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## PARAPHARYNGODON N. SPP. (NEMATODA: PHARYNGODONIDAE) PARASITES OF HYLID FROGS FROM MEXICO

--Manuscript Draft--

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<b>Abstract:</b>	Two new species of Parapharyngodon Chatterji, 1933 parasitizing 3 species of hylid frogs ( <i>Diaglena spatulata</i> , <i>Triprion petasatus</i> , and <i>Trachycephalus typhonius</i> ) from Mexico are herein described. The 2 new species share the presence of a gubernaculum with <i>Parapharyngodon lamothei</i> and belong to the group of those species with short spicule; both differ from the remaining species of the genus in the papillar pattern on ventrolateral and dorsal lips and, in the thickness of cuticular annulations and cuticular ornamentation in the female specimens. These are the third and fourth report of <i>Parapharyngodon</i> spp. parasitizing hylid frogs. Additionally to the egg characteristics, we propose that length of the lateral alae is also a taxonomically relevant feature to differentiate species of the genus.

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*PARAPHARYNGODON* N. SPP. (NEMATODA: PHARYNGODONIDAE)  
PARASITES OF HYLID FROGS FROM MEXICO AND REVIEW OF SPECIES  
INCLUDED IN THE GENUS

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**ABSTRACT:** Two new species of *Parapharyngodon* Chatterji, 1933 parasitizing 3 species of hylid frogs (*Diaglena spatulata*, *Triprion petasatus*, and *Trachycephalus typhonius*) from Mexico are herein described. The 2 new species share the presence of a gubernaculum with *Parapharyngodon lamothei* and belong to the group of those species with short spicule; both differ from the remaining species of the genus in the papillar pattern on ventrolateral and dorsal lips and, in the thickness of cuticular annulations and cuticular ornamentation in the female specimens. These are the third and fourth reports of *Parapharyngodon* spp. parasitizing hylid frogs. Additionally to the egg characteristics, we propose that length of the lateral alae is also a taxonomically relevant feature to differentiate species of the genus. A bibliographic review of all species historically assigned to *Parapharyngodon* is given, including those that have been declared *species inquirenda*, transferred to other genera, and those that are considered valid.

The number of studies carried out on helminth parasites of amphibians and reptiles from Mexico has increased considerably in the last 15 yr. Those studies generally have covered topics such as taxonomic record of helminth species in amphibians and reptiles

from a specific geographic area (Guillén-Hernández et al., 2000; Pérez-Ponce de León et al., 2000, 2001; Bursey and Goldberg, 2001; Goldberg and Bursey, 2002, among others), helminth parasites of a particular species of host (Paredes-Calderón et al., 2004; Cabrera-Guzmán et al., 2007; Espínola-Novelo and Guillén-Hernández, 2008; Yáñez-Arenas and Guillén-Hernández, 2010) or on the taxonomy of a particular helminth species (León-Règagnon and Brooks, 2003; Razo-Mendivil et al., 2004; Mata-López and León-Règagnon, 2006; León-Règagnon, 2010; Martínez-Salazar and León-Règagnon, 2010). As a result of these studies, a significant number of new species of different taxonomic groups have been described. Particularly for nematodes, several new species have been described (Jiménez-Ruiz et al., 2003; Martínez-Salazar, 2006, 2008; Martínez-Salazar and León-Règagnon, 2005, 2006, 2007; Jiménez et al., 2008; Mata-López et al., 2008). The high number of new nematode species is likely due to the increasing number of species being examined.

This is the case for the veined tree frog, *Trachycephalus typhonius* (Linnaeus, 1758) (= *Trachycephalus venulosus*), the Yucatecan casque headed treefrog, *Tripriion petasatus* (Cope, 1865) and the Mexican shovel-headed tree frog *Diaglena spatulata* (Günther, 1882) (= *Tripriion spatulatus*), for which little has been done regarding their parasites in México (Mata-López et al., 2008). *Trachycephalus typhonius* is distributed from central Tamaulipas to southern Sinaloa in Mexico, southward on both coasts to the Pacific lowlands through Panama and central Nicaragua. In South America it is present throughout the Amazon basin, south to Paraná in Brazil, Paraguay, and northern Argentina. It is also present in Trinidad and Tobago, in the Caribbean (La Marca et al., 2010). *Tripriion petasatus* is distributed in southern Mexico, through Belize and throughout Guatemala with an isolated record in northern Honduras (Frost, 2014). Its natural habitats are subtropical or tropical dry forests (Duellman, 2001; Santos-Barrera et al., 2004). *Diaglena spatulata* is an endemic

hylid distributed in Pacific lowlands of western Mexico (Sinaloa to Oaxaca), inhabiting tropical deciduous forest, tropical semideciduous forest, riparian vegetation and xerophilous scrub (García and Ceballos, 1994). Extending the studies of the helminth fauna of amphibians in Mexico, where the diversity and endemism of this group is one of the highest in the world, but where the extinction rates are also very high (Parra-Olea et al., 2014), is of crucial importance. The knowledge of the helminth fauna provides valuable information about host habits and ecosystem interactions, information that can be used in monitoring and conservation programs (Horwitz and Wilcox, 2005).

The aim of the present paper is to describe 2 new species of *Parapharyngodon* from the intestine of these 3 species of Hylidae from various localities in Mexico, giving new taxonomic information at the specific level, as well as to present a review of the species historically assigned to *Parapharyngodon*, identifying those that have been transferred to other genera, whose names have been misspelled, or have been inappropriately described.

