (MNRJ); Laboratório de Ictiologia de Ribeirão Preto, Faculdade de Filosofia Ciências e Letras de Ribeirão Preto, Universidade de São Paulo (LIRP); Departamento de Zoologia, Universidade Estadual Paulista, Campus de São José do Rio Preto, São Paulo (DZSJRP); and the Smithsonian Institution, National Museum of Natural History (USNM). Comparative glandulocaudi-

ne and other characid specimens used in this report are listed in Weitzman & Fink (1985: Appendix 1), Weitzman et al. (1994), Burns et al. (1995, 1997), Weitzman & Menezes (1998:176), and Weitzman et al. (2004).

Planaltina Böhlke

Planaltina Böhlke, 1954:265 (type species: *P. myersi* Böhlke, 1954:267 by monotypy and original designation).

Definition.—1) There are fewer scales forming the dorsal border of the caudal pouch in *Planaltina* (1–2) than in *Acrobrycon* (4–7 or 8) and *Diapoma* (3–6). 2) In *Planaltina* one of the scales forming the dorsal border of the pouch opening is elongate and forms most of that border, whereas in *Acrobrycon* and *Diapoma*, even when one of the dorsal border scales of the pouch opening is somewhat elongate or larger, its actual contribution to the length of the dorsal pouch border is little more than that of the other dorsal border scales of the pouch opening. 3) The three species of *Planaltina* produce aquasperm, the nuclei of which vary in shape from spherical to slightly elliptical, whereas both *Acrobrycon* and *Diapoma* have elongate sperm cell nuclei.

Key to the species of *Planaltina*

The characters used in this key, except those in couplet 1a, are not necessarily synapomorphies and the key is not intended to reflect phylogenetic relationships, only information for species identification. The key assumes that at least adult male specimens are available and have a caudal organ consisting of hypertrophied scales enclosing a pouch that is in part open to the surrounding water and that the specimens do not fit the diagnosis of the Cheirodontinae proposed by Malabarba (1998:199–205).

1a. Male and female caudal organs as indicated by caudal squamation nearly equivalent in size and morphological development; three or more scales im-

mediately ventral to lateral-line series extend posteriorly to form dorsal border of pouch opening *Diapomini* (2)

- 1b. Female caudal organs as expressed by caudal squamation never as hypertrophied as that of males; arrangement of scales bordering pouch opening not as above other *Glandulocaudinae*
- 2a. Dorsal border of pouch opening formed by one or two enlarged and elongate dorsal scales; sperm cell nuclei spherical to slightly elliptical (aquasperm) *Planaltina* (3)
- 2b. Dorsal border of pouch opening without especially enlarged scales or one somewhat enlarged scale present, but its perimeter entering pouch border not especially large; sperm-cell nucleus somewhat elongate *Acrobrycon* and *Diapoma*
- 3a. One much enlarged and elongate scale along dorsal border of pouch opening; adipose fin present *Planaltina myersi*
- 3b. Three enlarged and somewhat elongate scales along dorsal border of pouch opening; adipose fin present or absent (4)
- 4a. Six or seven scale rows between dorsal-fin origin and lateral line; 5 scale rows between anal-fin origin and lateral line; 16–17 scale rows around caudal peduncle ($X = 16.2$); 17–20 predorsal scales ($X = 18.0$); adipose fin absent *Planaltina glandipedis*
- 4b. Five scale rows between dorsal-fin origin and lateral line; 4 scale rows between anal-fin origin and lateral line; 12–14 scale rows around caudal peduncle ($X = 13.1$); 14–16 predorsal scales ($X = 15.2$); adipose fin present *Planaltina britskii*

Planaltina myersi Böhlke

Figs. 1–3, Table 1

Planaltina myersi Böhlke, 1954:267, original description, Brazil, “Goyaz, Sarandi brook, Planaltina,” now in Distrito Federal.—Weitzman & Fink, 1985:106–107, listed specimens from several localities.—Burns et al. (1995:135–143) presented evidence that species is inseminating with aquasperm.—Weitzman &



Fig. 1. *Planaltina myersi*, USNM 221202, adult male above, SL 35.9 mm and adult female, below, SL 32.0 mm; córrego Pipiripau near Planaltina, Distrito Federal, Brazil, about 15°40'S, 47°39'W.

Table 1.—Morphometrics of *Planaltina myersi*. Standard length is expressed in mm; measurements through head length are percentages of standard length; the last four entries are percentages of head length. Minimum, maximum, *n*, *X*, and *SD* are based on the holotype, SU 18636 (now at CAS) and the following specimen lots: MNRJ 10634, MNRJ 10635, USNM 363088, USNM 2210202, USNM 236416, USNM 258458, USNM 278966, USNM 278986, USNM 278987, USNM 278989, and MUSP 63588.

	Holo- type	Males				Females			
		<i>n</i>	Range	<i>X</i>	<i>SD</i>	<i>n</i>	Range	<i>X</i>	<i>SD</i>
Standard length (mm)	36.8	14	22.3–38.0	33.7		33	19.0–43.0	30.7	
Body depth at dorsal fin origin	24.7	14	22.2–26.2	24.0	1.0	33	21.1–28.3	24.9	1.8
Snout to dorsal-fin origin	54.3	14	54.3–61.6	59.2	1.8	33	53.7–61.1	59.1	1.5
Snout to pectoral-fin origin	25.5	14	24.5–26.2	25.3	0.6	33	22.2–28.6	25.0	1.4
Snout to pelvic-fin origin	46.2	14	45.1–47.1	45.8	0.6	33	46.7–50.0	46.4	1.4
Snout to anal-fin origin	58.4	14	57.3–61.0	59.2	1.0	33	57.1–64.9	60.9	2.0
Caudal peduncle depth	10.9	14	09.3–11.1	10.0	0.5	33	0.84–10.6	09.8	0.5
Caudal peduncle length	12.8	14	10.8–14.2	12.7	1.0	33	11.1–17.1	13.1	1.0
Pectoral-fin length	20.9	14	20.1–24.2	22.1	1.0	33	18.8–25.3	21.7	1.2
Pelvic-fin length	14.4	14	12.5–16.1	15.1	1.1	33	12.0–15.6	14.1	0.7
Dorsal-fin base length	10.9	14	08.9–12.5	10.5	0.8	33	0.93–12.9	10.4	0.8
Dorsal-fin height	19.8	14	18.7–21.4	20.2	0.8	33	18.2–21.3	19.8	0.8
Anal-fin base length	29.9	14	27.6–33.3	30.6	1.4	33	26.0–32.0	28.6	1.5
Anal-fin lobe length	17.7	14	16.8–18.8	17.9	0.7	33	16.1–19.6	18.1	1.0
Eye to dorsal-fin origin	46.5	14	44.6–47.9	46.1	1.0	33	41.7–48.6	45.7	1.5
Dorsal-fin origin to caudal-fin base	43.5	14	40.1–43.9	42.2	1.1	33	38.7–47.7	42.2	1.6
Bony head length	23.4	14	22.6–25.4	23.7	0.8	33	20.5–26.4	24.1	1.1
Horizontal eye diameter	35.4	14	35.0–37.7	36.2	0.7	33	33.7–42.6	36.7	1.8
Snout length	22.1	14	18.8–23.7	21.2	1.6	33	17.8–23.4	21.2	1.2
Least interorbital width	31.4	14	31.4–36.1	33.8	1.4	33	31.1–38.3	33.5	1.5
Upper jaw length	43.0	14	40.0–45.9	43.1	1.4	33	40.3–47.7	43.8	1.5



Fig. 2. *Planaltina myersi*, USNM 221202, adult male, SL 35.9 mm; córrego Pípiripau near Planaltina, Distrito Federal, Brazil, about 15°40'S, 47°39'W. Displays pigment pattern of head and anterior part of body.

Menezes (1998:184) discussed relationships and assigned it to Diapomini.

Specimens examined.—All specimens are from Brazil, Distrito Federal, drainage basin of rio Corumbá, tributary of upper rio Paraná.

Holotype.—SU 18636 (now at CAS), 1 male, 36.8 mm SL. Type locality: Brazil: "Goyaz, Sarandi brook, Planaltina" (approximately 15°40'S, 47°45'W). Now in Distrito Federal, see discussion below regarding type locality.

Additional specimens.—Brazil: Distrito Federal. MNRJ 10634, 24 (2 mature males, from 30.5 to 31.5 mm SL; 22 immatures of either sex to mature females, from 22.3 to 36.6 mm SL), córrego Fumal, where crosses road between Brasília and Planaltina, near Planaltina, about 15°20'S, 47°50'W, 11 Apr. 1982, L.E. de Macedo Cordoso. MNRJ 10635, 13 (including 1 c&s male, 33.3 mm SL; 1 c&s female, 36.4 mm SL), córrego Fumal, where it crosses road between Brasília and Planaltina, near Planaltina, about 15°20'S, 47°50'W, 5 Aug. 1981, L. E. de Macedo Cordoso. USNM 363088, 1 (ma-

ture male, 46.0 mm SL), rio Pípiripau near Planaltina, about 15°40'S, 47°39'W, 30 Sept. 1977, N. Menezes & party. USNM 221202, 6 (1 mature male, 35.9 mm; 5 mature females, 32.0–43.1 mm SL), rio Pípiripau near Planaltina, about 15°40'S, 47°39'W, 30 Sept. 1977. N. Menezes & party. USNM 236416, 3 (immatures to 1 mature female, 19.0–39.7 mm SL), córrego Vargem de Trás, rio Pípiripau, near Planaltina, about 15°40'S, 47°39'W, 1 Jun. 1979, N. Menezes & E. Bastos. USNM 258458, 1 (mature female, c&s, 41.0 mm SL), rio Pípiripau near Planaltina, about 15°40'S, 47°39'W, 19 Jan. 1976, E.C. Calaf. USNM 278966, 8 (7 mature sexually active males, 35.5–38.3 mm SL; 1 mature female, 37.8 mm SL), córrego Papuda, tributary of rio São Bartolomeu, about 40 km south east of Brasília, 1 Feb. 1985, M. Ribeiro & party. USNM 278985, 1 (mature male, 36.4 mm SL), rio Pípiripau near Planaltina, about 15°40'S, 47°39'W, 1985, M. Ribeiro. USNM 278986, 1 (mature female, 39.6 mm SL), córrego Papuda, tributary to rio São Bartolomeu, 28 Aug. 1985, M. Ribeiro &

R.C. Mendonça. USNM 278987, 1 (mature male, 37.1 mm SL), córrego Forquilha, tributary to rio São Bartolomeu, Sept. 1985, M. Ribeiro. USNM 278989, 3 (mature females, 28.7–37.4 mm SL), rio Taboca, tributary to rio São Bartolomeu, Sept. 1985, M. Ribeiro & J. Dalmaco. MZUSP 63588, 3 (mature females, 34.3–41.3 mm SL), córrego Vargem de Trás, rio Pípiripau, near Planaltina, 1 Jun. 1979, N. Menezes & E. Bastos.

Note.—Böhlke (1954:267) with the aid of other Dr. Carl Ternetz localities of about the same date discussed the type locality “as a small brook somewhere along the Chapadão do Sarandy, lying between the headwaters of the Rio Maranhão (which empties into the Tocantins) and those of the Rio São Bartholomeo [= rio São Bartolomeu] (which empties into the [rio] Corumbá and then into the [rio] Paranaíba [=

rio Paranaíba].” Böhlke continued: “Thus the particular brook which Ternetz collected may drain into the Amazon system to the north or into the Paraná to the south, but more likely the latter . . .” Subsequent to the original description, several collections were made in this region as listed above and in Weitzman & Fink (1985:106). *Planaltina myersi* so far has been found only in the upper rio Paraná system.

Definition.—Following features distinguish *Planaltina myersi* from *P. glandipedis* and *P. britskii*: One much enlarged and elongate scale along dorsal border of pouch opening; adipose fin present. In addition, anterior teeth of inner tooth row of premaxilla of *P. myersi* pentacuspoid, and dentary with its anterior large teeth pentacuspoid or quadricuspoid. Lower jaw not extending beyond upper. *Planaltina glandipedis* with tri-

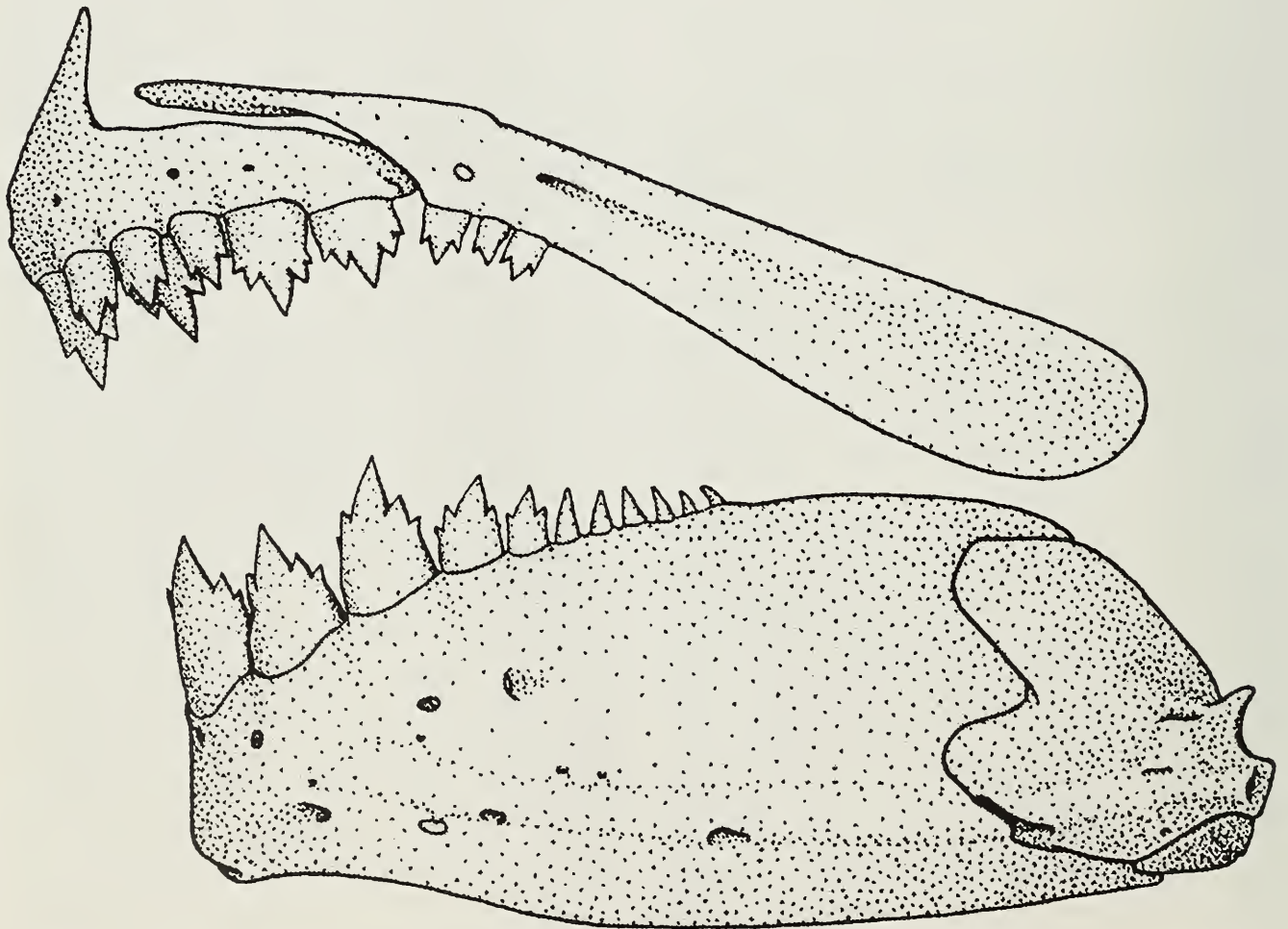


Fig. 3. *Planaltina myersi*, MNRJ 10635, c&s, sexually active male, SL 33.3 mm. Premaxilla, maxilla and mandible, left side, external view. Note relative positions of maxilla and premaxilla with dentary not normal so that all jaw teeth can be illustrated.

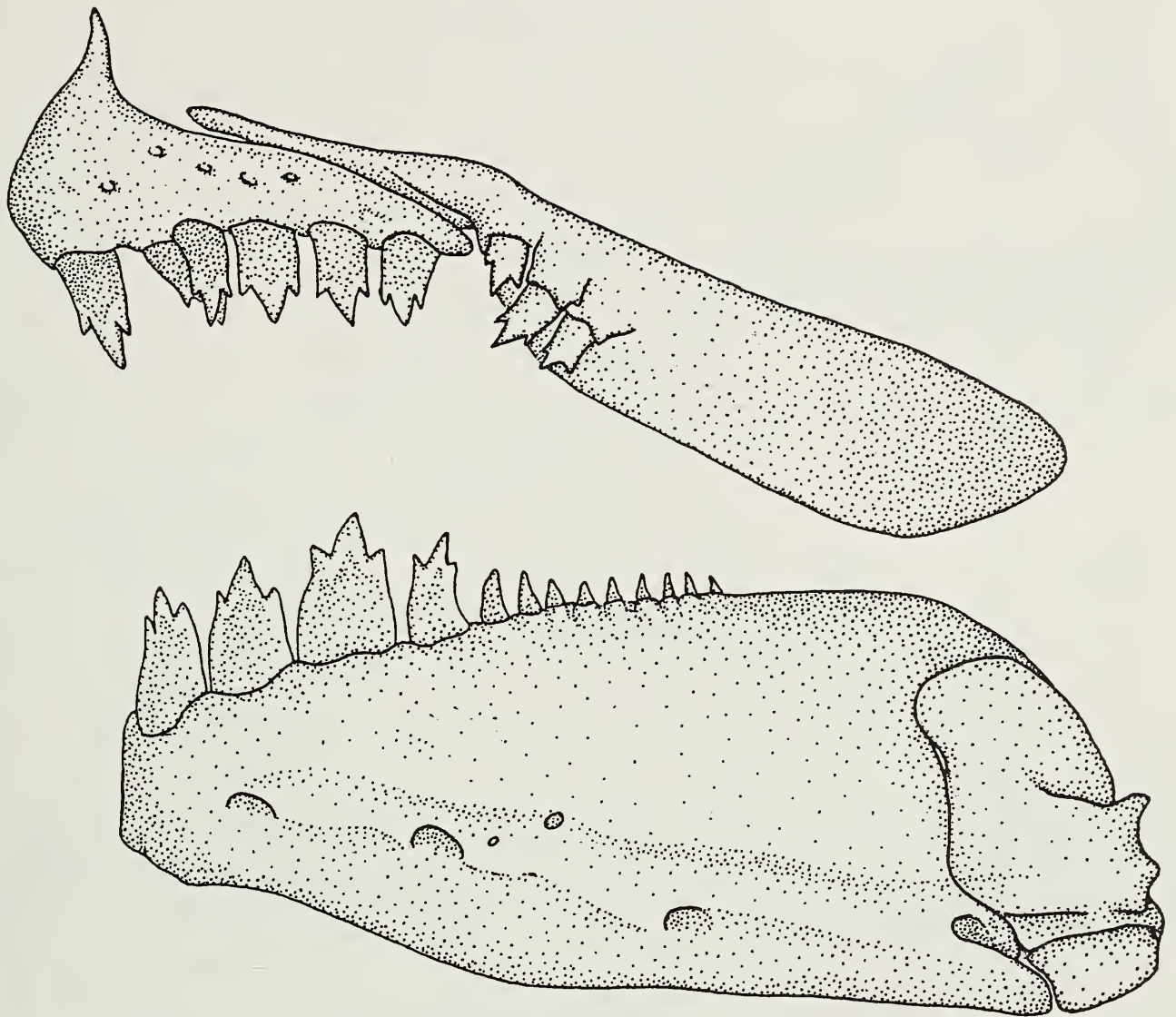


Fig. 4. *Planaltina glandipedis*, new species, paratype, USNM 362135, sexually active male, c&s, SL 24.3 mm. Premaxilla, maxilla and mandible, left side, external view. Note relative positions and premaxilla with dentary not normal so that all jaw teeth can be illustrated.

cuspid teeth in inner row of premaxilla; dentary with tricuspid anterior large teeth, lower jaw protrudes somewhat beyond upper jaw. *Planaltina britskii* with teeth of inner row of premaxilla and large anterior teeth of dentary pentacuspoid and lower jaw included by upper (Figs. 3–5, but note: in drawings upper and lower jaws reproduced from independent drawings and not in a natural position in relation to one another, thus some dentary teeth not hidden by upper jaw teeth).

Figures 6–13 illustrate Tukey Box Plot distributions of population sample data for species of *Planaltina*. Captions of these figures provide results of Mann-Whitney rank

sum tests regarding differences and similarities among *P. myersi*, *P. britskii*, and *P. glandipedis* in number of lateral-series scales, Fig. 6; number of predorsal scales, Fig. 7; number of branched anal-fin rays, Fig. 8; total number of vertebrae including those of Weberian apparatus, Fig. 9; least number of scale rows around caudal peduncle, Fig. 10; number of lower-limb gill rakers, Fig. 11; number of scale rows between dorsal-fin origin and lateral line, Fig. 12; and number of scale rows between anal-fin origin and lateral line, Fig. 13.

Description.—Morphometrics of the holotype and additional specimens presented in Table 1. Tables, graphs, and descriptions

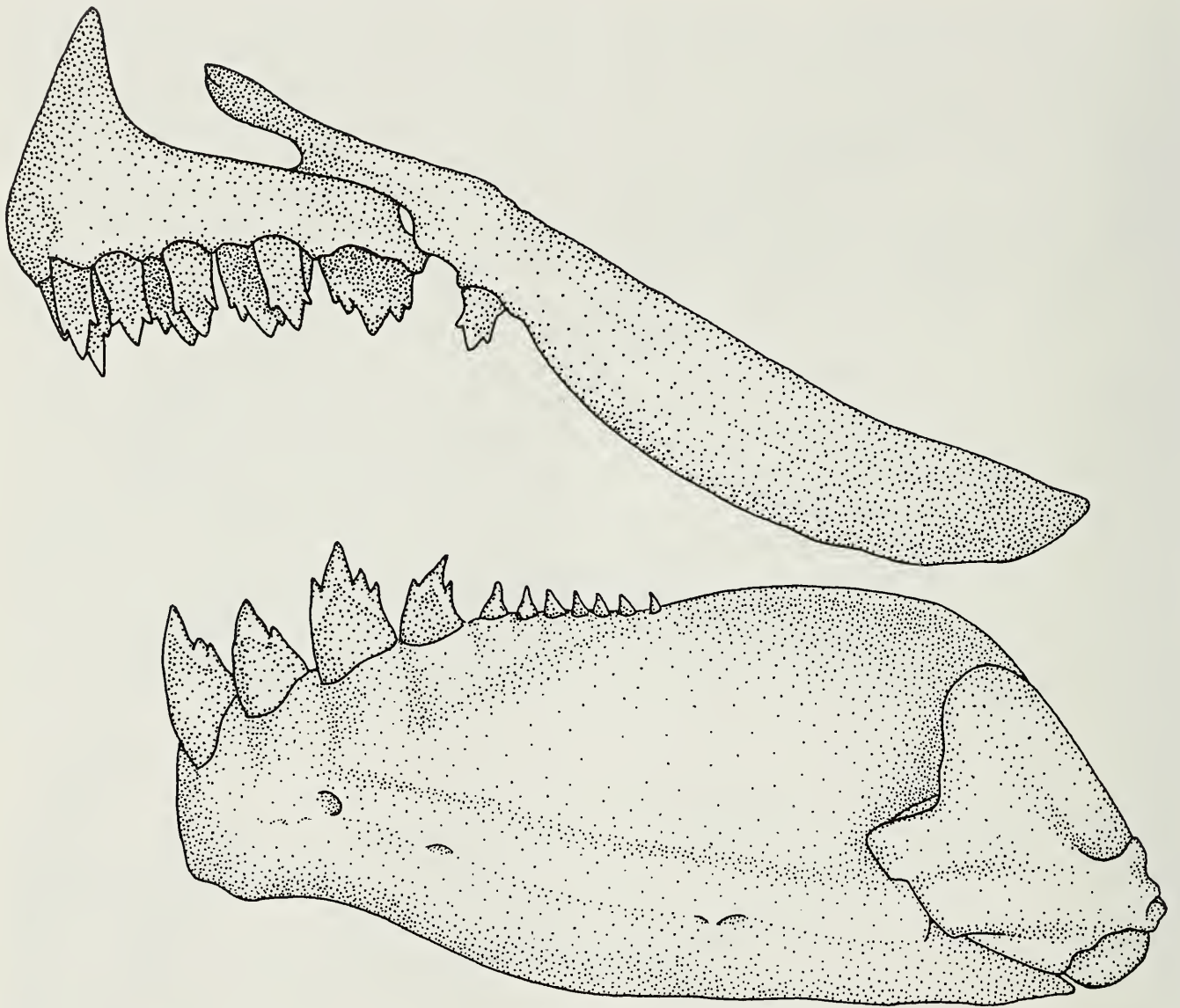


Fig. 5. *Planaltina britskii*, new species, paratype, MZUSP 62758, c&s, sexually active male, SL 35.6 mm. Premaxilla, maxilla and mandible, left side, external view. Note relative positions of maxilla and premaxilla with dentary not normal so that all jaw teeth can be illustrated.

provided below based on combined lots of this species because no statistical differences were found among examined same-sex population samples. All collection localities geographically close and in one drainage system, rio Corumbá, upper rio Paraná.

Body large, compressed and moderately elongate; greatest body depth between snout tip and dorsal-fin origin, near origin of pelvic fin. Dorsal body profile somewhat convex between nape and just anterior to dorsal-fin origin, only slightly elevated at dorsal-fin origin. Head profile to snout tip slightly convex. Snout rounded. Body profile nearly straight along dorsal-fin base and slightly concave in region of caudal pedun-

cle. Dorsal-fin origin nearer to caudal-fin base than snout tip. Ventral body profile convex from tip of lower jaw to anal-fin origin, nearly straight along anal-fin base and slightly concave from end of anal fin to origin of procurrent caudal-fin rays.

Lower jaw terminal or only slightly protruding anterior to upper jaw. Mouth gape somewhat inclined posteroventrally towards mandibular joint. Maxilla extending posteriorly beyond vertical line passing through anterior border of orbit, but falling short of reaching a vertical line passing through anterior border of pupil of eye (see Fig. 2).

Dorsal-fin rays ii, 8 in 44 of 45 specimens including holotype, I, 7 in one spec-

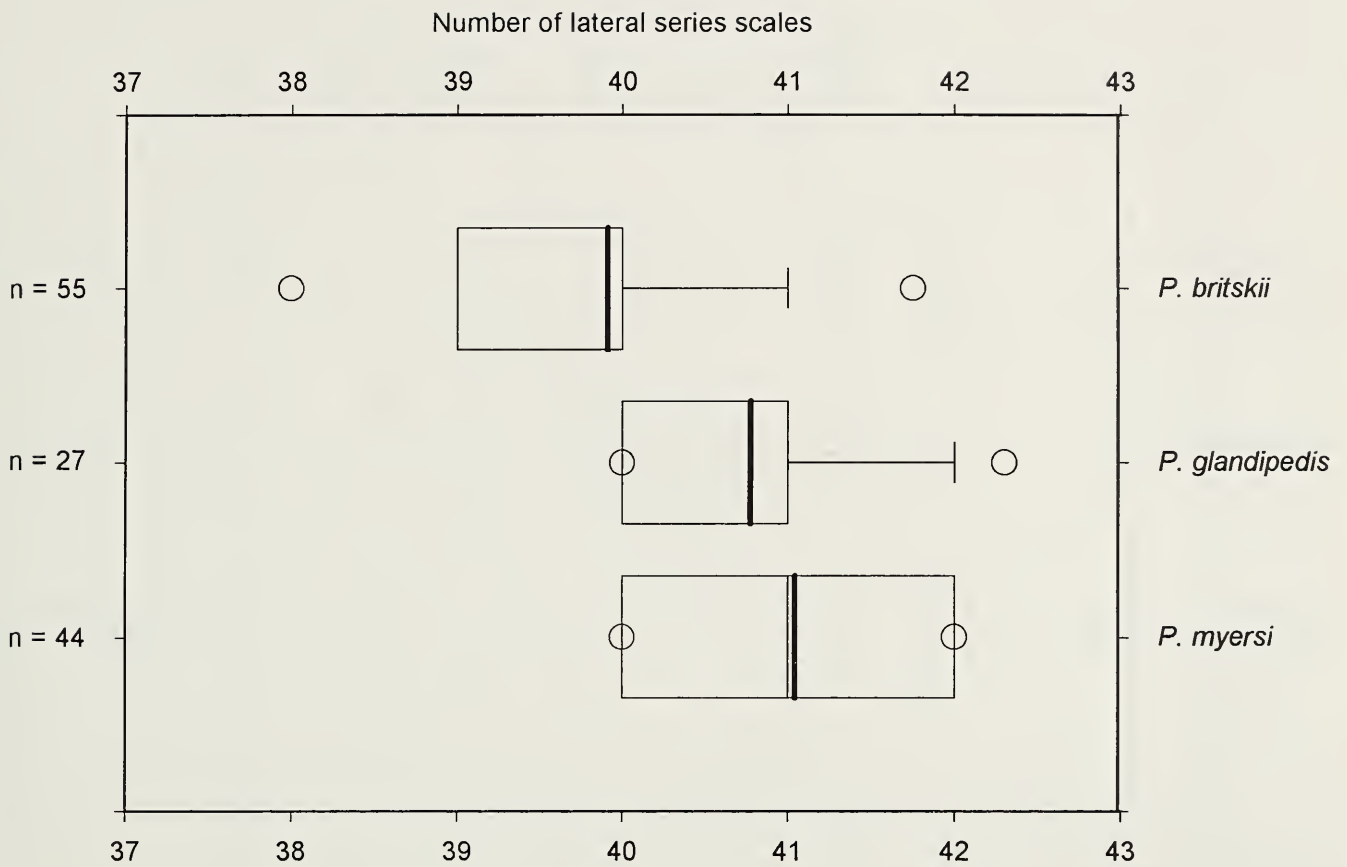


Fig. 6. Tukey box plots showing the statistical distribution of number of lateral-series scales for species of *Planaltina*. No significant difference in number of lateral series scales was found using a Mann-Whitney rank sum test for *P. myersi* and *P. glandipedis*. However, using this test a statistically significant difference was found between *P. myersi* and *P. britskii* ($T = 3021.00$, $P = <0.001$) and between *P. glandipedis* and *P. britskii* ($T = 1733.0$, $P = <0.001$). The median for *P. myersi* and *P. glandipedis* is 41 and for *P. britskii* it is 40.

imen. Posterior most ray unbranched in all but one specimen in which count appears as ii, 9, but is actually ii, 8, posteriormost ray being branched, $n = 45$. Adipose fin present. Anal-fin rays iv, 21 (iv or v, usually v, branched rays $X = 20.8$, range 19–23, $n = 45$). Moderately developed anterior anal-fin lobe including anterior unbranched rays and first 4–5 branched rays. Anal fin of sexually mature males with bilateral hooks on fifth unbranched and anterior 9 or 10 branched rays distributed as in Fig. 14. Pectoral-fin rays i, 11 (anterior unbranched ray i in all specimens, posterior ray actually unbranched, but counted as a branched ray), branched rays $X = 10.3$, range 9–11, $n = 45$. Posterior tips of longest pectoral-fin rays not reaching pelvic-fin origin; pectoral fin about same length in both sexes, without hooks. Pelvic-fin rays i, 6, $n = 45$ (posterior most ray unbranched). Sexually mature

males with hooks present on rays of pelvic fin, distributed as in Fig. 15. Number of hooks per ray varying among different males, but usually approximately as shown in Fig. 15; a mature male (30.5 mm SL) with 0 hooks on first ray, 8 on second, 10 on third, 13 on fourth, 15 on fifth, 16 on sixth, 3 on seventh ray, all on ventral surface of right side pelvic fin. Pelvic fins of adult males longer than those of adult females (see Table 1 and Fig. 15); distal tips of longest pelvic-fin rays extending to, or slightly beyond, anal-fin origin in adult males, but pelvic fins falling short of anterior origin of anal fin in adult females. Compare Figs. 1a, b. See also discussion under “Sexual dimorphism.” Scales cycloid, with few radii, often 3–6 along posterior exposed field, more numerous, to approximately 10, on enlarged scale bordering dorsal border of pouch opening.

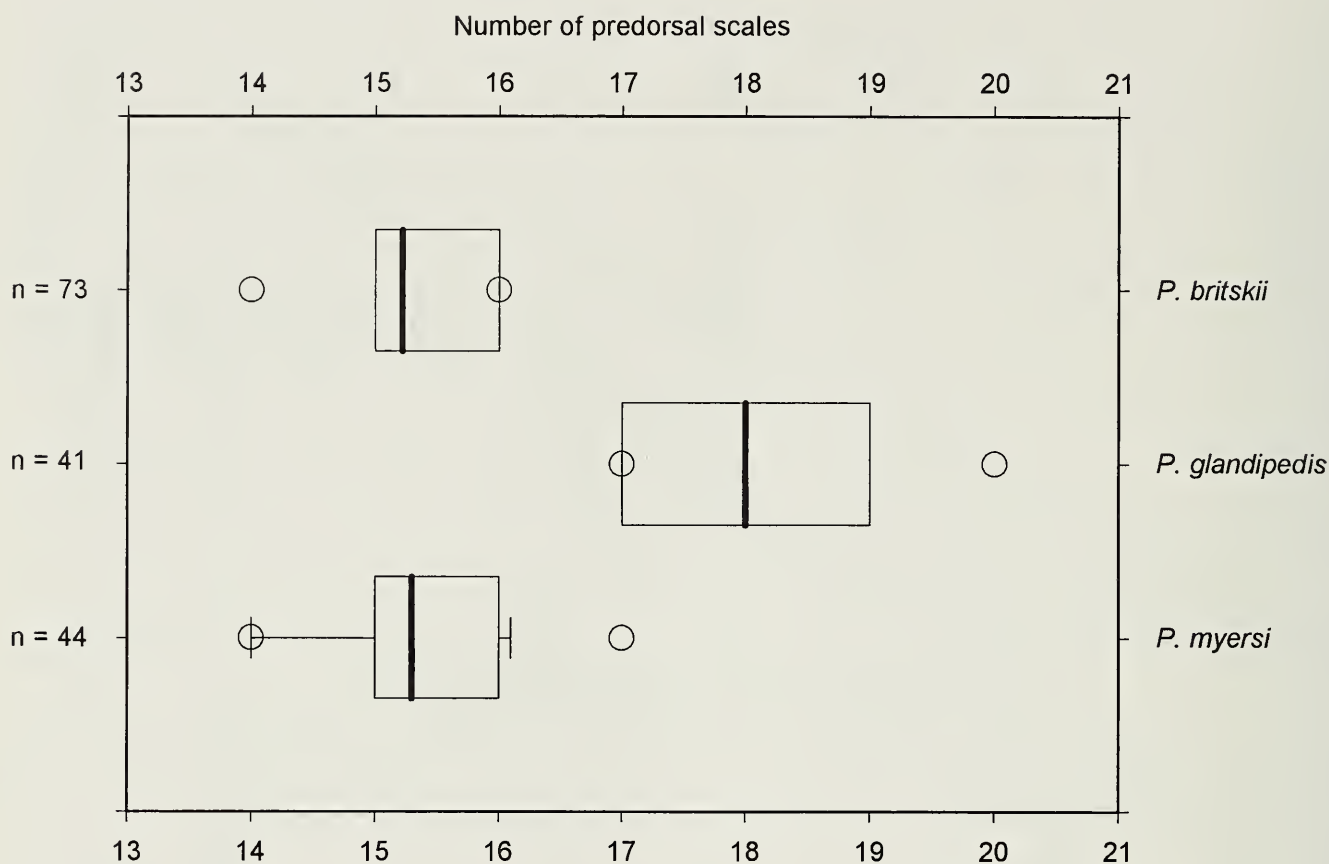


Fig. 7. Tukey box plots of number of predorsal scales for species of *Planaltina*. A Mann-Whitney rank sum tests found no significant difference in the number of those scales for *P. myersi* and *P. britskii*, but a significant difference was found between *P. myersi* and *P. glandipedis* ($T = 2633.000$, $P = <0.001$) and between *P. glandipedis* and *P. britskii* ($T = 3854.000$, $P = <0.001$). The median for *P. myersi* = 15, for *P. glandipedis* = 18 (= the same as mean), and for *P. britskii* = 15.

Lateral line complete, perforated scales 42 ($X = 41.0$, range 39–43, $n = 44$). Predorsal scales 15 ($X = 15.3$, range 13–17, $n = 44$). Scale rows between dorsal-fin origin and lateral line 6 ($X = 5.9$, range 5–6, $n = 45$). Scale rows between anal-fin origin and lateral line 5 ($X = 4.9$, range 4–5, $n = 45$). Scale rows around caudal peduncle 16 ($X = 15.5$, range 15–16, $n = 45$).

Premaxillary teeth in two distinct rows (see Fig. 3). Larger teeth pentacuspoid; smaller teeth tricuspid or with less well-developed and sometimes vestigial additional lateral cusps. Outer row teeth 3 ($X = 3.2$, range 2–4, $n = 47$). Inner row teeth 4 ($X = 4.0$, range 4–5, but only one specimen had 5 teeth, $n = 47$). Maxillary teeth 1 (number of teeth does not appear to increase ontogenetically, $X = 2.1$, range 1–3, $n = 47$). Maxillary teeth tricuspid, occasionally bicuspid, (anterior tooth larger than

remaining teeth). Dentary with 4 large anterior pentacuspoid or sometimes quadricuspoid teeth, $n = 47$ and 7 smaller posterior teeth ($X = 7.0$, range 5–9, $n = 46$). Premaxillary, maxillary, and dentary teeth compressed so that flattened surfaces face both externally and internally.

Vertebrae 39 ($X = 39.3$, range 38–41, $n = 54$). Upper limb gill-rakers 5 ($X = 5.7$, range 4–7, $n = 47$); lower limb gill-rakers 10 ($X = 11.1$, range 10–13, $n = 47$). Branchiostegal rays 4 in two cleared and stained specimens, 3 rays originating from anterior ceratohyal and 1 ray from posterior ceratohyal.

Color in alcohol.—Males and females with approximately the same color pattern (Figs. 1a, b, 2). Body pale to light brown and a little darker dorsally than ventrally. Dorsal body surface dark due to scattered dark chromatophores and a clear reticulate

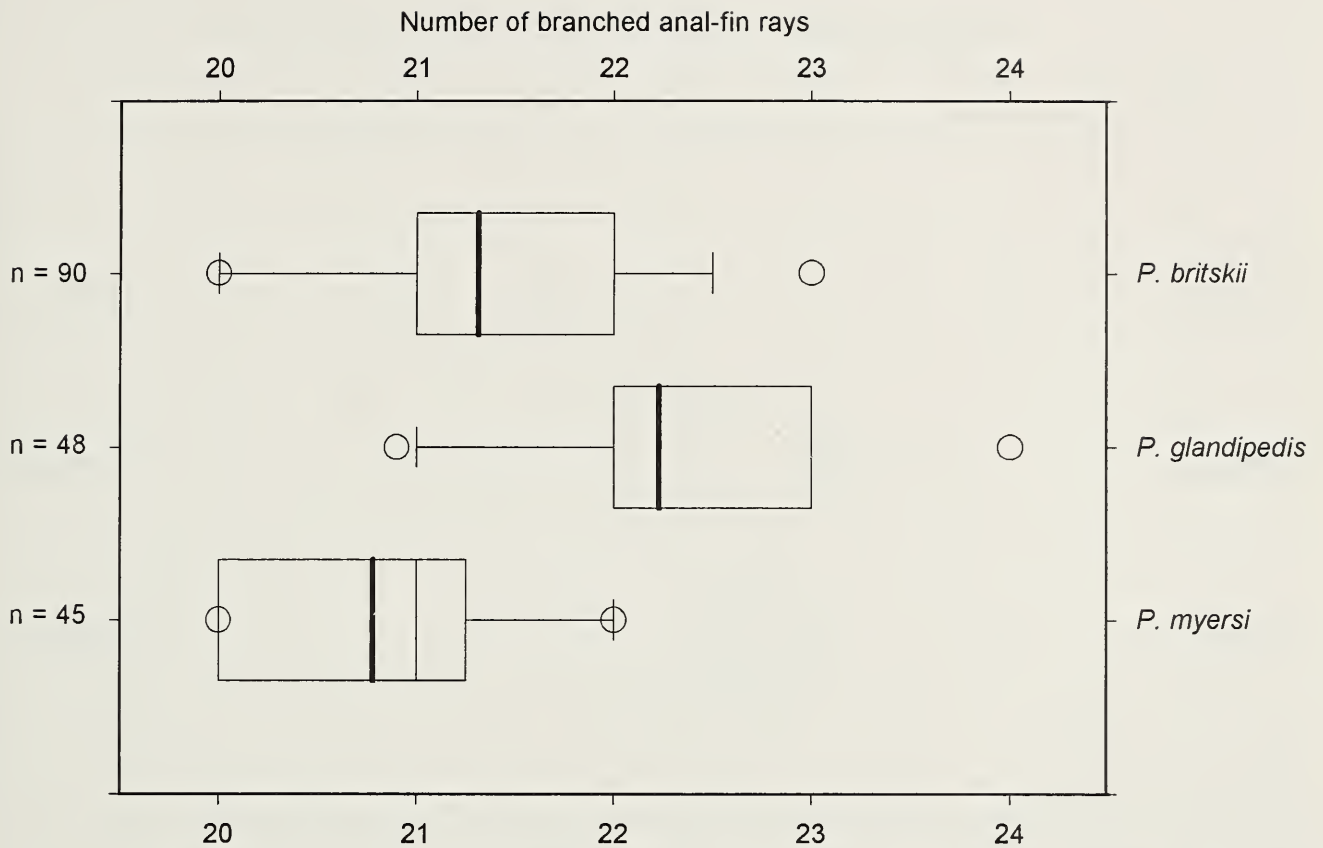


Fig. 8. Tukey box plots of number of branched anal-fin rays for species of *Planaltina*. A significant difference in number of these fin rays was found among all three species using a Mann-Whitney rank sum test. Between *P. myersi* and *P. britskii* ($T = 2449.000$, $P = 0.004$), between *P. myersi* and *P. glandipedis* ($T = 1376.000$, $P = <0.001$) and between *P. glandipedis* and *P. britskii* ($T = 4387.000$, $P = <0.001$). The median for *P. myersi* = 21, for *P. glandipedis* = 22 and for *P. britskii* = 21.

pattern of dark chromatophores associated with scale borders. Fewer dark chromatophores occurring on ventral posterior part of body where scattered concentration of chromatophores presents on body dorsal to anterior half of anal fin, most obvious in males. Dark lateral body stripe present, but mostly obscured by guanine pigment in freshly caught specimens or in specimens fixed in ethyl alcohol. This darkly pigmented stripe, when guanine pigment destroyed by formalin, extending from posterior part of dorsal opercular region to caudal-fin base and onto anterior part of median caudal-fin rays. Dark pigmentation of lateral stripe mostly concentrated along posterior two thirds of body and about equally evident on males and females. Also extending onto anterior part of median caudal-fin rays. Other median fins relatively free of pigment, but anal fin with considerable amount of dark pigment on the mem-

branes between rays. Pectoral and pelvic fins pale. Head dark dorsally and dark around mouth. Circumorbital bones and opercle silvery with very few scattered dark chromatophores.

Sexual dimorphism, reproductive mode and gonad anatomy.—The females lack the pelvic-fin and anal-fin hooks present in males as described above (see Figs. 14, 15). The pelvic fins are longer in adult males than in adult females. Our data indicate that sexual maturity is reached by about or at least by 30 mm SL and by this length the male's pelvic fins have also reached their proportionately greatest length relative to that of the females. Comparisons of Fig. 16 of *P. myersi*, Fig. 17 of *P. glandipedis* and Fig. 18 of *P. britskii* indicate that the relative pelvic-fin length in males of *P. myersi* and *P. glandipedis* varies less than in *P. britskii*. Although our population samples are represented by males and females of

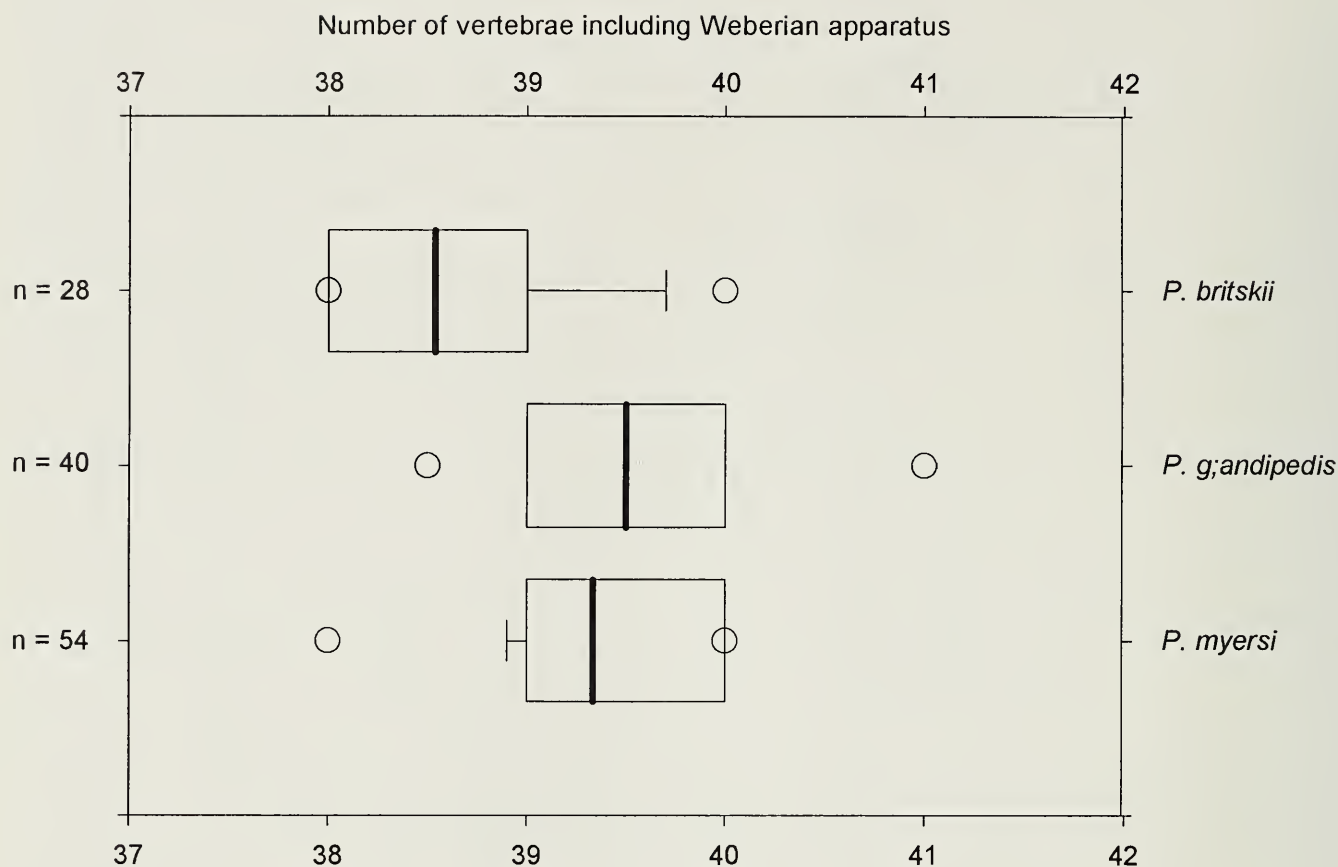


Fig. 9. Tukey box plots showing the distribution of number of vertebrae for species of *Planaltina*. A Mann-Whitney rank sum test found no significant difference between number of vertebrae in *P. myersi* and *P. glandipedis*, but a significant difference ($T = 612.500$, $P = <0.001$) was found between *P. britskii* and *P. glandipedis* as well as *P. britskii* and *P. myersi* ($T = 740.00$, $P = <0.001$). Median for *P. myersi* and *P. glandipedis* = 39, and for *P. britskii* = 38.

about equal length ranges for each sex, relatively few are fully sexually mature judging from visual inspection of the gonad state of development in some specimens. The scales bordering the dorsal margin of the mature male pouch opening (see Fig. 19) are more elongate than those of the mature females, but it is impossible to predict if greater elongation of scales dorsal to the pouch opening might be attained at comparatively larger sizes in females.

A gill gland as reported present in *Corynopoma riisei* Gill by Burns and Weitzman (1996) was reported as present by Bushmann et al. (2002: table 1) in a sexually mature male specimen of *P. myersi* (USNM 278966, 38.3 mm SL), but absent in a sexually mature female specimen (USNM 278966, 43.0 mm SL). In maturing males the presence of such a gland is uncertain. One maturing male specimen (MNRJ

10635, 33.0 mm SL) appeared to have several fused distal tips of anterior gill filaments, but no obvious gill gland was present.

Histological analysis revealed that the epithelium covering both the anal- and pelvic-fin rays was thicker in males than in females. Figure 20 shows the thickened epithelium along a pelvic-fin ray of a mature male (USNM 278966, 38.3 mm SL). Abundant club cells, some close to the surface, were present in the anal- and pelvic-fin epithelia of both sexes.

Histological analysis of ovaries of two mature females (MNRJ 10634, 30.9 mm SL; USNM 278989, 35.0 mm SL) revealed the presence of abundant spermatozoa (see Fig. 21) and large mature oocytes within the ovarian cavity (see also Burns et al., 1995: table 3 and fig. 1A). Longitudinal sections through the testes revealed a pos-

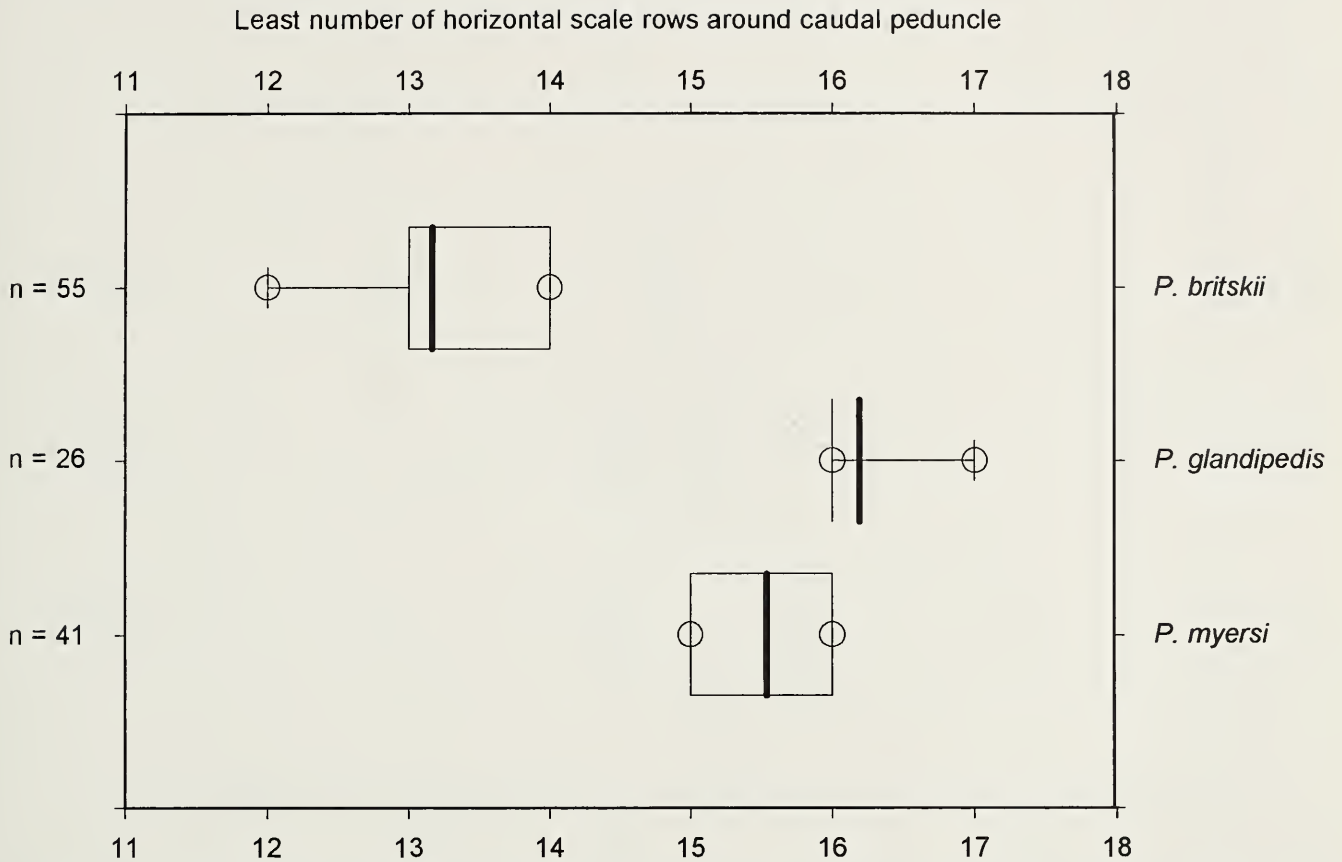


Fig. 10. Tukey box plots of least number of horizontal scale rows around caudal peduncle for species of *Planaltina*. A Mann-Whitney rank sum test indicated a statistically significant difference among all species. That between *P. britskii* and *P. glandipedis* and between *P. britskii* and *P. myersi* is obvious comparing the graphs, but that between *P. glandipedis* and *P. myersi*, although apparently statistically significant ($T = 1186.00$, $P < 0.001$) is not particularly useful for identification of the species. Median for *P. myersi* and *P. glandipedis* = 16, and for *P. britskii* = 13.

terior sperm storage area occupying 44.2% of the total testis area in a mid-sagittal testis section as was reported and discussed by Burns et al. (1995:134, fig. 2). Burns et al. (1995: table 3) also reported that the sperm cells are typical aquasperm, but with the nucleus spherical to slightly “deformed.” There appear to be no sperm cell modifications as found in typical glandulocaudines, but ultrastructure examination was not possible because only formalin-fixed specimens were available.

***Planaltina glandipedis*, new species**

Fig. 22, Table 2

Specimens examined.—All specimens from Brazil, Estado de São Paulo, Município de Corumbataí (except where noted), and tributaries to the drainage basin of the

rio Tietê, a tributary of the upper rio Paraná.

Holotype.—MZUSP 62752, male, 26.2 mm SL, Corumbataí, rio Corumbataí, approximately 22°13'S, 47°38'W, 19 Jan. 1976; H. A. Britski.

Paratypes.—MZUSP 62753, 11 (23.0–28.7 mm SL) and USNM 362135, 11 (immatures to adults, sex undetermined, both collected with holotype, 20.0–27.0 mm SL, 2 specimens, male 26.3 mm SL and female 27.0 mm SL used for histological information). Following 5 lots of immature to adult paratypes collected at Corumbataí, rio Corumbataí, approximately 22°13'S, 47°38'W. MZUSP 62754, 7 (19.7–23.0 mm SL). USNM 362136, 5 (21.7–25.3 mm SL), 25 Jan. 1976, H. A. Britski. MZUSP 62755, 1 (28.5 mm SL), Dec. 1962, H. A. Britski. USNM 362137, 2 (25.8 and 26.5 mm SL),

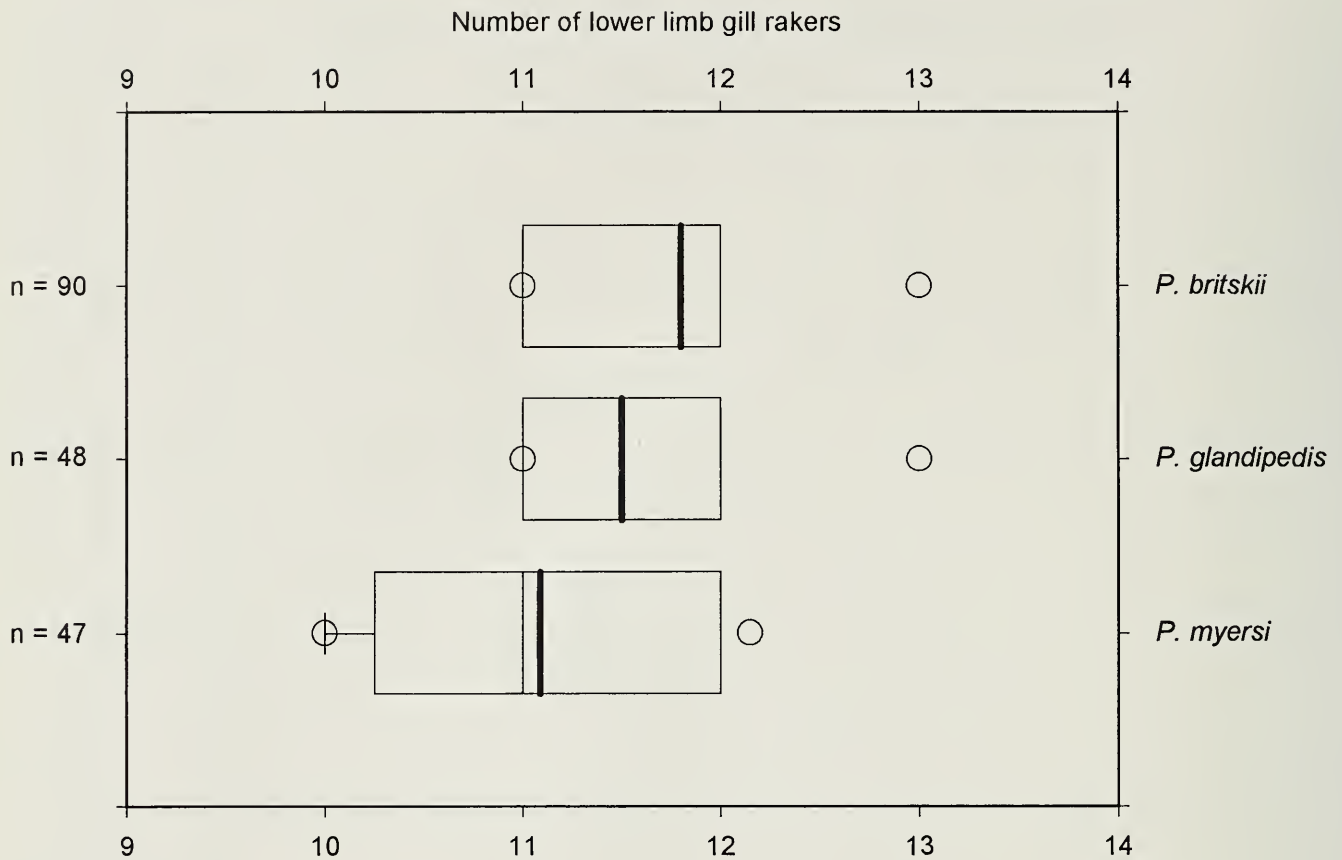


Fig. 11. Tukey box plots of number of lower limb gill rakers for species of *Planaltina*. The differences in the number of lower limb gill rakers among the species is relatively small and provide little if any useful information for identification of the species. However, a nonparametric Mann-Whitney rank sum test found a statistical difference between *P. britskii* and *P. myersi* ($T = 2192.500$, $P = <0.001$) and may indicate a genetic difference in these species. However, using the same type of test, differences between the other two species combinations suggest that resulting differences should be interpreted cautiously and considering the numbers of specimens used we reserve judgment about any possible genetic differences in these species. Differences for *P. britskii* and *P. glandipedis* are $T = 1936.5$, $P = 0.017$ and for *P. glandipedis* and *P. myersi* are $T = 2752.0$, $P = 0.009$. Median for *P. myersi* and *P. glandipedis* = 11, and for *P. britskii* = 12.

2 Nov. 1963, H. A. Britski & A. E. Gomes. MZUSP 62756, 3 (matures 25.5–26.5 mm SL), 2 Nov. 1963, H. A. Britski & A. E. Gomes. DZSJP 671, 4 (22.0–25.0 mm SL) and MZUSP 63690, 3 (matures 25.5–26.5 mm SL), Brazil, São Paulo, Município de Brotas, basin of rio Jacaré-Pepira, approximately 22°17'S, 48°09'W, Jan. 1988, W. Barrela.

Definition.—*Planaltina glandipedis* is sympatric with *P. britskii*, but can be easily distinguished from that species and the allopatric *P. myersi* by lacking an adipose fin and by characters provided in the key. Furthermore, *P. glandipedis* has tricuspid jaw teeth (see Figs. 3–5) and the lower jaw protrudes somewhat beyond upper, whereas in *P. britskii* the teeth of the inner row of the

premaxilla and the large anterior teeth on the dentary are pentacuspoid, and the lower jaw is included by the upper jaw.

Description.—Morphometrics of the holotype and paratypes presented in Table 2. Description based on all lots of this species examined because no statistical differences found among lots from different localities.

Body relatively small, compressed and moderately elongate; greatest body depth between snout tip and dorsal-fin origin, near distal tip of adpressed pelvic fin. Dorsal body profile elevated at dorsal-fin origin, slightly convex from this point to snout tip, nearly straight along dorsal-fin base and slightly concave dorsal to caudal peduncle. Dorsal-fin origin nearer to caudal-fin base than to snout tip. Ventral body profile con-

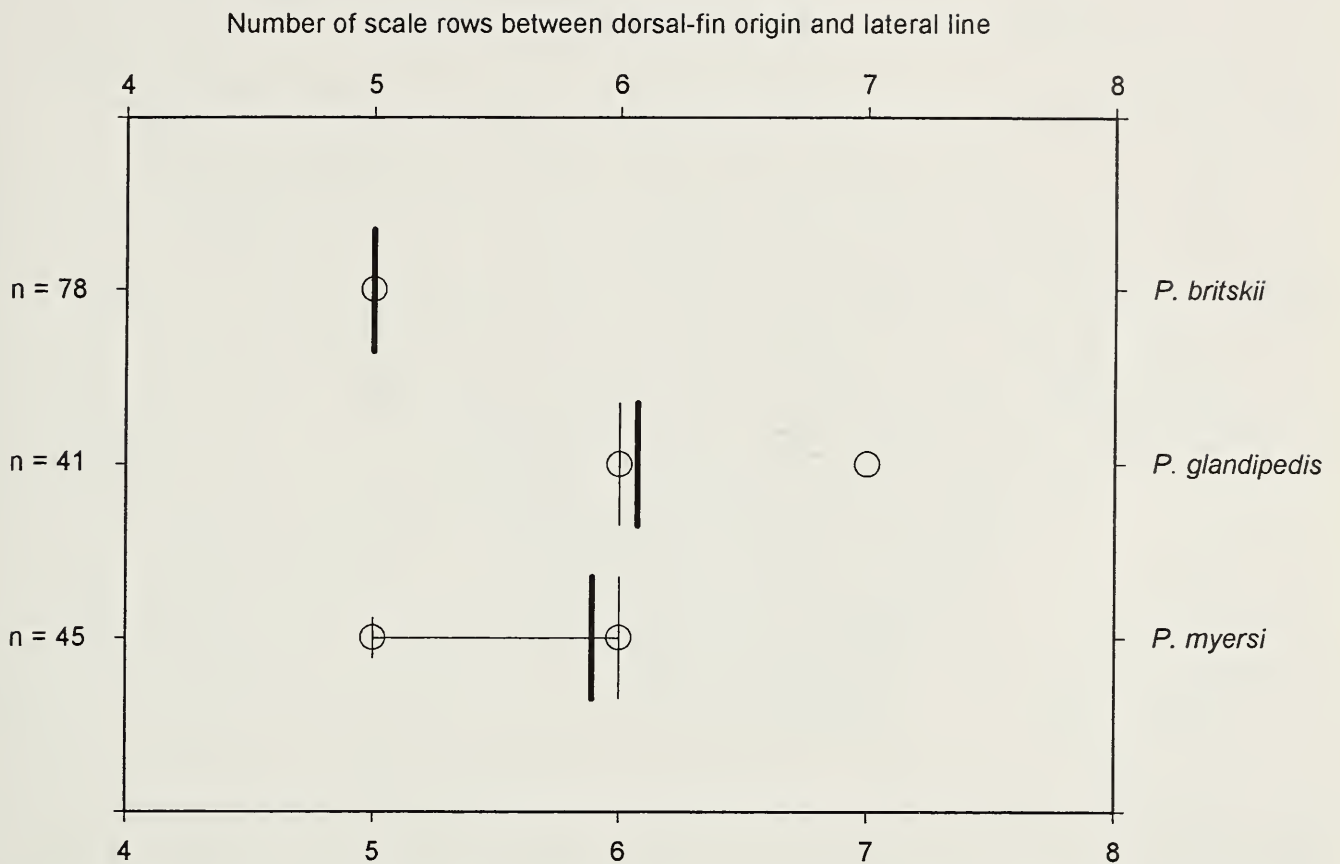


Fig. 12. Tukey box plots of number of scale rows between dorsal-fin origin and lateral line for species of *Planaltina*. A nonparametric Mann-Whitney rank sum test detected a statistically significant difference between *P. britskii* and both other species, *P. britskii* and *P. glandipedis* ($T = 4059.000$, $P = <0.001$) and for *P. britskii* and *P. myersi* ($T = 4350.000$, $P = <0.001$). The same test for differences between *P. myersi* and *P. glandipedis* indicated no significant difference. Median for *P. myersi* and *P. glandipedis* = 6, and for *P. britskii* = 5.

vex from tip of lower jaw to anal-fin origin, nearly straight along anal-fin base and concave from end of anal fin to origin of procurrent caudal-fin rays.

Lower jaw protruding, anterior to upper jaw. Mouth gape inclined posteroventrally towards mandibular joint. Maxilla extending posteriorly beyond vertical line passing through anterior border of orbit, but not reaching vertical line passing through anterior border of eye pupil.

Dorsal-fin rays ii, 8, $n = 47$. Adipose fin absent. Anal-fin rays iv, 22 (iv or v, usually iv, branched rays $X = 2.2$, range 20–25, $n = 48$). Anterior anal-fin lobe moderately developed and includes fourth or fifth unbranched ray and first 5–6 branched rays. Anal fin of sexually mature males with bilateral hooks on fourth or fifth unbranched and anterior 10 branched rays (Fig. 23). Anal fin of sexually active males with glan-

dular cells on fin's anterior region (see "Sexual dimorphism, . . ." below and Fig. 24). Pectoral-fin rays i, 9 (anterior unbranched ray i in all specimens) branched rays $X = 9.7$, range 9–11, $n = 48$. Distal tips of longest pectoral-fin rays extending posteriorly beyond pelvic-fin origin. Pectoral fins of about equal length in both sexes and without hooks. Pelvic-fin rays i, 6 (posteriormost ray unbranched in most specimens, branched in two adult males, but always considered as "branched" in counts, $n = 48$). Sexually mature males with hooks present on rays of pelvic fin, distributed as in Fig. 25. Number of hooks per ray in males varies; mature male (26.0 mm SL) with 7 hooks on first, 18 on second, 16 on third, 10 on fourth, and 13 on fifth branched rays of right pelvic fin. Pelvic fins of adult males somewhat longer than those of most adult females (see Fig.

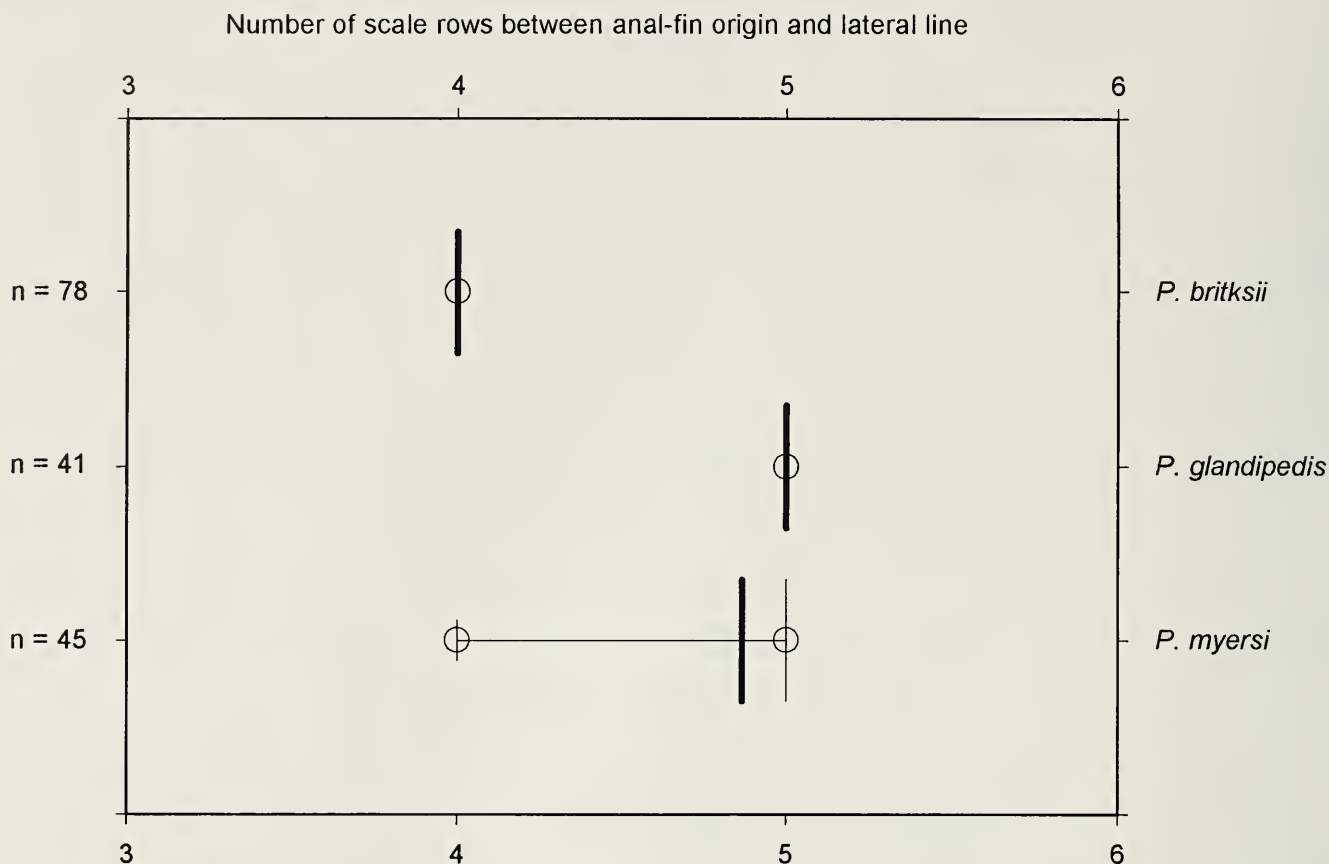


Fig. 13. Tukey box plots of number of scale rows between anal-fin origin and lateral line for species of *Planaltina*. A nonparametric Mann-Whitney rank sum test found a statistically significant difference between *P. britskii* and *P. myersi* ($T = 4311.00$, $P = <0.001$). The same test for *P. myersi* and *P. glandipedis* indicated no significant difference. The difference between *P. britskii* (all 4) and *P. glandipedis* (all 5) was absolute. Median for *P. myersi* = 5.

17); distal tips of longest pelvic-fin rays extending to anal-fin origin in adult males but not in adult females. Males and females with pads of glandular tissue on pelvic-fin rays (see Figs. 26 and 27 and discussion in "Sexual dimorphism, . . ." below).

Scales cycloid with few radii along posterior border, more numerous on enlarged scales bordering and covering caudal pouch of male and female (see Fig. 28a, b).

Lateral line complete, perforated scales 41 ($X = 40.7$, range 40–44, $n = 27$). Pre-dorsal scales 18 ($X = 18$, range 17–20, $n = 41$). Scale rows between dorsal-fin origin and lateral line 6 ($X = 6.1$, range 6–7, $n = 41$). Scale rows between anal-fin origin and lateral line 5 in all specimens ($n = 41$). Scale rows around caudal peduncle 16 ($X = 16.2$, range 16–17, $n = 26$).

Premaxillary teeth in two distinct rows. Larger teeth distinctly tricuspid, smaller

teeth with less well-developed, sometimes vestigial, lateral cusps (see Fig. 4). Outer row teeth 3 ($X = 2.5$, range 1–4, $n = 48$). Inner row teeth 4 ($X = 4.9$, range 4–6, $n = 44$). Maxillary teeth 3, (increasing in number with increasing SL from $X = 3.6$ in 10 specimens between 20.0 and 24.7 mm SL to $X = 4.2$ in 7 specimens between 22.0 and 26.5 mm SL). Maxillary teeth tricuspid, first 2 or 3 larger than remaining teeth. Dentary with 4 large anterior tricuspid teeth in all specimens, $n = 48$ and 8 ($X = 7.2$, range 5–11, $n = 48$) posterior small teeth. Premaxillary, maxillary, and dentary teeth compressed, having flat inner and outer surfaces.

Vertebrae 39 ($X = 39.5$, range 38–41, $n = 39$). Upper limb gill-rakers 6 ($X = 5.6$, range 5–6, $n = 48$); lower limb gill-rakers 12 ($X = 11.5$, range 10–13, $n = 48$). Branchiostegal rays 4 in two cleared and stained

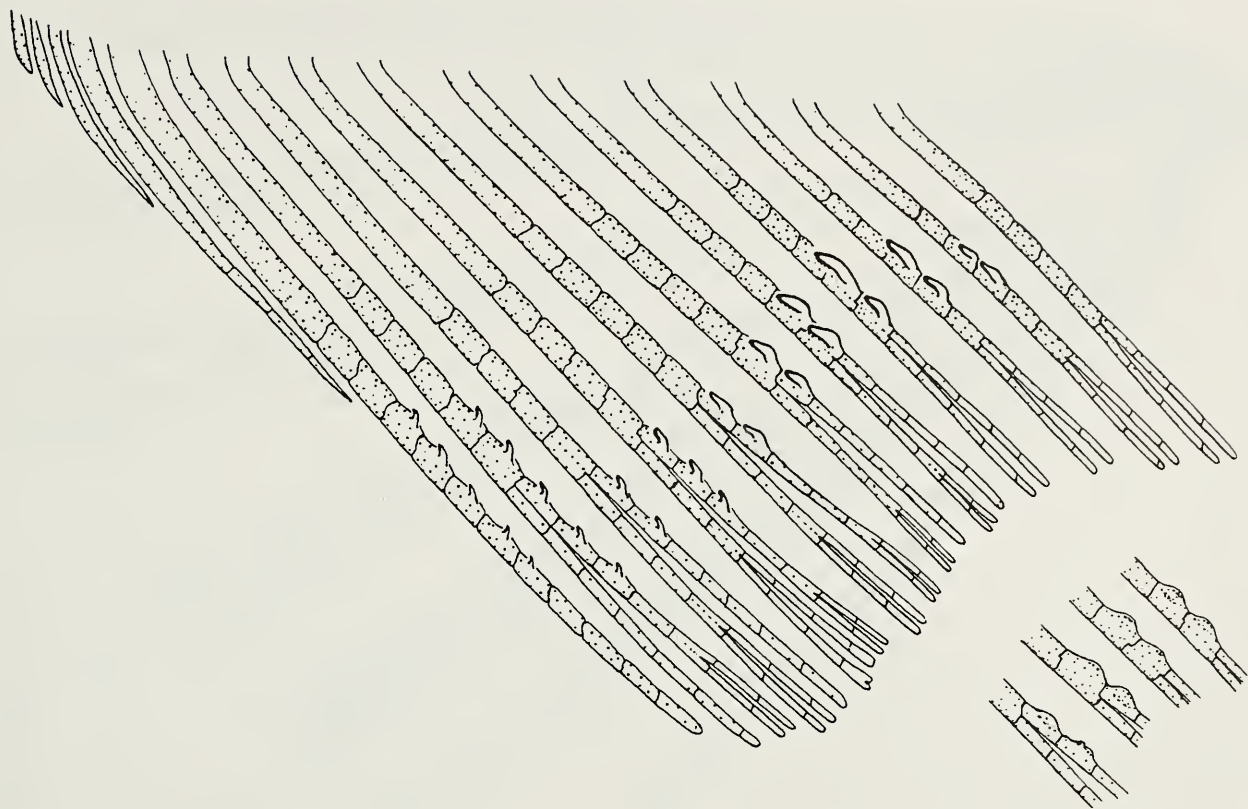


Fig. 14. *Planaltina myersi*, MNRJ 10635, c&s, sexually active male, SL 33.3 mm. Anterior portion of anal fin, left side. Figure shows anal-fin hooks positioned along posterolateral border of anal-fin rays, larger more posterior hooks bent dorsoanteriorly. Inset drawing at right shows anal-fin hook remnants of a sexually inactive adult male or perhaps developing hooks of a maturing male.

specimens, 3 rays originating from anterior ceratohyal and 1 ray from posterior ceratohyal.

Color in alcohol.—Males and females with approximately same color pattern (Fig. 22) at least in specimens preserved in alcohol for more than 20 years. Body pale to light brown and slightly darker dorsally than ventrally. Dorsal body surface dark due to scattered dark chromatophores. Fewer dark chromatophores on the ventral posterior part of body. Dark lateral body stripe mostly obscured by guanine pigment when such pigment not destroyed by formalin and extending from posterior part of dorsal opercular region to caudal-fin base. Visible dark pigmentation of lateral stripe mostly concentrated on caudal peduncle and more evident on males. This dark pigment continuing on anterior part of median caudal-fin rays. Pectoral and pelvic fins pale, dorsal and anal fins dusky with scattered dark chromatophores along fin rays. Head darker

dorsally and around mouth. Circumorbital bones and opercle silvery with few scattered dark chromatophores.

Ecology.—Dr. Heraldo Britski (pers. comm.) reports that the rio Corumbataí, where most of the samples were collected, is a clear-water river with a sandy bottom, approximately 8 meters wide and 1 meter deep at the collecting site. The area was almost entirely deforested and the marginal vegetation predominately represented by grasses.

Sexual dimorphism, mode of reproduction, and gonad anatomy.—Histological analysis revealed a thickened epithelium along the anal-fin rays of a mature male (26.3 mm SL; Fig. 24). Only a slight thickening was evident in the anal fin of a mature female (27.0 mm SL). Club cells were abundant in some areas, particularly in the epithelium near the anal-fin base. Although some club cells were present near the epithelial surface, no definitive secretion of the

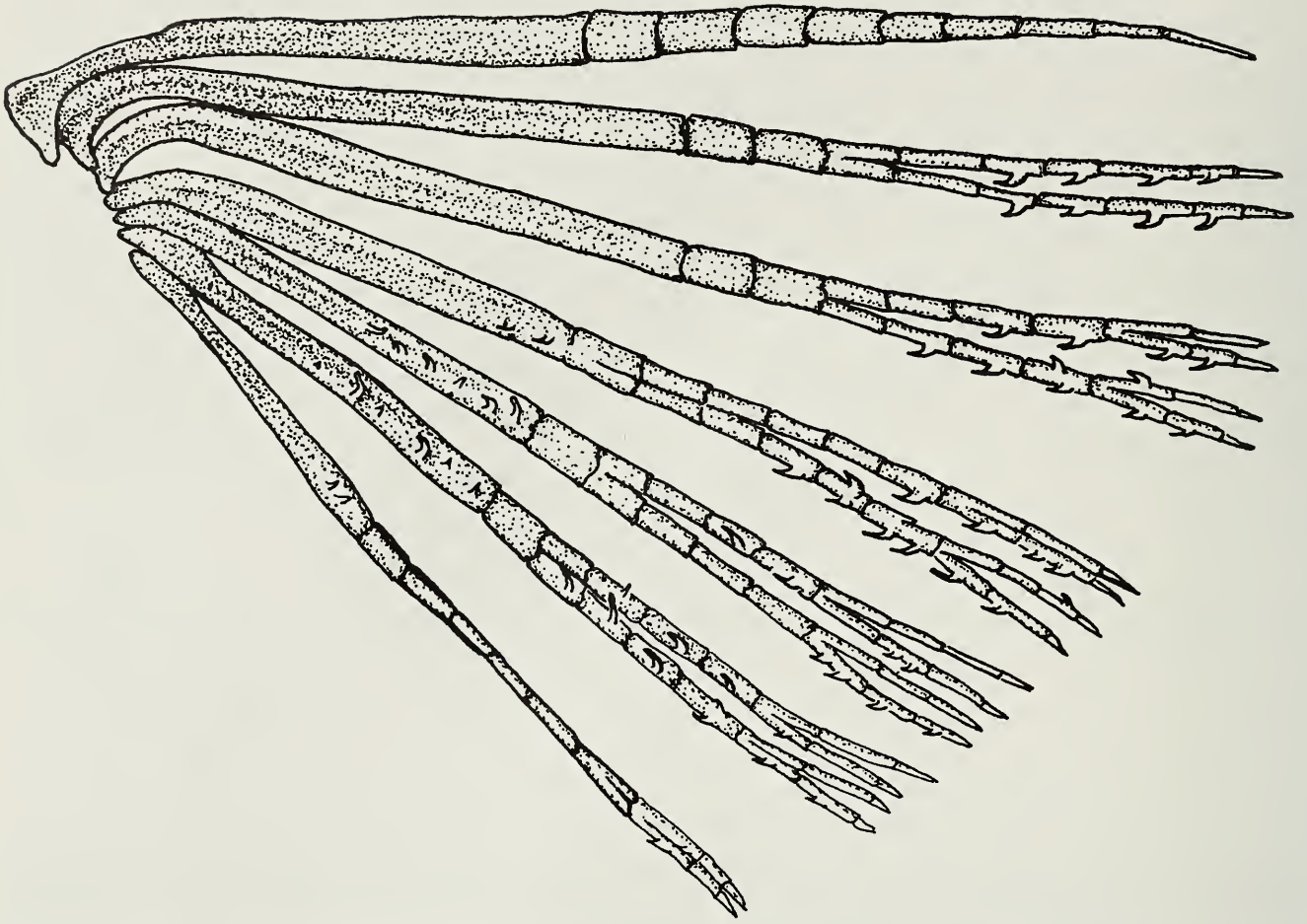


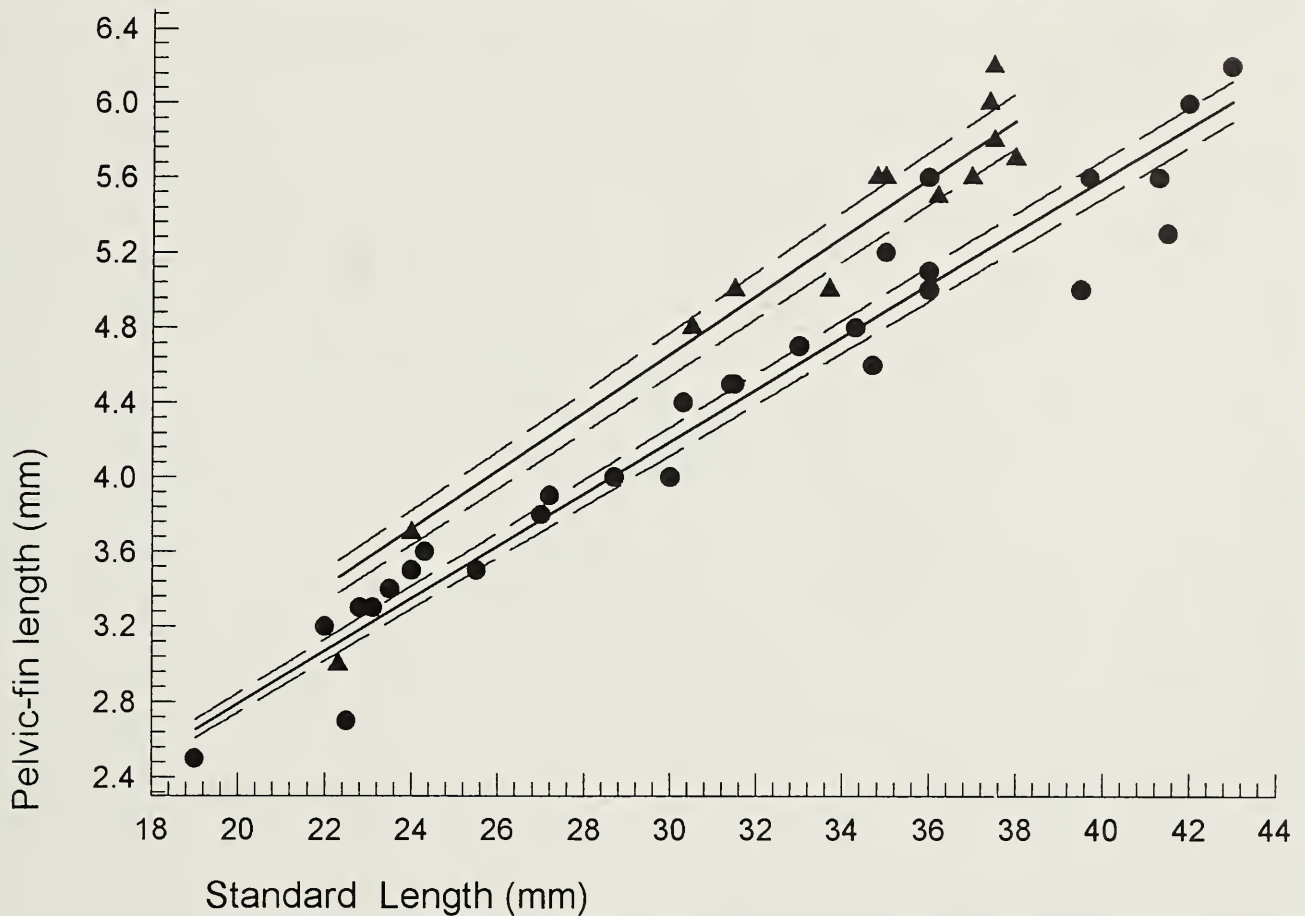
Fig. 15. *Planaltina myersi*, MNRJ 10634, c&s, sexually active male, SL 30.5 mm. Pelvic-fin rays, left side. Ventral surface showing pelvic-fin hooks.

cell contents was observed. The females lack the anal-fin and pelvic-fin hooks present in the males as described above (Fig. 25). The mean pelvic-fin length is longer in adult males than in adult females (Fig. 17) and although difficult to document from our limited data, this divergence in relative length may begin at approximately 24.0–25.0 mm. The skin is thickened along the ventral surface of the pelvic-fin rays of reproductively active males and forms a linear and turgid mound of tissue. Histological analysis of pelvic fins of a mature male (26.3 mm SL) and a mature female (27.0 mm SL) revealed that the marked thickening of the skin in the male was due to both growth of the epithelium and underlying connective tissue (Figs. 26, 27b). Club cells were particularly abundant near the pelvic-fin base, some near or at the surface. Unfortunately we were not able to observe cells at the surface undergoing active ho-

locrine secretion as was observed for similar cells of the anterior region of the anal fin of a species of *Attonitus* and the new genus. See Weitzman et al. (2004) for a more complete description of the gland cells and their mode of secretion in species of *Attonitus*. In the related undescribed genus and species these glandular cells resemble the classic “club” cells known to be present in most ostariophysan fishes (Pfeiffer 1977:660). There is a great amount of evidence that most ostariophysan club cells produce a pheromone that serves as an alarm signal (Pfeiffer 1967:389–390). Classic alarm substance cells (ASC’s) are club cells that do not open onto the epithelial surface and are said to release their contents only if the epithelium is damaged (Pfeiffer 1977:660–662). The club cells seen along the anal fin of *Attonitus* and the possibly closely related new genus and species do reach the epithelial surface and undergo de-

▲ = 13 males plus juvenile males, $Y = -0.628 + 0.174X$; $r^2 = 0.951$; adj. $r^2 = 0.947$

● = 32 females plus juvenile females, $Y = 0.098 + 0.137X$; $r^2 = 0.946$; adj. $r^2 = 0.944$



Planaltina myersi

Fig. 16. *Planaltina myersi*, pelvic-fin length as a function of SL by sex. Males and females were identified by external features and sometimes by examination of gonads through a slit in right side of body. Below 30 mm SL, the data is essentially useless for indicating differences in male and female pelvic-fin length, but beyond 30 mm SL, where most mature males occur and primarily where sex of both could males and females could be identified by gonad examination, all males have longer pelvic fins than females.

generation with the contents of the entire cell being secreted (holocrine secretion). These cells may therefore have a function other than of ASC's as may be the case in several catfish species (Pfeiffer 1967:389–390, 1977:663). Some club cells observed in the species of *Planaltina* also appeared to be located near the epithelial surface, although cell degeneration and release was not observed in our histological sections. More specimens need to be analyzed histologically to see if some club cells of *Planaltina* resemble those present on the anal fins of species of *Attonitus* and the new species and genus possibly closely related to *Attonitus*.

Although our population samples of *P. glandipedis* are represented by males and females of about equal length ranges from 24 to about 28.5 mm SL, only a few are sexually mature judging from visual inspection of the gonads. The scales bordering the dorsal border of the mature male pouch opening are more elongate than those of the mature females (Fig. 28a, b), but it is impossible to predict that greater elongation of scales dorsal to the pouch opening might be attained at comparatively larger sizes in females based only on the few available adult specimens of both sexes.

Histological analysis of ovaries from a mature female (27.0 mm SL) revealed the

▲ = 27 males plus juvenile males, $Y = -1.180 + 0.180X$; $r^2 = 0.859$; adj. $r^2 = 0.853$

● = 19 females plus juvenile females, $Y = 0.186 + 0.117X$; $r^2 = 0.829$; adj. $r^2 = 0.819$

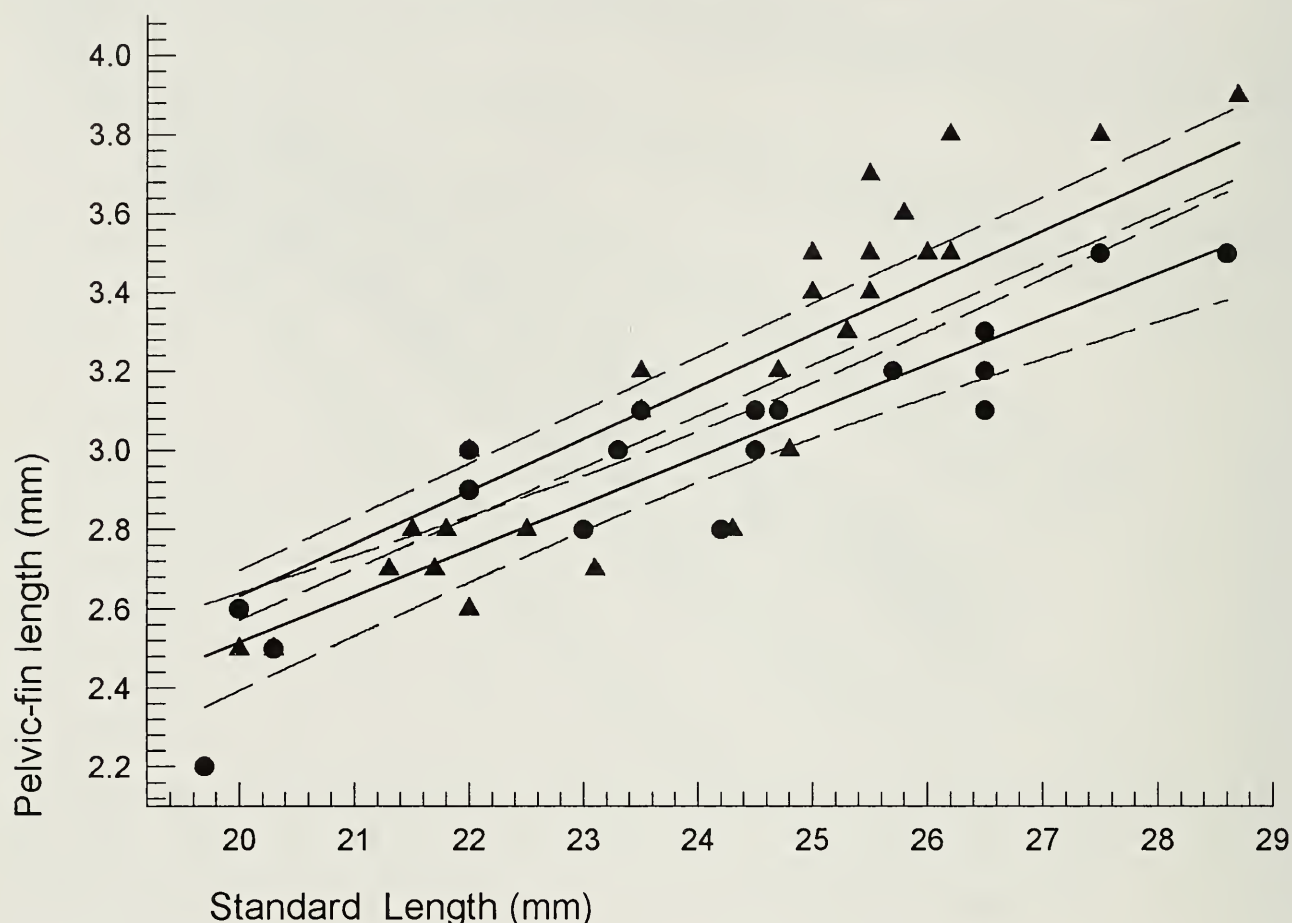


Fig. 17. *Planaltina glandipedis*, pelvic-fin length as a function of SL by sex. Males and females identified by external features and sometimes by examination of gonads by a slit in right side of body. Sexual maturity according to relative pelvic-fin length in males versus those of females appears to strikingly occur at least by standard lengths of about 25 mm SL where there appears a sudden increase in male pelvic-fin length. However, the data in other regions of the graph are insufficient to confirm this estimate. Also, at these lengths the male's testes become active and gland cells appear present in the pelvic fins.

presence of spermatozoa within the ovarian cavity (Fig. 29). Longitudinal sections through the testes revealed a posterior sperm storage area like that described for *P. myersi* by Burns et al. (1995:134, fig. 2). This posterior sperm storage region in a mature male *P. glandipedis* male (26.3 mm SL) occupied 23.3% of the area of a mid sagittal testis section. In *P. myersi* the storage area occupied 44.2% of the total testis area while equivalent regions in outgroup glandulocaudine species ranged from 4.3–12.2% (Burns et al. 1995). As reported for *P. myersi* by Burns et al. (1995: table 3) the sperm cell nucleus is spherical to slightly

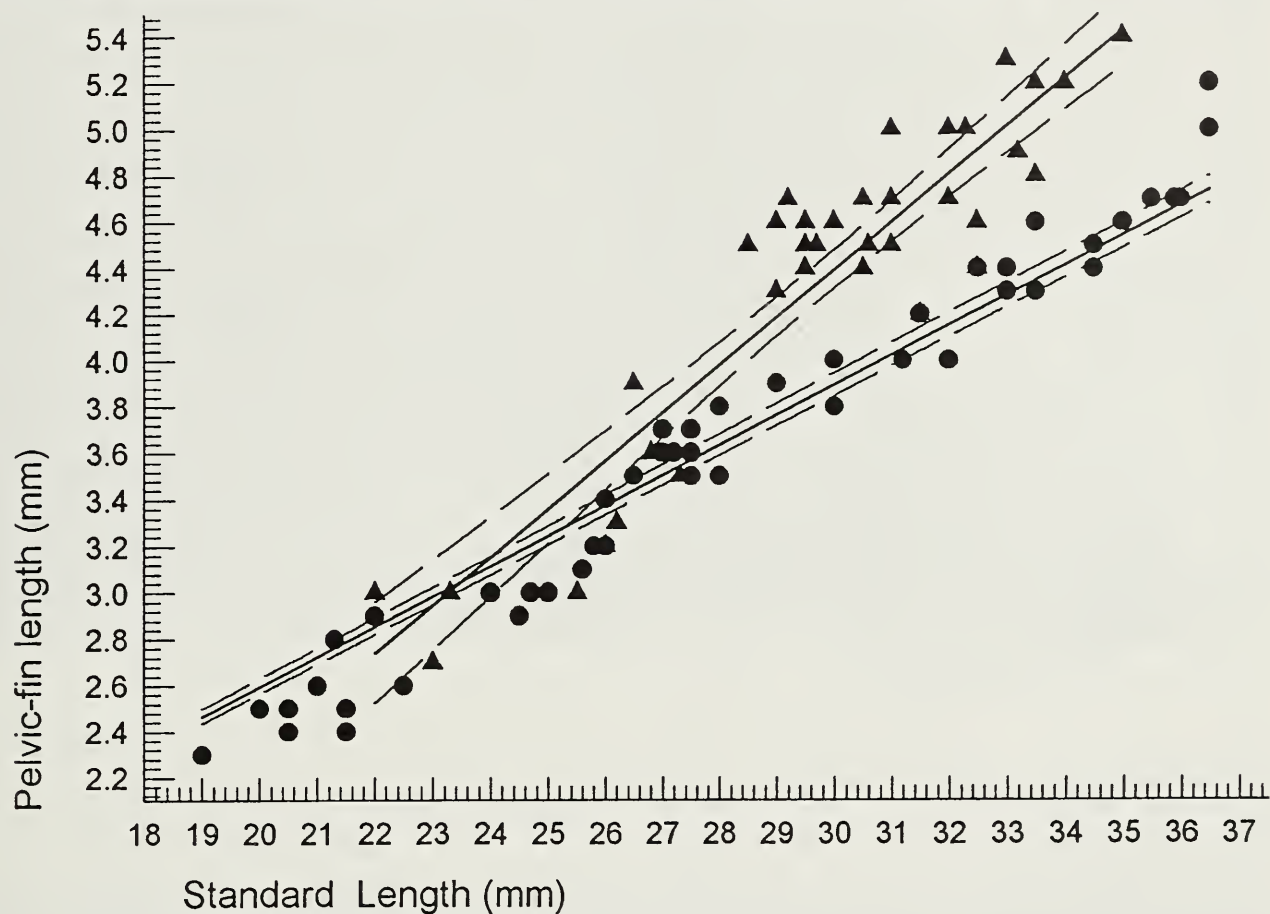
deformed. There appears to be no sperm cell modifications as are found in typical glandulocaudines, but ultrastructure examination was not possible. There were no gill glands as reported in *Corynopoma riisei* Gill by Burns and Weitzman (1996) and other glandulocaudines by Bushmann et al. (2002).

Distribution.—*Planaltina glandipedis* is known from the rio Corumbataí and rio Jacaré-Pepira, both tributaries of the rio Tietê, upper rio Paraná basin, in the State of São Paulo.

Etymology.—The name *glandipedis* is derived from Latin *glandula*, diminutive for

▲ = 41 males plus juvenile males, $Y = -1.809 + 0.207X$; $r^2 = 0.865$; adj. $r^2 = 0.861$

● = 51 females plus juvenile females, $Y = -0.591 + 0.150X$; $r^2 = 0.970$; adj. $r^2 = 0.969$



Planaltina britskii

Fig. 18. *Planaltina britskii*, pelvic-fin length as function of SL by sex and maturity. Males and females identified by external features and sometimes by examination of gonads by a slit in right side of body. Sexual maturity according to relative pelvic-fin length in males versus that of females appears to occur by lengths close to 28–29 mm SL. At these lengths male's pelvic fins become longer relative to those of females. Also, at these lengths, male's testes become active.

acorn, hence gland, and *pedis*, Latin for foot, in this case referring to the pelvic fins. A noun in apposition. The name is meant to signify a fish with a pelvic-fin gland or organ.

Planaltina britskii, new species

Fig. 30, Table 3

Specimens examined.—All type specimens are from Brazil, Estado de São Paulo, drainages, tributary to rio Grande or rio Tietê, both tributaries of the rio Paraná or in small streams directly tributary to the rio Paraná.

Holotype.—MZUSP 62757, male, 35.0

mm SL, Município de São José do Rio Preto, córrego da Barra Funda, tributary of rio Preto and tributary of rio Turvo, tributary of rio Grande, approximately, 20°37'S, 49°23'W, 7 Dec. 1998, V. Garutti.

Paratypes.—MZUSP 62758, 5 (33.0–36.5 mm SL) and DZSJRP 668, 7 (immature to adults, 22.0–36.5 mm SL), collected with holotype. Following 4 lots of immature to adult paratypes collected in Município de São José do Rio Preto, córrego da Barra Funda, tributary of rio Preto and then rio Turvo, tributary of rio Grande, approximately 20°37'S, 49°23'W. MZUSP 62759, 4 (17.0–31.0 mm SL), 30 Dec. 1980, V. Ga-

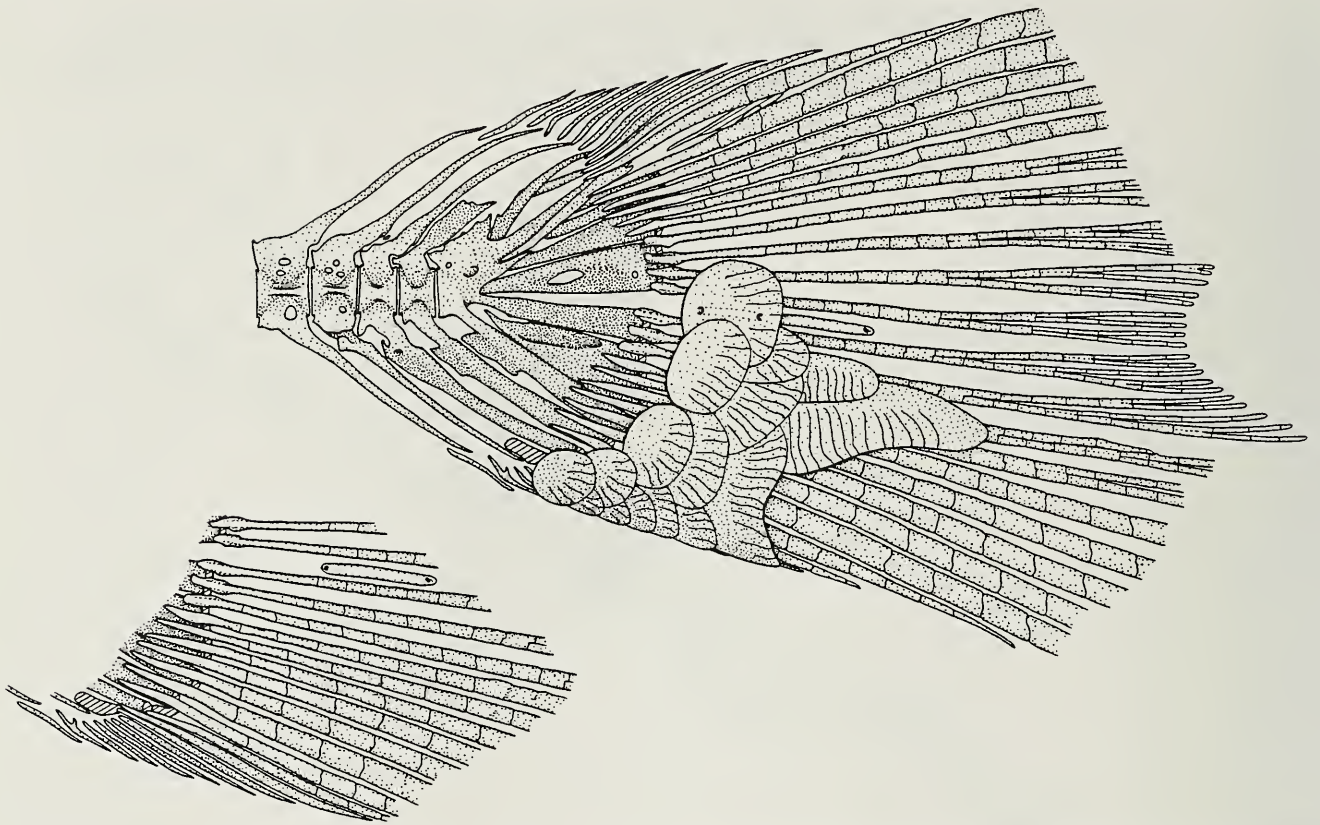


Fig. 19. *Planaltina myersi*, MNRJ 10635, c&s, sexually active male, SL 33.3 mm. Caudal skeleton, lateral view, left side. Inset at left shows modified scales removed.

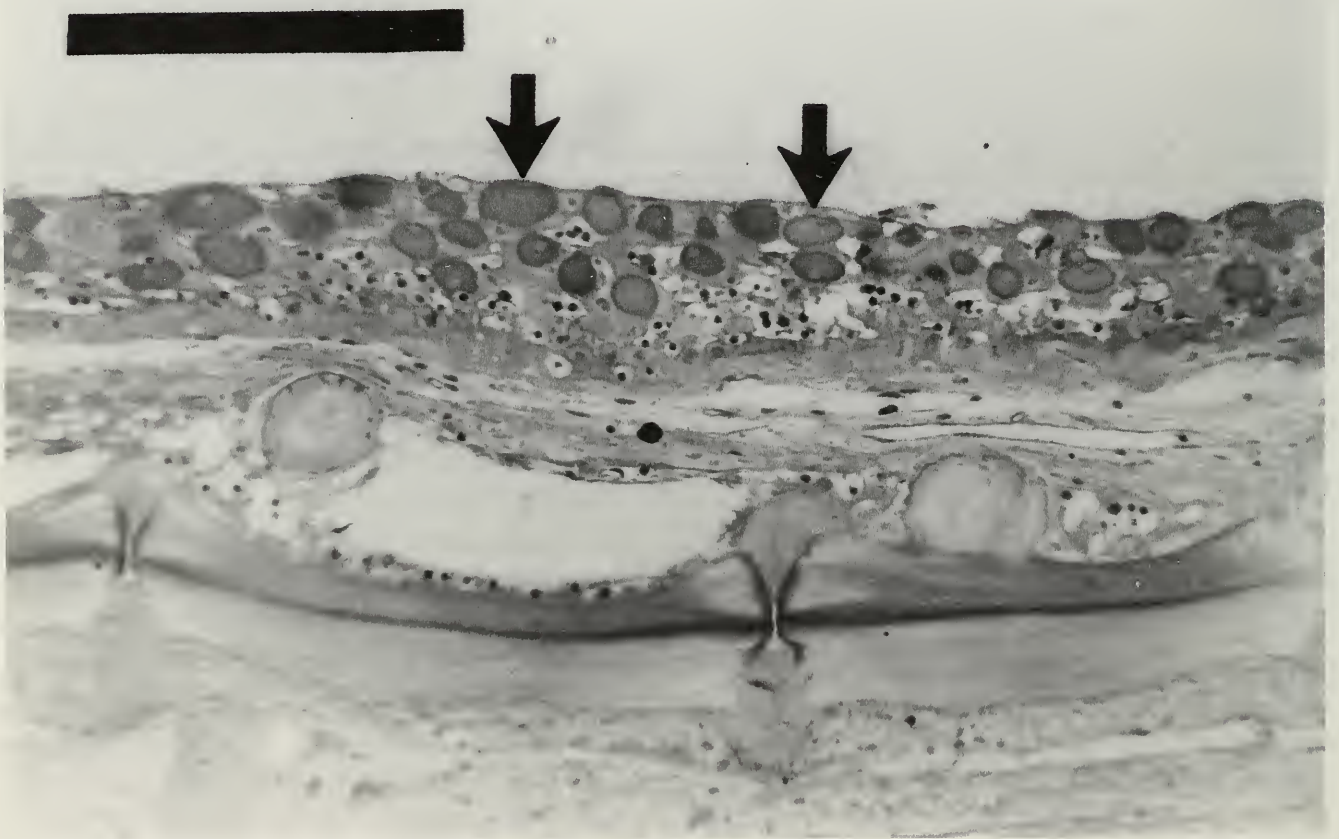


Fig. 20. *Planaltina myersi*, USNM 278966, histological section of pelvic fin showing abundant club cells (arrows), adult male SL 38.3 mm. Bar = 100 μ m.

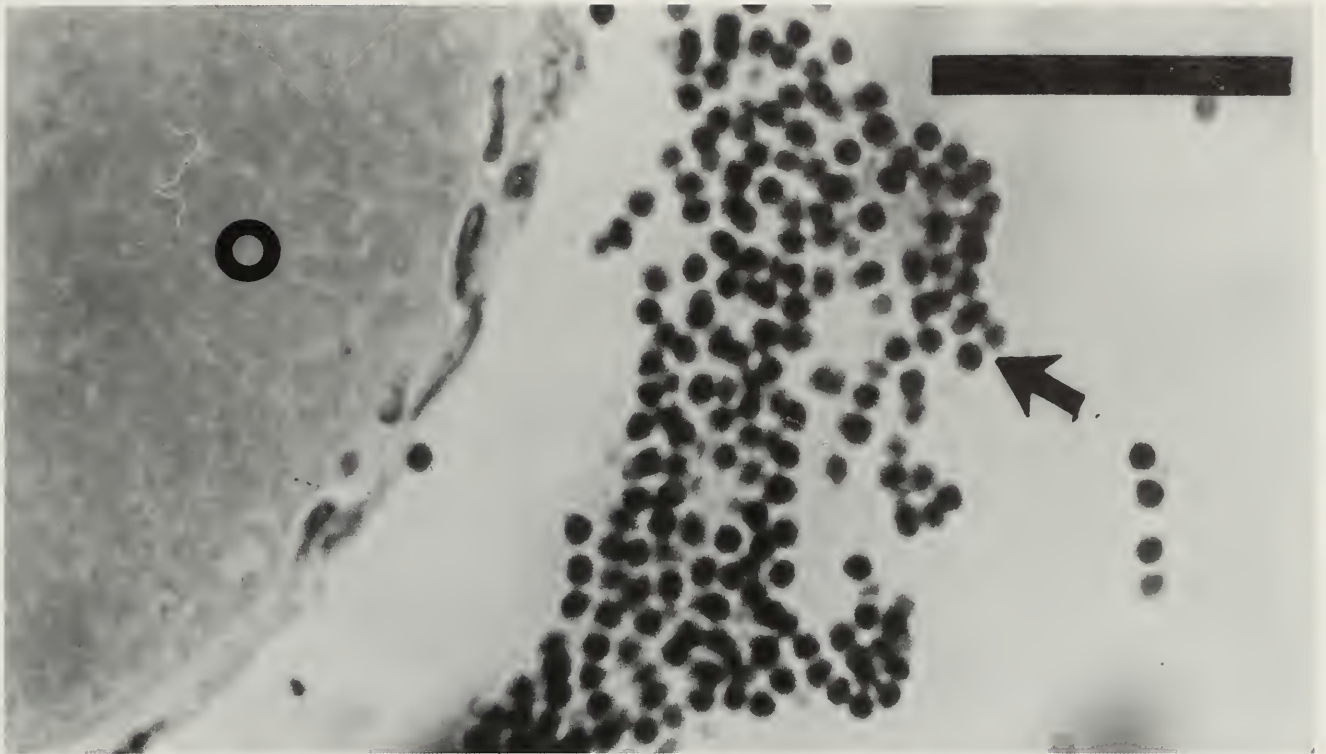


Fig. 21. *Planaltina myersi*, USNM 278989, histological section of ovary of adult female, 35.0 mm SL, arrow points to spermatozoa, o = oocyte cytoplasm. Bar = 20 μ m.

rutti & party; DZSJRP 674, 5 (immatures, 26.0–27.0 mm SL), 30 Dec. 1980, V. Garutti & party; MZUSP 26911, 10 (21.0–26.2 mm SL), 4 Jul. 1980, V. Garutti; USNM 362134, 10 (immatures to adults,

25.5–31.2 mm SL), 4 Jul. 1980, V. Garutti. MZUSP 62760, 10 (immatures to adults, 19.0–32.5 mm SL); LIRP 2255, 10 (immatures to adults, 31.5–33.5 mm SL), Município de Auriflama, Fazenda Itapuã, cór-

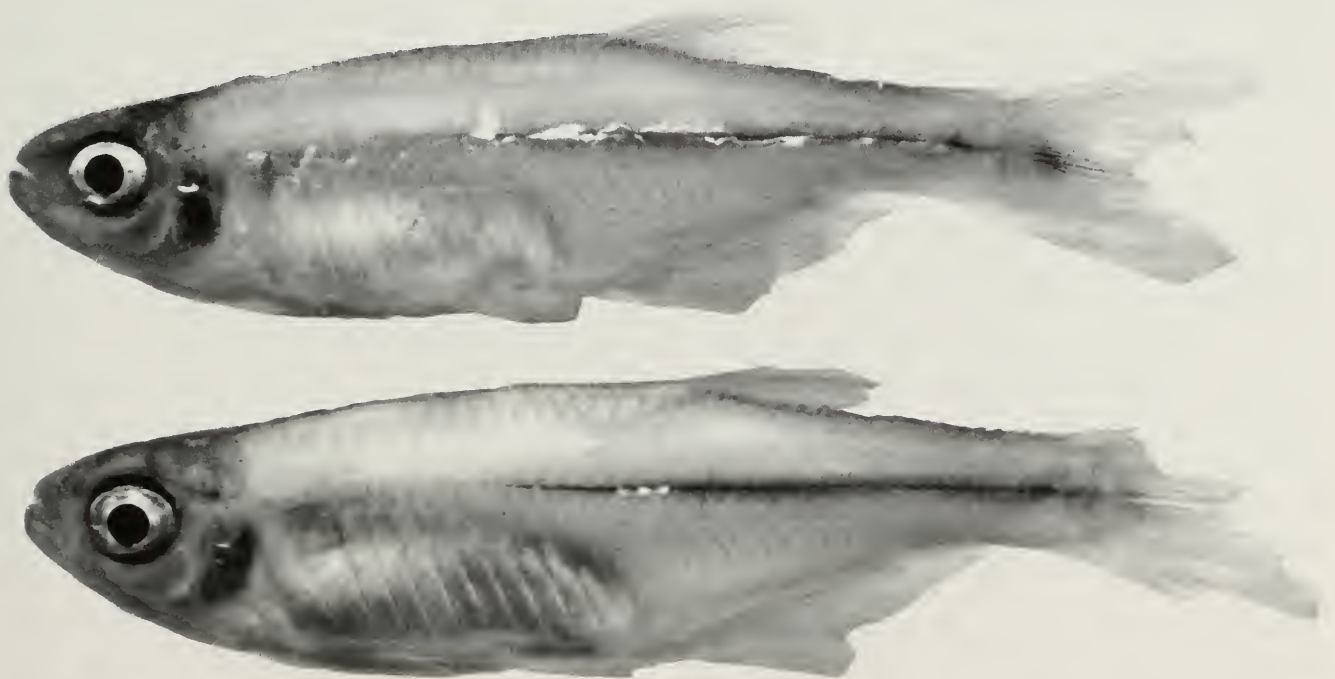


Fig. 22. *Planaltina glandipedis*, new species, holotype, adult male above, MZUSP 62752, SL 26.2 mm and paratype, adult female below, MZUSP 62753, SL 28.6 mm. Corumbataí, rio Corumbataí, approximately 22°13'S, 47°38'W, Estado de São Paulo, Brazil.

Table 2.—Morphometrics of *Planaltina glandipedis*. Standard length is expressed in mm; measurements through head length are percentages of standard length; the last four entries are percentages of head length. Minimum, maximum, *n*, *X*, and *SD* are based on the holotype, MZUSP 62752, and the following paratype lots: MZUSP 62753, USNM 362135, MZUSP 62754, USNM 362136, MZUSP 62755, USNM 362137, MZUSP 62756, and DZSJRP 671.

	Holotype	Males				Females			
		<i>n</i>	Range	<i>X</i>	<i>SD</i>	<i>n</i>	Range	<i>X</i>	<i>SD</i>
Standard length (mm)	26.2	27	20–28.7	24.0		20	19.7–28.6	24.2	
Body depth at dorsal fin origin	26.7	27	18.6–28.8	23.5	3.0	20	21.8–28.7	24.3	2.0
Snout to dorsal-fin origin	61.5	27	54.4–64.0	58.9	2.6	20	54.7–62.8	59.5	2.5
Snout to pectoral-fin origin	25.6	27	21.4–28.0	24.2	1.6	20	23.0–27.6	24.9	1.1
Snout to pelvic-fin origin	45.8	27	42.4–50.0	45.2	2.0	20	42.1–49.1	45.7	1.7
Snout to anal-fin origin	58.8	27	53.0–64.0	57.7	2.6	20	55.8–61.5	59.0	1.6
Caudal peduncle depth	10.7	27	07.9–12.0	09.9	1.2	20	07.6–11.5	09.9	1.1
Caudal peduncle length	12.6	27	10.6–14.4	12.4	0.9	20	07.6–14.5	12.0	1.6
Pectoral-fin length	26.7	27	20.6–26.9	23.4	1.2	20	21.8–26.4	23.4	0.1
Pelvic-fin length	14.5	27	12.5–14.5	13.4	0.5	20	11.2–14.4	12.5	0.7
Dorsal-fin base length	09.9	26	08.0–12.0	09.8	0.1	20	08.2–12.7	10.0	1.2
Dorsal-fin height	19.8	27	15.9–22.4	19.6	1.7	20	17.2–22.1	19.7	1.3
Anal-fin base length	29.3	27	26.5–32.8	29.0	1.6	20	26.0–33.2	28.7	2.0
Anal-fin lobe length	17.9	27	13.6–19.5	17.2	1.6	20	13.0–20.4	17.3	1.8
Eye to dorsal-fin origin	46.9	27	43.1–49.6	46.0	2.1	20	43.0–50.0	46.5	1.6
Dorsal-fin origin to caudal-fin base	38.2	27	36.3–42.0	39.3	1.5	20	36.4–40.7	38.7	1.1
Bony head length	24.8	27	21.6–25.8	23.3	1.2	20	21.5–25.4	23.3	1.1
Horizontal eye diameter	35.4	27	35.4–42.6	38.9	1.8	20	33.8–42.6	38.7	2.1
Snout length	23.1	27	17.0–26.9	21.0	2.5	20	17.8–25.4	21.9	2.6
Least interorbital width	33.8	27	27.0–34.9	30.8	2.1	20	26.7–36.2	31.5	2.6
Upper jaw length	43.1	27	37.0–44.8	40.7	2.1	20	38.6–44.0	41.3	1.4

rego do Limoeiro, tributary of rio São José dos Dourados, tributary of rio Grande, 20°33'32.9"S, 50°35'29"W, altitude 350 m, 28 Jul. 1999, Ricardo M. C. Castro & party. MZUSP 62761, 6 (29.5–35.0 mm SL).

DZSJRP 656, 7 (immatures to adults, 22.0–29.2 mm SL), José Bonifacio, km 88 of road BR-153, stream ultimately tributary to rio Tietê, approximately 21°03'S, 49°41'W, 12 Feb. 1988, D. Brandão & party. MZUSP

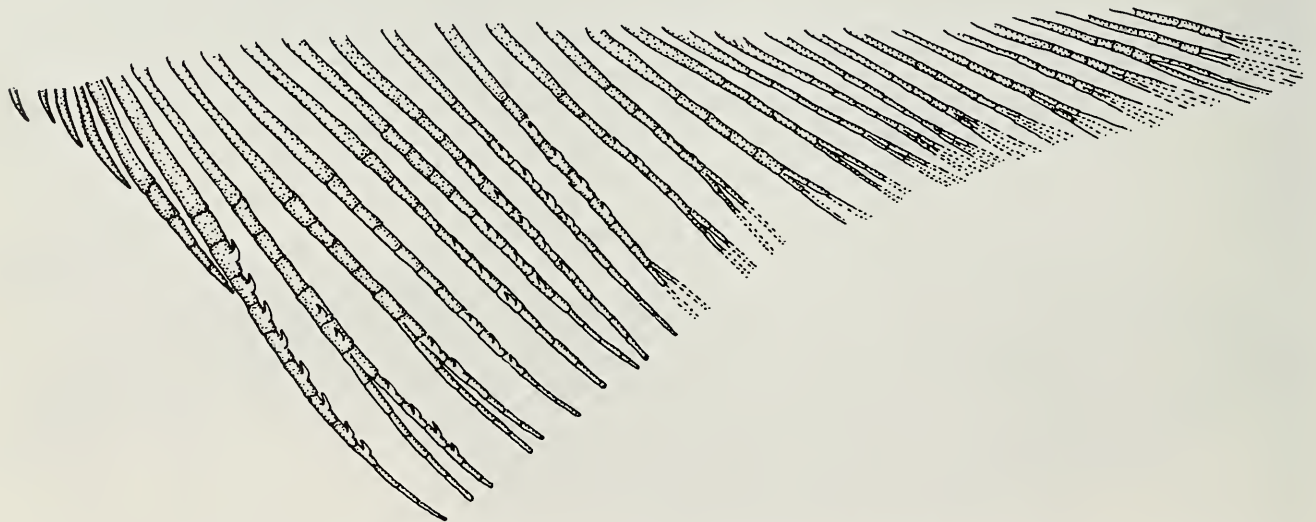


Fig. 23. *Planaltina glandipedis*, USNM 362385, c&s, sexually active male, SL 24.3 mm. Anterior portion of anal fin, left side. Figure shows anal-fin hooks positioned along posterolateral border of anal-fin rays, larger more posterior hooks bent dorsoanteriorly.



Fig. 24. *Planaltina glandipedis*, USNM 362136, histological section through anterior anal fin of mature male, SL 26.3 mm. Arrow indicates thickened epithelium. Bar = 100 μ m.

62762, 3 (immatures to adults, 30.0–33.5 mm SL); DZSJRP 670, 3 (adults, 27.5–30.0 mm SL), Município de Mirassolândia, Macaúbas, approximately 20°34'S, 49°28'W, 30 Apr. 1988, Marcelo Garcia. MZUSP 27138, 2 (immatures, 18.5 and 20.5 mm SL). USNM 367195, 1 (27.3 mm SL), Miguelópolis, represa de Volta Grande, rio Grande, approximately 20°12'S, 48°07'W, 6–7 Nov. 1975, CETESB. MZUSP 62763, 4 (immatures, 21.5–23.3 mm SL), Conchal, rio Mogi-Guaçu, tributary of rio Tietê, approximately 22°19'S, 47°07'W, 20 Apr. 1997, Flavio C. T. Lima & party. MZUSP 62764, 2 (immatures, 27.2 and 29.5 mm SL), Corumbataí, rio Corumbataí, tributary of rio Piracicaba, tributary of rio Tietê, approximately 22°13'S, 47°38'W, 25 Jan. 1976, Heraldo A. Britski.

Non-type material.—MZUSP 62808, 4 (adults, 27.5 and 31.5 mm SL), Ilha Soltei-

ra, rio Paraná, approximately 20°23'S, 51°167'W, Sept. 1965. LIRP 2256, 1 (adult, 32.0 mm SL), Município de Olímpia, Córrego das Laranjeiras 20°44'11.3"S, 49°02'50.3"W, 15 July 2001, Ricardo M. C. Castro & party. LIRP 2257, 2 (immatures, 22.3 and 27.0 mm SL), Município de Guapiaçu, Córrego do Modesto, 20°43'52.4"S, 49°14'35.5"W, 14 July 2001, Ricardo M. C. Castro & party.

Definition.—*Planaltina britskii* and *P. glandipedis* sympatric in rio Corumbataí drainage and both with a scale arrangement on dorsal border of pouch scale different from that of *P. myersi* (key above and compare Figs. 19, 28, 33a, b). These two species readily distinguished from each other by characters provided in key and in definitions of *P. myersi* and *P. glandipedis*.

Description.—Morphometric data presented in Table 3. Description based on all

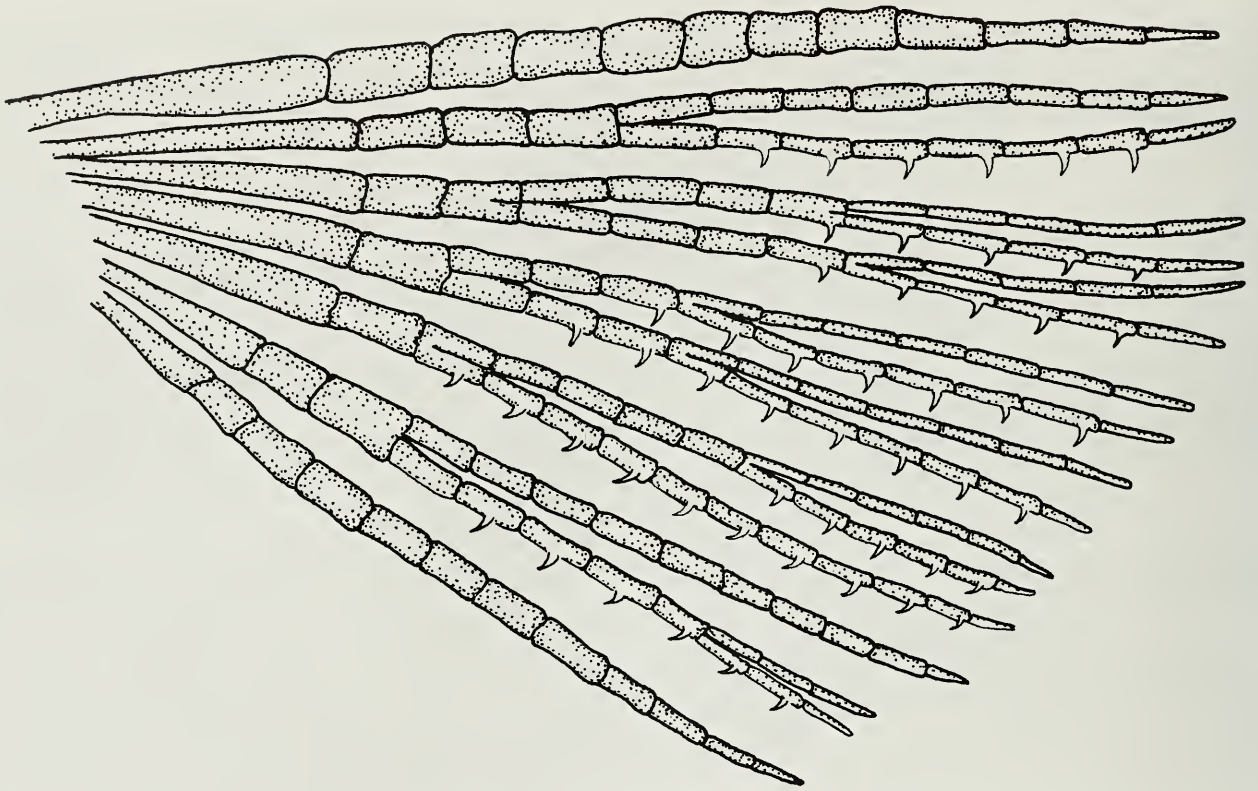


Fig. 25. *Planaltina glandipedis*, USNM 362135, c&s, sexually active male, SL 24.3 mm, pelvic-fin rays, left side. Ventral surface showing pelvic-fin hooks.

lots since no significant differences found among them.

Body compressed and slender; greatest body depth located slightly anterior of dorsal-fin origin at vertical crossing pelvic-fin origin. Dorsal body profile slightly convex from tip of snout to dorsal-fin origin, almost straight from this point to anterior to caudal peduncle and slightly concave dorsal to caudal peduncle. Dorsal-fin origin nearer to caudal-fin base than to snout tip. Ventral body profile convex from tip of lower jaw to anal-fin origin, almost straight from this point to posterior end of anal-fin base and slightly concave ventral to caudal peduncle.

Snout conical, shorter than orbital diameter. Mouth subterminal, lower jaw included in upper when mouth closed. Maxilla ventrally convex, extending posteriorly to vertical line crossing anterior border of pupil of eye.

Dorsal-fin rays ii, 8 (with posteriormost ray unbranched in all but two specimens in which count appears as ii, 9 but is actually ii, 8), $n = 90$. Adipose fin present. Anal-fin

rays iv, 21 (iv or v, usually iv, unbranched rays, branched rays $X = 21.3$, range 19–24, $n = 90$). Anterior anal-fin lobe weakly developed and including fourth and/or fifth unbranched rays and first 6–7 branched rays. Anterior part of anal fin in sexually mature males with bilateral hooks on anterior fourth or fifth unbranched and anterior 9–10 branched rays (Fig. 31). Pectoral-fin rays i, 11 (anterior unbranched ray i in all specimens; branched rays $X = 10.4$, range 9–11, $n = 90$). Distal tips of longest pectoral-fin rays not reaching pelvic-fin origin in juveniles, just extending to pelvic-fin origin in immatures and slightly beyond pelvic-fin origin in adult specimens; pectoral fin about same relative length in both sexes and without hooks. Pelvic-fin rays i, 6 (posteriormost ray unbranched in most specimens, branched in 2 adult males, $n = 90$). Sexually mature males with hooks present on rays of pelvic fin, distributed as in Fig. 32. Number of hooks per ray varying among males; in mature male (43.0 mm SL) no hooks present on first branched ray,

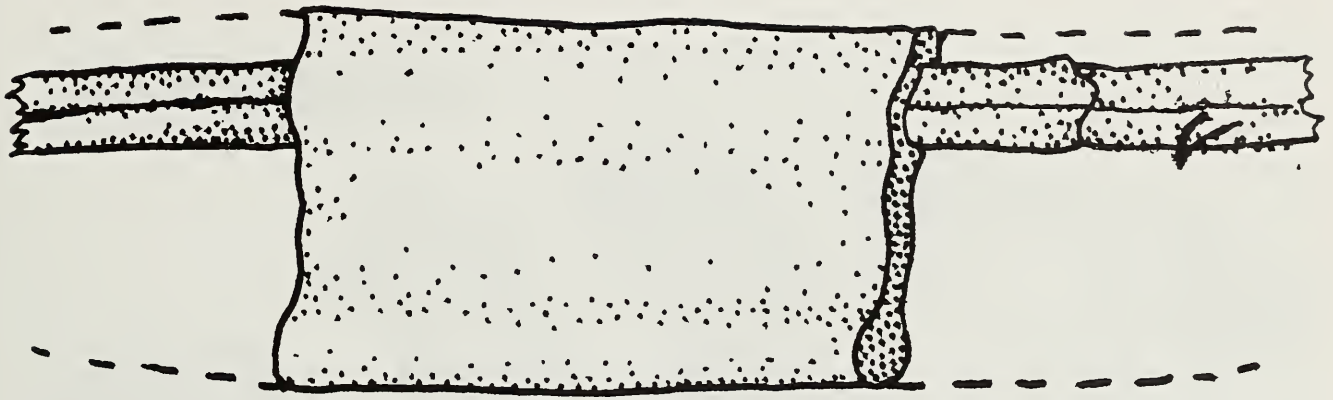


Fig. 26. *Planaltina glandipedis* drawing of a section of the ventral external surface of pelvic-fin glandular pads of a sexually active male, USNM 362135, SL 24.3 mm. The fin ray section displays its two halves or lepidotrichs and the proximal portion of this ray extends to the left and the distal portion extends to the right. A hook, at the right, is shown extending ventrally from the surface of the ventral lepidotrich. The fold of tissue extending ventrally from the fin ray constitutes a section of this particular ray's glandular pad. The ventral dashed lines extending to the right and left of the fold of tissue indicate the continuation of the ventral border of the fold or pad that has been cut away. The dorsal dashed lines are continuous with the area where the pad of tissue has been cut from the membrane that extends between the pelvic-fin rays adjacent to the illustrated ray.

25 present on second, 23 on third, 30 on fourth, and 15 on fifth branched ray of right pelvic fin. Pelvic fins of adult males longer than those of females (Fig. 18); distal tips of longest pelvic-fin rays of males extending slightly beyond anal-fin origin, but falling short of anal-fin origin in adult females. See discussion under "*Sexual dimorphism*" for explanation of Fig. 18 and pelvic-fin length differences between males and females. Principal caudal-fin rays 10/9, $n = 90$.

Scales cycloid with few radii (3–5) along posterior border, more numerous and conspicuous on enlarged scales bordering dorsal edge of pouch opening (Fig. 33a).

Lateral line complete, perforated scales 38 ($X = 39.9$, range 38–42, $n = 55$). Predorsal scales 14 ($X = 15.2$, range 14–16, $n = 73$). Scale rows between dorsal-fin origin and lateral line 5 ($n = 75$). Scale rows between anal-fin origin and lateral line 4 ($n = 75$). Scale rows around caudal peduncle 13 ($X = 13.1$, range 12–14, $n = 54$).

Premaxillary teeth in two distinct rows. Outer row of premaxillary teeth tricuspid, inner row pentacuspoid. Outer row teeth 3 ($X = 3.4$, range 2–5, $n = 90$). Inner row teeth 4 ($X = 4.0$, range 4–5, $n = 90$). Maxillary teeth 2 ($X = 1.7$, range 1–3, $n = 90$).

Maxillary teeth tricuspid, first usually larger than remaining. Dentary with 4 large anterior pentacuspoid teeth in all specimens, $n = 90$ and 6 ($X = 6.2$, range 4–9, $n = 90$) slightly tricuspid to nearly unicuspid teeth posteriorly. Premaxillary, maxillary and dentary teeth compressed.

Vertebrae 38 ($X = 38.7$, range 38–41, $n = 41$). Upper limb gill-rakers 6 ($X = 5.8$, range 4–7, $n = 88$); lower limb gill-rakers 12 ($X = 11.8$, range 11–13, $n = 89$). Branchiostegal rays 4 in 2 cleared and stained specimens, 3 rays originating from anterior ceratohyal and 1 ray from posterior ceratohyal.

Color in alcohol.—Males and females displaying an identical color pattern in preserved specimens (Fig. 30). Body light brown, darker on dorsum and top of head. Lateral body stripe dark with silvery reflections, especially along ventral region due to deposits of guanine. This stripe beginning anteriorly as thin line at dorsal region of opercle and widens progressively towards caudal-fin base, reaching a maximum width at caudal peduncle, where it narrows and extends dorsal to enlarged dorsal pouch scales and onto median caudal-fin rays. Dark chromatophores present on dorsal body surface, mostly concentrated along

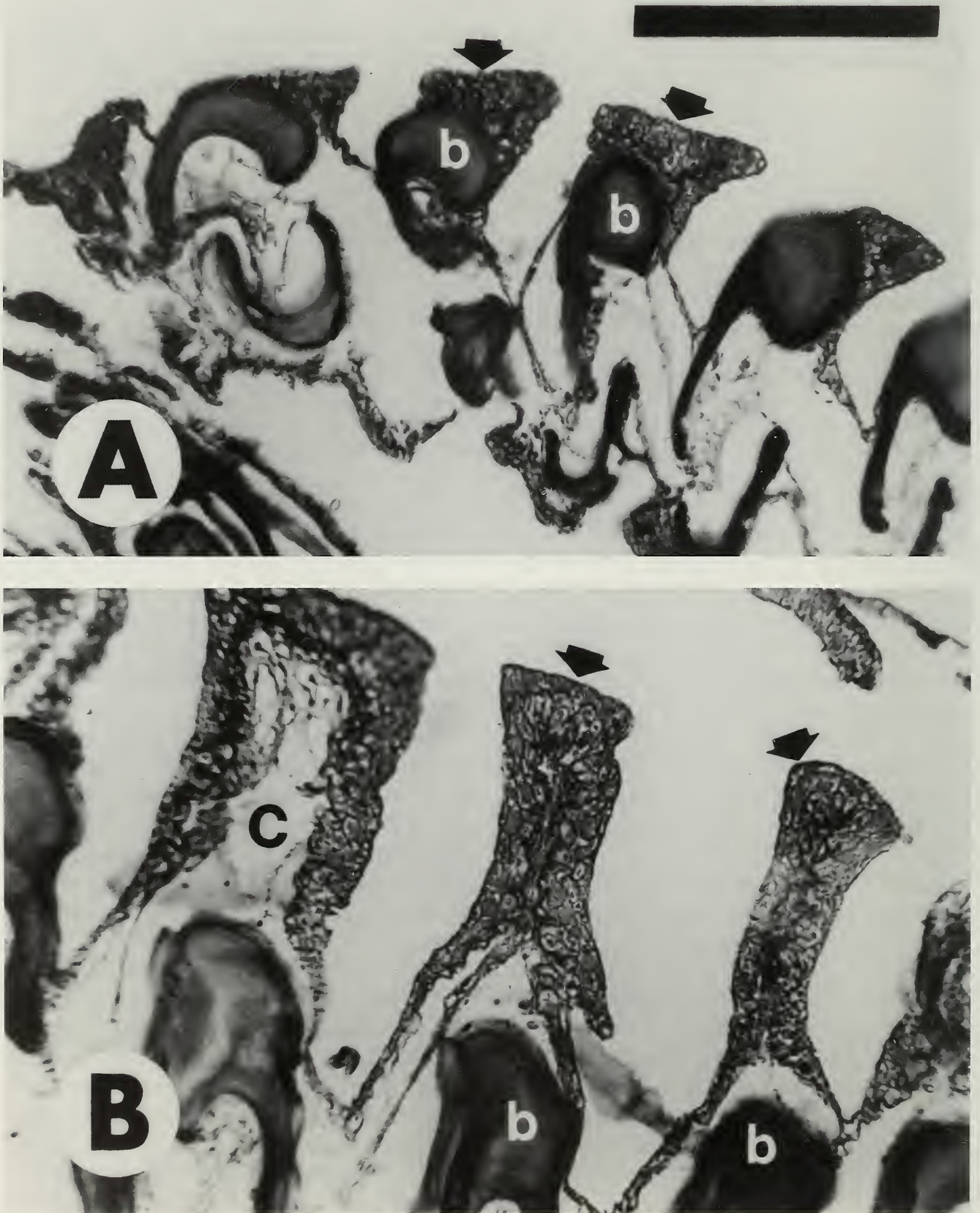


Fig. 27. *Planaltina glandipedis*, USNM 362136; A, histological cross sections of pelvic fins of female SL 27.0 mm and B, glandular pads of the male SL 26.3 mm. Arrows indicate epithelium covering pelvic-fin rays, b = bone of fin rays; c = expanded connective tissue of male. Bar = 100 μ m.

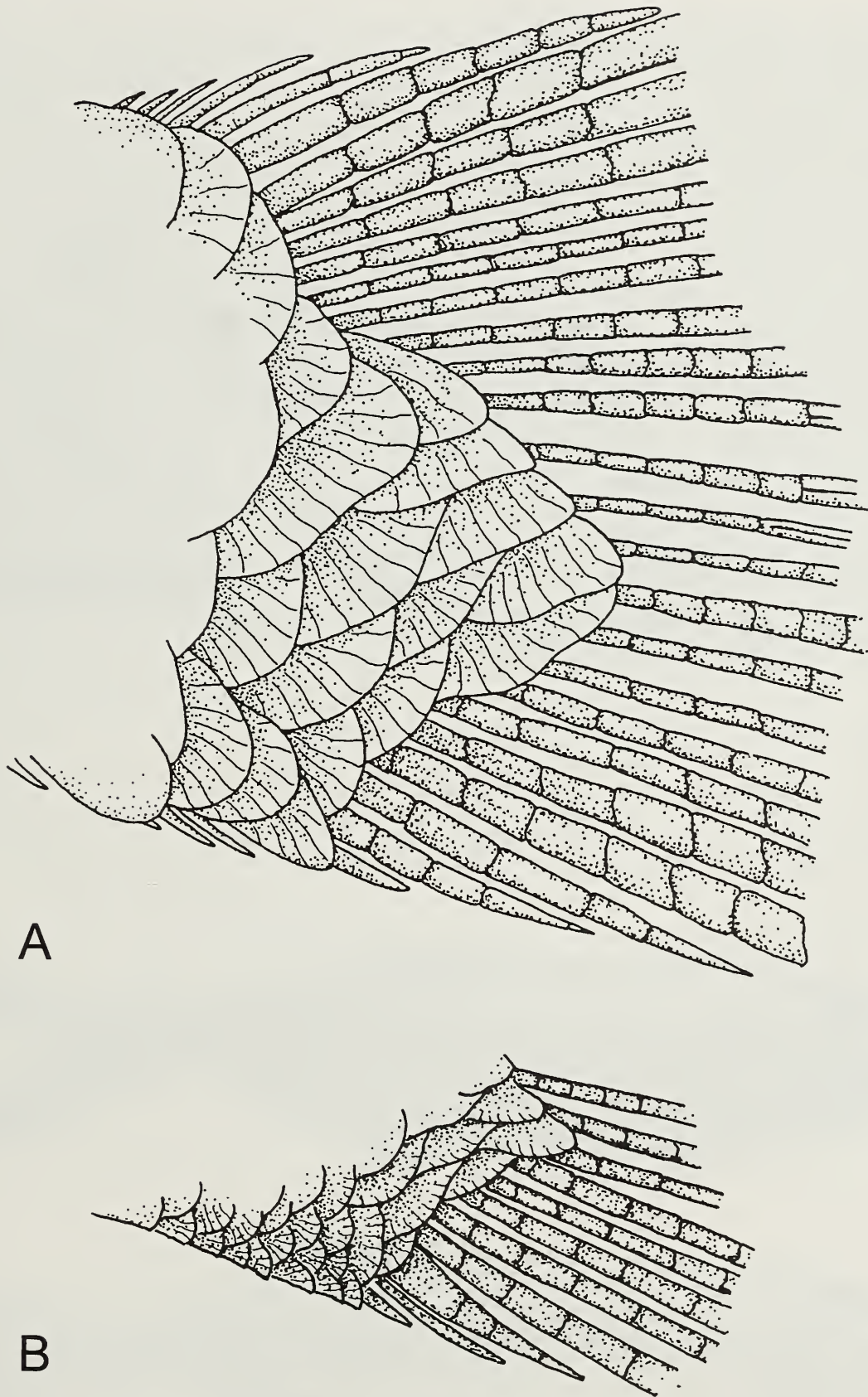


Fig. 28. *Planaltina glandipedis*. A, USNM 362135, c&s, sexually active male, SL 26.9 mm. Caudal skeleton, lateral view, left side; B, USNM 362135, c&s, sexually active female, SL 24.5 mm. Caudal skeleton, lateral view, left side.

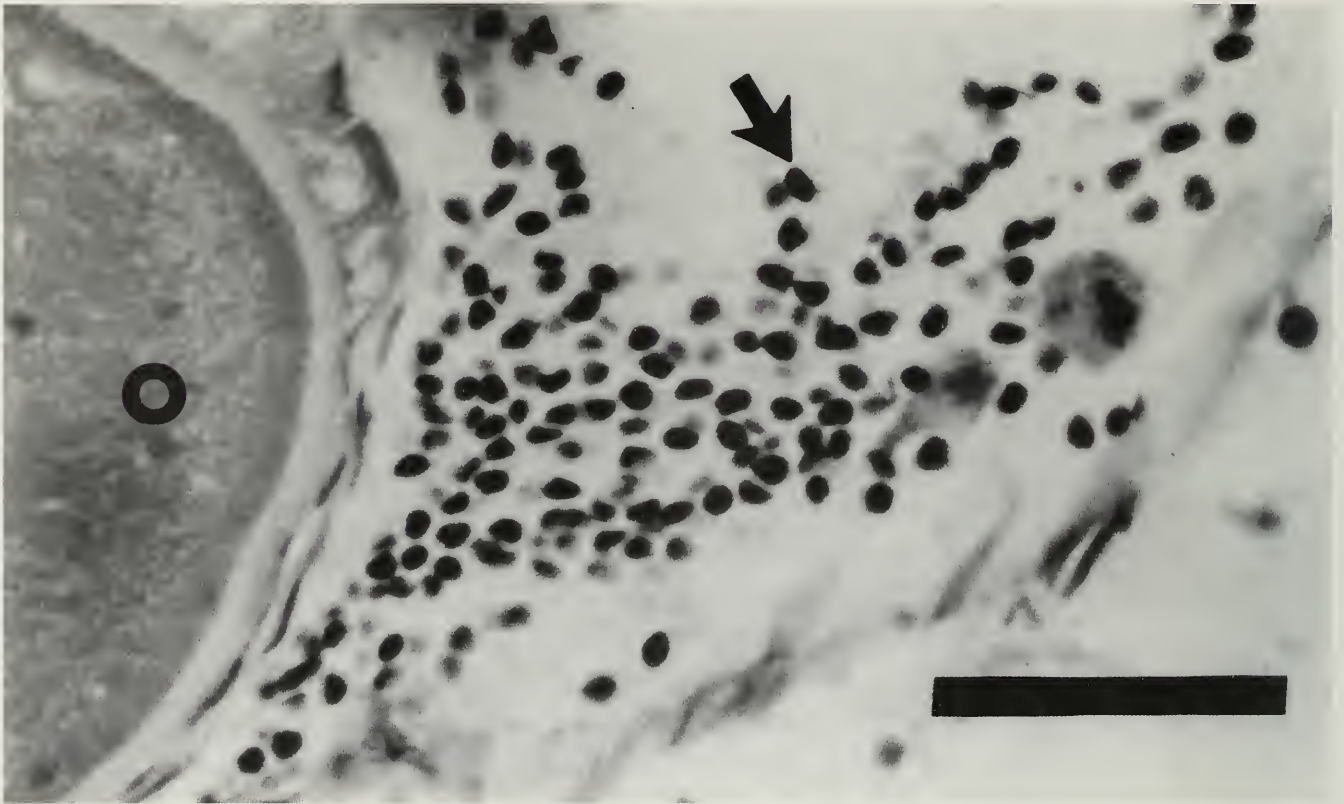


Fig. 29. *Planaltina glandipedis*, USNM 362136, histological section of ovary of adult female SL 27.0 mm. Arrow indicates spermatozoa; O = oocyte cytoplasm. Bar = 20 μ m.



Fig. 30. *Planaltina britskii*, new species, holotype, adult male above, MZUSP 62757, SL 35.0 mm, and paratype and adult female, MZUSP 62758, SL 36.5 mm; córrego da Barra Funda, tributary of rio Preto and tributary of rio Turvo, tributaries to rio Grande, Município de São José do Rio Preto, approximately 20°37'S, 49°23'W, Estado de São Paulo, Brazil.

Table 3.—Morphometrics of *Planaltina britskii*, new species. Standard length is expressed in mm; measurements through head length are percentages of standard length; the last four entries are percentages of head length. Minimum, maximum, *n*, *X*, and *SD* are based on the holotype, MZUSP 62757, and the following paratype lots: MZUSP 62758, DZSJRP 668, MZUSP 62759, DZSJRP 674, MZUSP 26911, USNM 362134, MZUSP 62758, LIRP XXX, MZUSP 62761, DZSJRP 656, MZUSP 62762, DZSJRP 670, USNM 367195, and MZUSP 62763.

	Holotype	Males				Females			
		<i>n</i>	Range	<i>X</i>	<i>SD</i>	<i>n</i>	Range	<i>X</i>	<i>SD</i>
Standard length (mm)	35.0	39	22.0–35.0	29.7		50	19.0–36.5	28.3	
Body depth at dorsal fin origin	22.9	39	18.6–25.0	22.5	1.8	50	16.9–25.5	22.2	2.5
Snout to dorsal-fin origin	59.1	39	53.8–61.9	57.9	1.8	50	55.3–61.0	58.3	1.5
Snout to pectoral-fin origin	23.7	39	22.3–26.8	24.2	1.0	50	22.4–27.3	24.4	1.0
Snout to pelvic-fin origin	46.6	39	42.9–50.9	45.6	1.8	49	42.8–51.1	46.5	1.8
Snout to anal-fin origin	60.0	39	53.6–63.5	59.1	1.8	50	54.7–65.7	60.2	2.1
Caudal peduncle depth	09.7	39	07.7–10.3	09.2	0.7	50	06.5–10.0	08.8	0.8
Caudal peduncle length	14.3	39	10.0–14.3	12.3	1.1	50	09.7–14.1	12.1	1.1
Pectoral-fin length	21.7	39	18.2–22.9	20.6	1.0	50	18.3–22.5	20.6	1.0
Pelvic-fin length	15.4	39	11.7–16.1	14.5	1.3	50	11.2–14.3	12.8	0.7
Dorsal-fin base length	09.7	39	08.5–11.3	10.0	0.8	50	08.0–11.7	09.9	0.7
Dorsal-fin height	19.1	37	17.6–20.6	19.2	0.7	48	17.5–20.2	18.9	0.6
Anal-fin base length	28.0	39	25.0–31.0	28.0	1.6	50	24.4–31.8	27.5	1.4
Anal-fin lobe length	16.3	38	15.2–18.9	16.9	0.9	50	14.6–19.2	17.1	1.1
Eye to dorsal-fin origin	47.1	39	41.5–49.4	45.2	1.6	50	41.3–48.6	45.6	1.7
Dorsal-fin origin to caudal-fin base	42.3	39	38.6–44.3	41.1	1.4	50	37.2–45.3	40.5	1.7
Bony head length	23.4	39	21.6–25.7	23.6	0.8	50	21.5–25.0	23.6	0.9
Horizontal eye diameter	36.6	39	34.9–41.8	37.7	1.6	50	34.5–41.8	38.0	1.9
Snout length	26.8	39	21.7–30.5	26.3	2.1	50	22.0–30.8	26.3	1.9
Least interorbital width	34.1	39	27.1–34.7	31.6	1.8	50	23.1–35.4	31.6	2.5
Upper jaw length	42.7	39	36.4–45.5	41.4	2.4	50	34.7–44.8	40.9	2.3

exposed borders of scales. Scattered dark chromatophores on snout, tip of lower jaw, and below eye. Inconspicuous patch of dark chromatophores present dorsal to anterior half of anal fin, extending ventrally onto most of anal fin.

Fins hyaline except faint scattered dark chromatophores present on basal portion of

dorsal fin and upper and lower lobes of caudal fin. Most of iris, as well as circumorbital, and opercular bones silvery.

Color in life.—Unknown.

Sexual dimorphism, mode of reproduction and gonad anatomy.—The typical hooks on the anal and pelvic fins of males are represented in Figs. 31 and 32. These

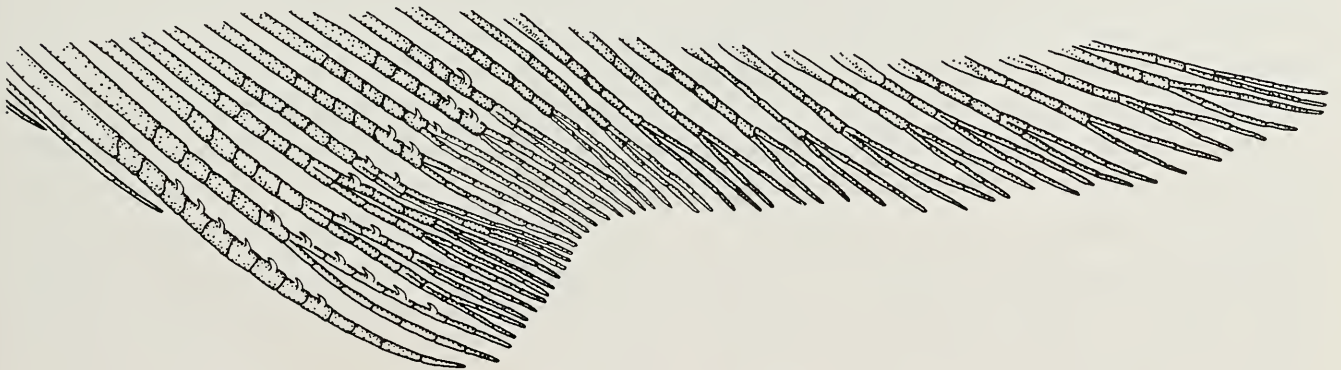


Fig. 31. *Planaltina britskii*, USNM MZUSP 62758, c&s, sexually active male, SL 35.6 mm. Anal fin, left side. Figure shows anal-fin hooks positioned along posterolateral border of anal-fin rays, hooks curved dorsoanteriorly.

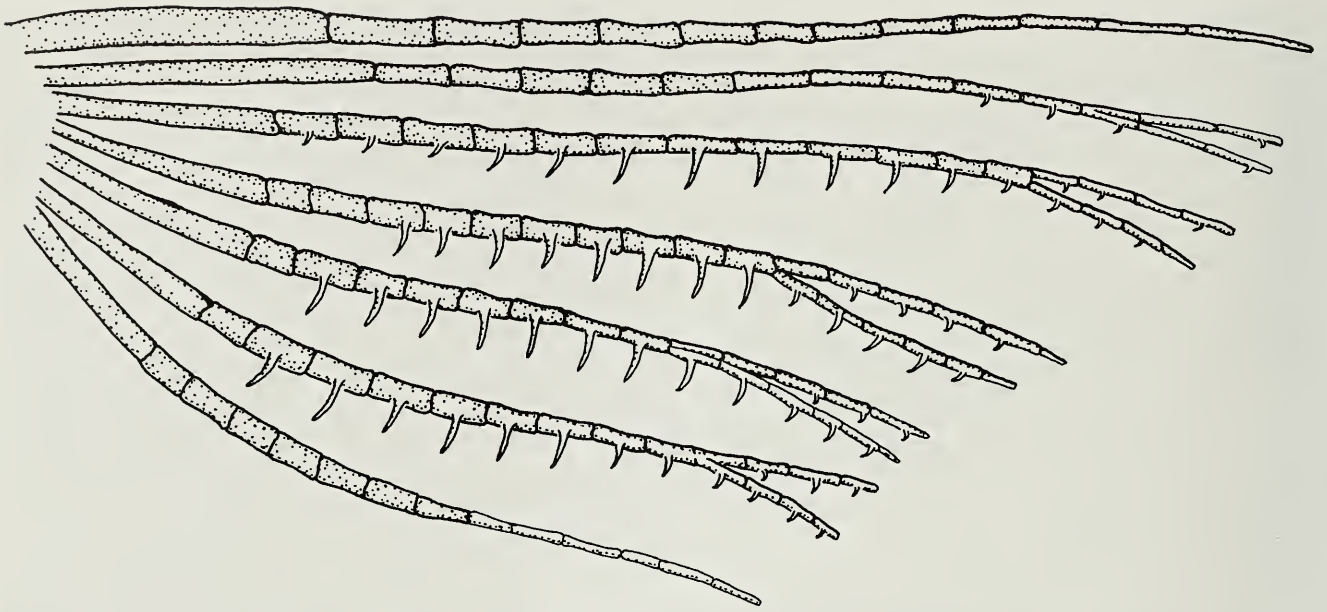


Fig. 32. *Planaltina britskii*, MZUSP62758, c&s, sexually active male, SL 35.6 mm. Pelvic-fin rays, left side. Ventral surface showing elongate narrow pelvic-fin hooks.

are absent on the pelvic and anal fins of females. Adult males have pelvic fins longer than adult females (see Fig. 18).

In our population samples males and females occur in equal length ranges, but very few adult females show the typical elongated scales on the dorsal border of the pouch opening that is present on the caudal fin of males of comparable lengths. The elongated scale pattern on the dorsal border of the pouch opening of adult males (illustrated in Fig. 33a) is present even in immature males of 30.0 mm in SL, but mature females in the size range between about 28.0 and 34.0 mm SL have the scales on the dorsal border of the pouch opening only slightly modified (see Fig. 33b). This suggests that the full elongation of scales on the dorsal border of the pouch opening in females is attained at comparatively longer sizes than in males.

A description of the ultrastructure of the sperm cell is not available. Histological analysis of mature ovaries revealed the presence of spermatozoa within the ovarian cavity (Fig. 34). Upon dissection, the testes of the only male specimen available for histological analysis (Fig. 35) were relatively thin, suggesting that it was not fully mature (holotype, MZUSP 62757, 35.0 mm SL).

However, a distinct posterior sperm storage region was present in the testis, occupying 13.1% of the total testis area in a mid-sagittal section. This is slightly larger than the percent area range (4.3–12.7%) for the out-group glandulo-caudine species in the study of Burns et al. (1995:134, fig. 2). Considering that this male was not fully mature, a distinct posterior sperm storage region comparable to that found in the other *Planaltina* species probably occurs in *P. britskii*. As reported for *P. myersi* by Burns et al. (1995: table 3) the sperm cells are typical aquasperm with the cell nuclei spherical to slightly deformed. There appears to be no sperm cell modifications as are found in typical glandulo-caudines. A gill gland, comparable to that seen in *P. myersi* (Bushman et al. 2002) was present in the holotype (Fig. 36).

Data from Garutti (1983) indicate that in córrego da Barra Funda the main reproductive period of the species is coincident with that area's rainy season, September through March, incidentally also the longest photo period of the year. The majority of the males and females, 98.3%, collected during the dry season, April through August, had undeveloped testes and ovaries, but 82.2% of the specimens of both sexes collected

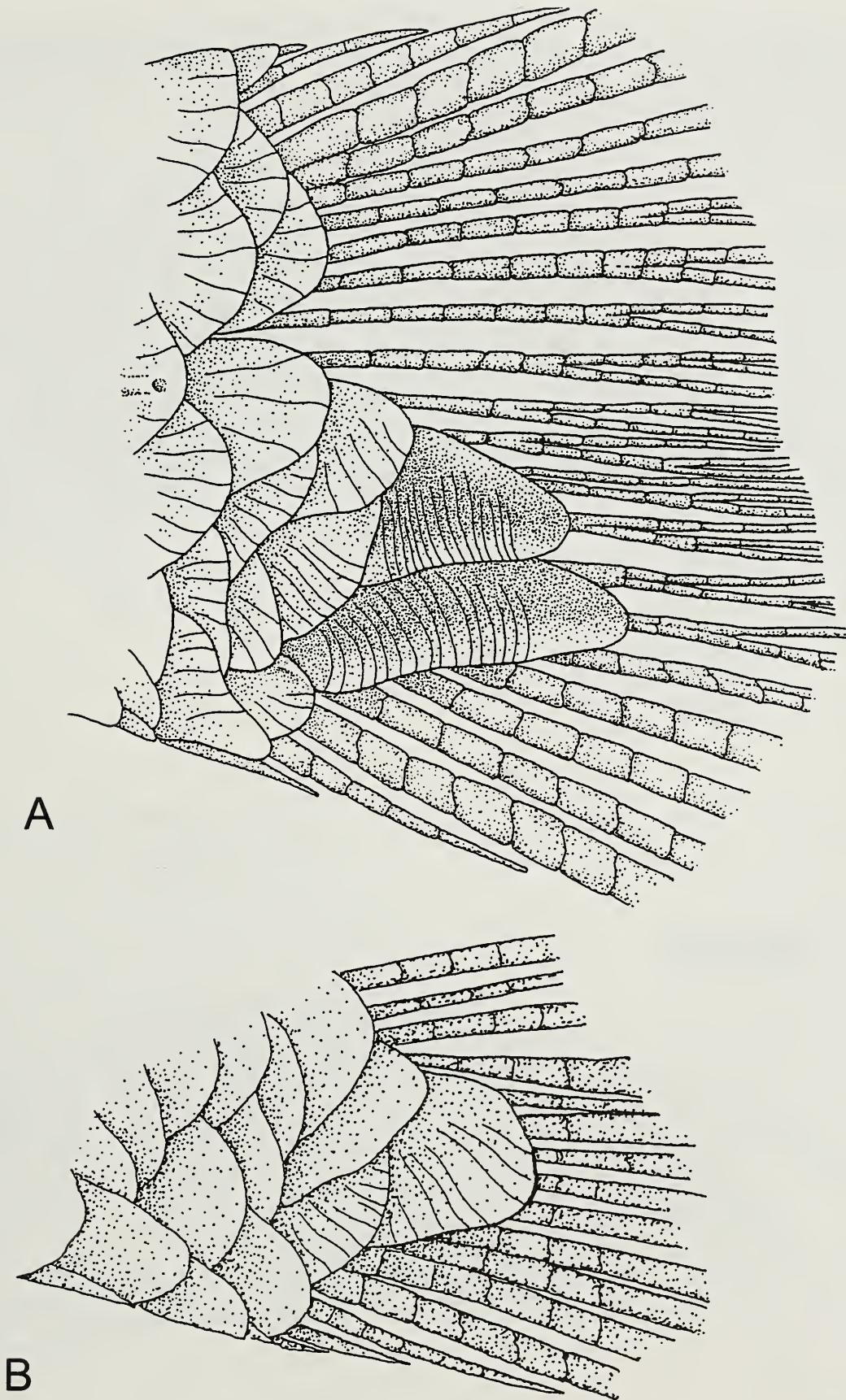


Fig. 33. *Planaltina britskii*, MZUSP62758, A, c&s, sexually active male, SL 35.1 mm. Caudal skeleton, lateral view, left side; B, sexually active female, SL 33.8 mm. Caudal skeleton, lateral view, left side.

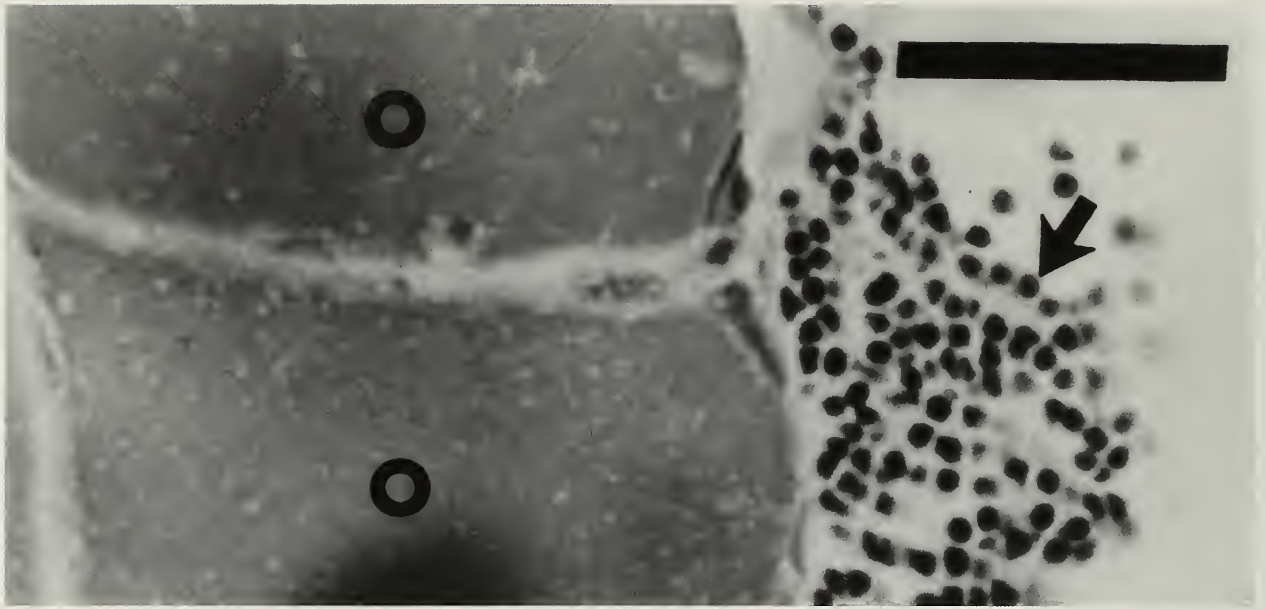


Fig. 34. *Planaltina britskii*, MZUSP 26911, histological section of ovary of an adult female SL 32.0 mm. Arrow indicates spermatozoa; O = oocyte cytoplasm. Bar = 20 μ m.



Fig. 35. *Planaltina britskii*, MZUSP 62757, holotype, SL 35.0 mm, mid-sagittal histology section through posterior testis showing more anterior spermatogenic regions (SG) and posterior sperm storage region (PS). Bar = 200 μ m.

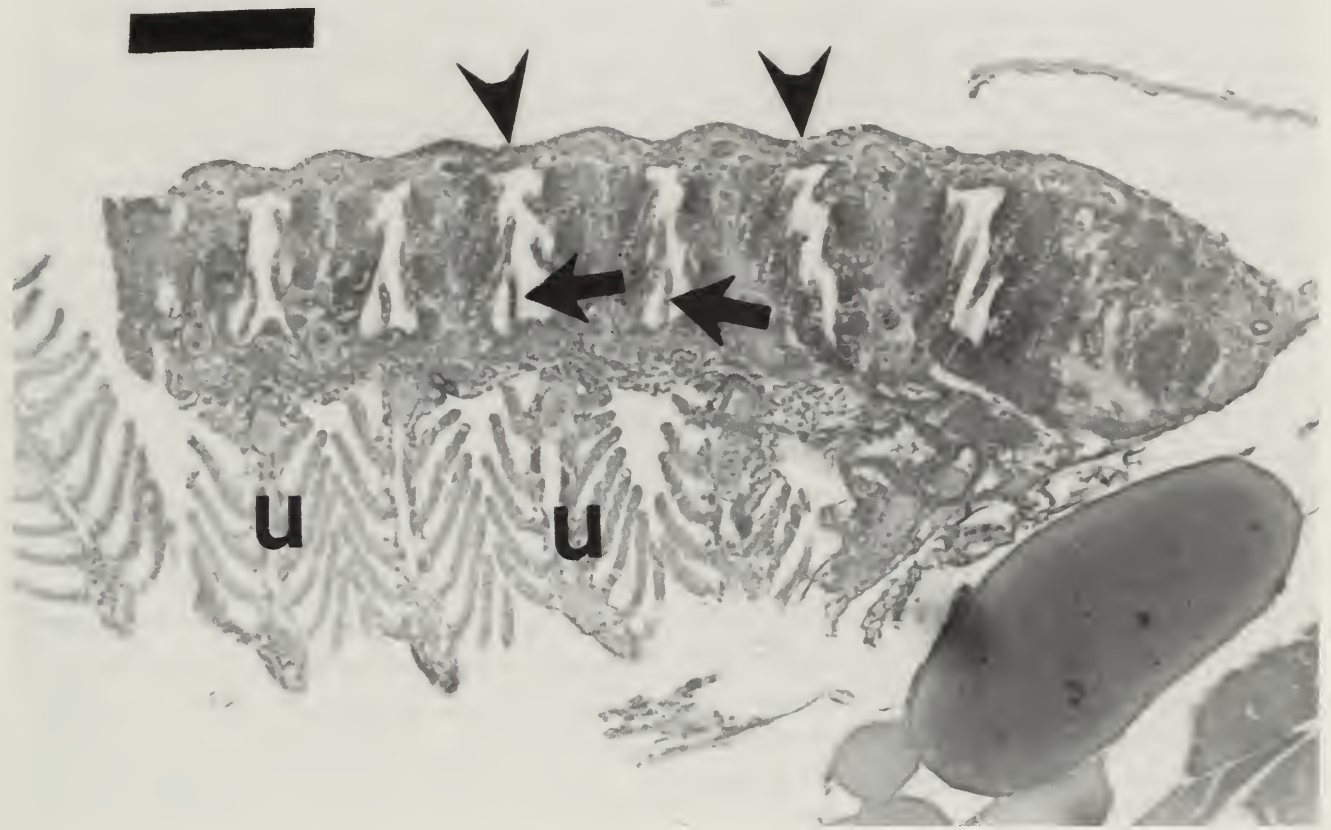


Fig. 36. *Planaltina britskii*, holotype MZUSP 62757, holotype, SL 35.0 mm, frontal histological section through anteriormost gills showing gill gland with its epithelial covering (arrowheads) and reduced secondary lamellae (arrows) within gill gland chambers which number nine. Unmodified gills (u) with secondary lamellae of usual length also shown. Bar = 100 μ m.

during the rainy season were mature, the males having well-developed testes and the females well-developed oocytes. Garutti also found that the males reach larger sizes than the females.

Ecology.—The population sample from Córrego do Limoeiro, rio São José dos Dourados sub-basin (MZUSP 62760 and LIRP 2255) was collected in a fourth order stream running in gallery forest represented by old cerrado vegetation. The stream width varied from 2.3–3.2 meters and the water depth from 0.07–0.08 meters. Rapids and small pools were found along the stream and the bottom consisted mostly of sand. Marginal vegetation was mostly represented by palm trees (Arecaceae), ferns (Pteridophyta) and lichens. At the time of collecting activities the following data were taken: air temperature 35.5°C, water temperature 21.5°C, pH = 7.24, dissolved ox-

ygen = 9.6 mg/l, and conductivity = 125.5 S/cm.

Other species taken at this site were: *Astyanax bimaculatus*, *Astyanax eigenmanniorum*, *Moenkhausia sanctaefilomenae*, *Piabina argentea*, *Characidium* sp., *Hypostomus ancistroides*, *Hypostomus* sp., *Sternopygus macrurus* and *Poecilia reticulata*.

The population samples from córrego da Barra Funda, rio Preto sub-basin (MZUSP 62757, 62758, 62759, 26911, DZSJRP 647 and USNM 362134), were all collected near the mouth where this stream empties into a larger stream called ribeirão da Barra Grande at an altitude of about 440 meters. According to Garutti (1983) the collecting site included a circular pool approximately 8 meters in diameter with a maximum depth of 2 meters. The pool lacked marginal vegetation. Rapids occurred downstream from the pool and ran through a gallery forest to

a pool of the ribeirão da Barra Grande. The maximum stream width along the rapids was two meters, the water depth varied from 0.4–1.5 meters and the marginal vegetation was grass.

During the period collections were made, from March 1980 through February 1982 the near surface water temperature varied between 19° and 30°C and the pH between 5.0 and 6.0. The water current in the gallery forest stream varied between 0.244 and 0.600 meters per second.

Other species at this collecting site were: *Serrapinnus piaba*, *Odontostilbe stenodon*, “*Cheirodon*” sp., *Astyanax bimaculatus*, *Astyanax fasciatus*, *Hemigrammus marginatus*, *Moenkhausia sanctaefilomenae*, *Piabina argentea*, *Serrasalmus spilopleura*, *Acestrorhynchus lacustris*, *Oligosarcus pintoii*, *Salminus hilarii*, *Characidium* sp., *Hoplis malabaricus*, *Pyrrhulina australis*, *Cyphocharax gilberti*, *Cyphocharax vanderi*, *Leporinus friderici*, *Leporinus octofasciatus*, *Leporinus striatus*, *Eigenmannia* sp., *Cetopsorhamdia iheringi*, *Nannorhamdia schubarti*, *Pimelodella* cf. *gracilis*, *Rhamdella minuta*, *Rhamdia hilarii*, *Aspidoras fuscoguttatus*, *Hypostomus ancistroides*, *Microlepidogaster francirochai*, *Poecilia reticulata*, *Cichlasoma portalegrense*, *Crenicichla britiskii*, *Tilapia* sp. and *Synbranchus marmoratus*.

Distribution.—This species is known to occur in the State of São Paulo in tributaries to rio Grande and rio Tietê, both tributaries of the upper rio Paraná basin.

Etymology.—The specific name, *britiskii*, is a patronym for Dr. Heraldo A. Britski, ichthyologist at the Museu de Zoologia da Universidade de São Paulo, in recognition of his many contributions to the ichthyology of Brazil. Dr. Britski collected the first two known specimens and recognized that they represented a new species of glandulo-caudine fish.

Discussion of generic and subfamily phylogenetic relationships.—Böhlke (1954: 265) placed *Planaltina* in the Glandulo-caudinae and noted a physical similarity be-

tween *Planaltina* and *Bryconamericus*. However, he set aside the question of glandulo-caudine relationships to other characid genera, suggesting that the Glandulo-caudinae are probably polyphyletic and that perhaps its various component taxa had origins among several tetragonopterine genera. Böhlke (1958:43) and Géry (1977:35) also thought it likely that the Glandulo-caudinae are polyphyletic. Weitzman et al. in Weitzman & Fink (1985:112–117) discussed the question of glandulo-caudine monophyly versus polyphyly at some length and concluded that there was not enough information to settle the question. Weitzman & Menezes (1998:178–180) hypothesized the subfamily as monophyletic based on a phylogenetic analysis of the seven tribes of the Glandulo-caudinae and used four unequivocal synapomorphies to unite the members of all of these tribes. Outgroup information relative to the Glandulo-caudinae and its tribes, as well as the synapomorphies used to diagnose the subfamily, were based on what was then known about the absence or near absence of the distribution of these four features in species of the non-glandulo-caudine genera of the Tetragonopterinae. Recently discovered information that some species of the tetragonopterine genus *Knodus* and all of the species of *Attonitus* and the related new genus and species are inseminating and that the anatomy of the primary and secondary sexual systems of these species display some to several of these same features used as synapomorphies for the Glandulo-caudinae by Weitzman & Menezes (1998) suggest that the phylogenetic relationships of the tribes of the Glandulo-caudinae need re-examination. We review at least some of the implications of this new information in our discussion below concerning the phylogenetic position of *Planaltina* and the other Diapomini. See also Weitzman et al. (2004) for a more detailed discussion of *Attonitus*, *Bryconamericus*, *Knodus* and the new genus and species regarding their possible relationships to the

Glandulocaudinae and other characids known to be inseminating.

The four synapomorphies for the Glandulocaudinae, each discussed at length by Weitzman & Menezes (1998:178), are as follows: 1) the presence of insemination, 2) the presence of a sperm storage area in the testes, 3) the presence of elongate sperm-cell-nuclei, and 4) the presence of an elongate cytoplasmic collar binding the flagellum to the sperm-cell nucleus in at least some stage of spermiogenesis (see Burns et al. 1998). So far as we know these characters remain valid for all species of the Glandulocaudinae with the exception of *Planaltina*, which differs by having essentially spherical sperm-cell nuclei and apparently lacks an elongate cytoplasmic collar binding the flagellum to the sperm-cell nucleus. However, their status as synapomorphies at the levels proposed by Weitzman & Menezes (1998) for most if not all glandulocaudines must now be reconsidered because Weitzman et al. (2004) found that these features are present in tetragonopterine species placed in *Attonitus*, some of the species currently placed in *Knodus*, the new genus and species and the species of a few other possibly related genera, for example *Brittanichthys* Géry and *Monotocheirodon*. However, all the species of these genera appear to lack the caudal-fin pheromone organ found in a variety of derived states, each characteristic for one of the various tribes of the Glandulocaudinae. It should be noted at this point that the putative homology of the caudal-gland cells among the glandulocaudine tribes remains to be investigated and therefore the homology of the caudal organs in the subfamily is a not a fully defended hypothesis.

It was recently discovered (Weitzman et al. 2004), that the species of these apparent glandulocaudine outgroup genera as well as at least some species of the Glandulocaudinae have pheromone organs and in some cases simple putative pheromone secretory cells on raised integumentary pads of the anal fin and sometimes the pelvic fins of

mature, sexually active males. These features, when present, were also described and discussed above for the species of *Planaltina*. Until further research reveals the distribution of these primary and secondary sexual structures among the above discussed genera, and among other inseminating characids such as *Brittanichthys* and *Monotocheirodon*, we decline to discuss the phylogenetic significance of these features regarding the Glandulocaudinae as a whole. We suggest that new hypotheses concerning the phylogenetic relationships of the Glandulocaudinae to apparent outgroup taxa be held in abeyance until the distribution of the synapomorphies used by Weitzman & Menezes (1998) to diagnose the Glandulocaudinae can be delineated for the inseminating species currently placed in the non-glandulocaudine genera mentioned here. We further note that the inseminating characid genera of the cheirodontine tribe Compsurini, although inseminating, lack three of the four synapomorphies (numbers 2, 3 and 4 mentioned above) and have the sperm cell synapomorphies discussed for the Cheirodontinae by Malabarba (1998). Regarding synapomorphy number 3 of the glandulocaudines, their elongate sperm cell nuclei, it is true that the sperm nuclei of the species of the Compsurini are somewhat elongate, but they are never as elongate as in nearly all the glandulocaudine species and apparently the centrioles are located posterior to the nucleus rather than anterior to it as in most of the glandulocaudines. Thus nuclear elongation appears to occur through forward growth in the cheirodontines rather than backward growth in the glandulocaudines (Burns et al. 1998). However, these putative characteristics of the ultrastructure of glandulocaudine and compsurin cheirodontine sperm cells need confirmation in many species and genera of both groups.

Planaltina was considered by Weitzman & Menezes (1998:184) to belong in the glandulocaudine tribe Diapomini because *P. myersi* shares with the species of the other two genera of the tribe, *Acrobrycon* and

Diapoma, two unequivocal synapomorphies. 1) The male and female caudal organs are nearly equivalent in size. 2) A multiple series of caudal scales, at least three or more, occur immediately ventral to the lateral-line series and extend posteriorly to form the dorsal border of a pouch opening of the caudal gland.

Planaltina myersi is distinguished from the species of *Acrobrycon* and *Diapoma* by the possession of separate dorsal and ventral enlarged pouch scales and only three scales across the dorsal opening of the pouch (Weitzman & Menezes 1998:184, figs. 13–16 and Weitzman & Fink 1985:17, fig. 15). The two diapomin synapomorphies are shared with the two new species herein described (compare Figs. 19, 28, 33). However, the description of caudal-organ features separating *Planaltina* from the species of *Acrobrycon* and *Diapoma* need some modification based on the inclusion of the two new *Planaltina* species. 1) The species of *Planaltina* have between two and six scales forming the dorsal region of the pouch while the number of scales in the dorsal region of the pouch in *Acrobrycon* and *Diapoma* exceeds eight or nine. 2) The number of scales forming the dorsal border of the pouch is greater in *Acrobrycon* and *Diapoma* than in *Planaltina*. The species of *Planaltina* have one or two scales forming the dorsal border of the pouch while in the species of *Diapoma* the number varies between three and six. In *Acrobrycon* this number varies from four to at least seven. In *Planaltina* one of the scales forming the dorsal border of the pouch is elongate and forms most of that border while in *Acrobrycon* and *Diapoma*, even when one of the dorsal border scales is somewhat elongate or larger, its actual degree of entry into the pouch border is little longer than that of the other dorsal border scales. At this time we are not prepared to hypothesize with confidence which of the characters listed above to separate these diapomin genera are plesiomorphic or apomorphic relative to these three genera. In our view, the position and

number of adnate scales on ventral lobe of the caudal fin of the inseminating or even non-inseminating species of *Knodus* (some of which may form an outgroup for the Diapomini) must be described and recorded before such hypotheses can be proposed. However, in view of the apparently more plesiomorphic nature of the sperm-cell nuclei of the species of *Planaltina* compared to those of *Acrobrycon* and *Diapoma*, as discussed here, we suggest that the species of *Acrobrycon* and *Diapoma* with a greater number of caudal scales may be the more derived and that a greater number of caudal scales may be a synapomorphy for *Acrobrycon* and *Diapoma*.

Histological examination and measurement of the sperm cell bodies of the three species of *Planaltina* recognized herein show that their sperm cells are aquasperm, but with sometimes a slight ellipsoid shape (see Appendix 1), while in *Diapoma speculiferum* and presumably the other species of *Diapoma*, the cell body is elongate and has the typical derived ultrastructure of glanduloaudine sperm cell with a cytoplasmic collar surrounding the flagellum as it parallels the side of the elongate sperm cell body (Burns et al. 1995:133, table 3, Burns et al. 1998:237, fig. 2). Although we have no information on the ultrastructure of the sperm cell of *Acrobrycon*, it has a cell body somewhat more elongate than that of the species of *Diapoma*. Thus in this respect, the three species of *Planaltina* appear plesiomorphic relative to the species of *Diapoma* and *Acrobrycon*. Although this information is useful for suggesting a hypothesis of the phylogeny of the genera and species of the Diapomini, confirmation of such relationships among all diapomin species and their relationships to outgroup inseminating species currently in *Knodus* must await detailed research on species of the latter genus in order to obtain a greater knowledge of the characids that apparently form an outgroup or outgroups to the glanduloaudine tribes as diagnosed by Weitzman & Menezes (1998). See also Weitzman

et al. (2004) for a more complete discussion of this problem.

One interesting undescribed species needs to be mentioned in regard to the statement just given above. Burns et al. (1995:133, table 3) recorded spherical sperm cell nuclei, aquasperm, in *Planaltina myersi*, USNM 278989, and in *Planaltina* sp. (this latter sample should have been listed as USNM 362836 but was also listed as USNM 278989 in the table by error). See Appendix 2 for field data and in Weitzman et al. (2004) for sexual characteristics. Both of these taxa have aquasperm and are inseminating. At this time we would place the population sample called *Planaltina* sp. in Burns et al. (1995) in *Knodus* because it has adnate scales on the lower caudal-fin lobe and therefore no caudal pouch. However, it is an inseminating species, and the type species of *Knodus*, *K. meridae* Eigenmann, although it too has adnate caudal scales and aquasperm, is apparently not an inseminating species according to our histological examination based on the specimens listed in Appendix 2 of Weitzman et al. (2004). The inseminating species currently in *Knodus* may belong to a series of species of that form a sister group to the Diapomini. However, the histological and ultrastructure characteristics of the primary sexual organs in those species up to the present referred to *Bryconamericus* and *Knodus* is complex and mostly unexplored. See Weitzman et al. (2004) for further discussion of these fishes. In our opinion the species traditionally referred to *Bryconamericus* and *Knodus* need a thorough phylogenetic study in order to better hypothesize possible relationships among the genera and species of the Diapomini.

Phylogenetic relationships among the three species of Planaltina.—The phylogenetic relationships among the species of *Planaltina* cannot be solved without better outgroup information than is currently available. There are over a dozen characters that provide information for distinguishing species; see especially the distinguishing

characters under the title “*Definition*” for each of the three species above and Figs. 3–13, 19, 28, 33. However, reliable outgroup information for many of these characters is unavailable and some of the characters that might be hypothesized to be derived compared to those found in characids usually considered members of the Tetraogonopterinae support contradictory hypotheses of phylogenetic relationships within the species of *Planaltina*. For example, *P. myersi* and *P. glandipedis* share the number of scale rows between the dorsal-fin origin and the lateral line, the number of scale rows between the anal-fin origin and the lateral line, the least number of scale rows around the caudal peduncle, and the number of vertebrae. We cannot at this time polarize any of these characters without appropriate outgroup information. Species in *Acrobrycon* and *Diapoma*, some undescribed in both genera, are not well known enough to be a source of outgroup information and some of the undescribed inseminating species currently referred to *Knodus* may in fact be the closest outgroup of the species of *Planaltina*. The species of *Acrobrycon* and *Diapoma* may be more derived diapomins than the species of *Planaltina* based on their more elongate sperm nuclei (in those so far investigated). Alternatively, if the less elongate and more numerous caudal organ scales of the species of *Acrobrycon* and *Diapoma* are considered plesiomorphic for the Diapomini and more like the caudal squamation in some of the inseminating species of *Knodus*, then we arrive at a different hypothesis. Parsimony ultimately must be used to settle these problems, but the available data is still insufficient for that purpose.

There is some evidence that *P. glandipedis* is a paedomorphic relative to *P. myersi* and *P. britskii*. It is smaller in size, has no adipose fin, and has fewer cusps on its jaw teeth than the other two species, all reductions common in relatively small characiform fishes (see Weitzman & Vari 1988, and Buckup 1993). On the other hand *P.*

glandipedis has a slightly greater number of scale rows around the caudal peduncle and more predorsal scales. In our view an analysis of the phylogenetic relationships among the species of *Planaltina* must await detailed descriptions of the characters of all diapomins so far described and yet to be described as well as a complete study of the inseminating species that are currently assigned to *Knodus*.

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Appendix 1

Sperm-cell dimensions for three species of Planaltina.—The following measurements were taken of sperm nuclei that exhibited a slightly non-spherical shape. These cells were clearly in the minority, but may give a more accurate assessment of the nuclear shape. Most views of the sperm nuclei were spherical. The cells measured varied from slightly ovoid, to pear shaped, to indented, to slightly elongate. The differences in measurements among the three species may be real or, alternatively, be due to variable shrinkage of cells having been treated differently in the past. For example separate collections may have been fixed in different concentrations of formalin. They may also have been slowly transferred to 70% ethyl alcohol by intermediate stages causing little or no shrinkage or, on the other hand, transferred from formalin fixative directly to 70% ethyl alcohol preservative, causing cell shrinkage.

Measurements were taken directly under oil immersion (100× lens) using an ocular micrometer or from photographic enlargements of negatives taken with a photomicroscope using an oil immersion (100×) lens. For each species, 20 cells were measured. Means ± standard deviations ($n - 1$ weighting) are given.

1. *Planaltina myersi*:

USNM 278989: Male 37.4 mm SL, female 35.0 mm SL.

$n = 20$:

Male SZ nuclear length: $1.73 \pm 0.12 \mu\text{m}$

Female SZ nuclear width: $1.16 \pm 0.11 \mu\text{m}$

2. *Planaltina glandipedis*:

USNM 362136: Paratype, male 26.3 mm SL, paratype, female 27.0 mm SL.

$n = 20$:

Male SZ nuclear length: $1.97 \pm 0.14 \mu\text{m}$

Female SZ nuclear width: $1.51 \pm 0.12 \mu\text{m}$

3. *Planaltina britskii*:

MZUSP 62757: Holotype, male 35.0 mm SL,

MZUSP 62757: paratype, female 36.5 mm SL.

$n = 20$:

Male SZ nuclear length: $1.89 \pm 0.11 \mu\text{m}$

Female SZ nuclear width: $1.48 \pm 0.11 \mu\text{m}$