## **MATERIALS AND METHODS**

Specimens of *D. spatulata*, *T. petasatus* and *T. typhoni* were collected by hand or with herpetological nets at localities of Jalisco and Yucatan states, Mexico. Specimens were collected under the scientific collection permit FAUT0056 issued to VLR. Hosts were killed with an overdose of sodium pentobarbital, were opened and examined for endoparasites under a stereoscope. Nematodes were counted in situ, recorded and fixed in 4% formaldehyde solution, cleared in Haman's lactophenol, and mounted on temporary slides for microscopic observation. Nematode specimens used for scanning electron microscopy (SEM) were fixed in 4% formaldehyde solution and dehydrated through an ethanol series, critical point dried with K850 Critical Point Drier (Emitech, Ashford, England), sputter-coated with gold with Q150R Modular Coating System (Quórum,

Ashford, England) and examined with a Hitachi S-2460N SEM (Hitachi, Tokyo, Japan), and SU1015 SEM (Hitachi). Original drawings were done with the aid of a drawing tube. Measurements are provided in millimeters, including the average and standard deviation, followed by range, the holotype or allotype measurements (in brackets), and the sample size in parentheses when different from the total number of specimens studied. Host specimens collected in Yucatan and Tepalcatepec, Jalisco were deposited in the Museo de Zoología, Facultad de Ciencias (MZFC), UNAM, and parasites were deposited in the Colección Nacional de Helminthos (CNHE), Instituto de Biología, UNAM. The following specimens from the CNHE were examined for comparison: *Parapharyngodon lamothei* 5,913 (paratypes); *Parapharyngodon maestro* 5,907 (paratypes).

In order to establish the number of the species historically included in the genus *Parapharyngodon*, to detect errors in the epithets of species, and comment about their actual status we used the information from a retrospective bibliographical search, using different databases (CAB Abstracts, Biological Abstracts, Zoological Record, and ISI Web of Science), we searched the databases of parasite collections, and consulted original descriptions of most species. To corroborate the host names, we consulted the following web pages: Amphibian species of the World (<http://research.amnh.org/vz/herpetology/amphibia/>) (Frost, 2014), The Reptile Database (<http://www.reptile-database.org>) (Uetz and Hošek, 2014) and Mammal Species of the World (<http://www.vertebrates.si.edu/msw/mswcfapp/msw/index.cfm>) (Wilson and Reeder, 2005). Biological realms classification is based on Holt et al. (2013). Morphological characters used to distinguish valid and *inquirenda* species are those proposed by Bursey et al. (2013).

## DESCRIPTION

### *Parapharyngodon chamelensis* n. sp.

(Figs. 1A-F, 2A-H)

*General:* Robust and fusiform nematodes, white, evident sexual dimorphism, males smaller than females. Cuticle with transversal striations in entire body excepting tail filament. Males with evident lateral alae extending from the level of excretory pore to the anterior part of the last third of body, females lacking alae. Oral opening triangular, surrounded by 3 lips; dorsal lip with 2 papillae; ventrolateral lips with 1 papilla and 1 amphid pore located laterally in males (Figs. 1B, 2A); females with 3 lips separated into 6 parts, single papillae on each part, amphids opening in ventrolateral lips (Figs. 1E, 2D). Excretory pore posterior to esophageal bulb. Males without caudal alae. Three pairs and 1 single caudal papillae. Caudal filament subterminal and directed dorsally in males (Fig. 1C). Vulva equatorial in females (Fig. 1D). Eggs with subpolar operculum containing embryo in early stages of cleavage (Fig. 1F).

*Male (based on holotype and 11 paratypes):* Small nematodes; blunt anterior end, distinctly truncate posterior end (Fig. 1A). Body length (MBL)  $1.47 \pm 0.14$  (1.31–1.78) [1.67]; maximum width at level of excretory pore  $0.12 \pm 0.01$  (0.10–0.15) (7.02–9.76% of MBL) [0.12, 7.02%]. Cuticle with wide transversal annulations. Lateral alae,  $0.79 \pm 0.10$  (0.69–0.96) [0.89, 53.47%] (49.45–58.31% of MBL) length, arising at mid-level of esophageal corpus and extending approximately to posterior end of body. Esophageal corpus  $0.23 \pm 0.02$  (0.21–0.27) (14.76–16.88% of MBL) [0.25, 14.96%] long by 0.03 (0.02–0.03) [0.03] wide; short isthmus; esophageal bulb length 0.06 (0.06–0.08) (3.90–4.70% of MBL) [0.07, 3.90%], width 0.07 (0.06–0.07) [0.07]. Nervous ring and excretory pore

0.09±0.01 (0.08–0.10) (4.94–6.61% of MBL) [0.09, 6.20%] and 0.46±0.05 (0.39–0.55) (27.17–33.66 % of MBL) [0.49, 29.40%] from anterior end respectively. Testis extending anteriorly from mid-body region, flexing posteriorly behind excretory pore; vas deferens not observed. Spicule length 0.05 (0.05–0.06) [0.05], spindle form (Fig. 1C). Cloaca opens terminally. Tail length 0.11±0.01 (0.09–0.12) (5.74–8.66% of MBL) [0.11, 6.50%]; tail filament length 0.10±0.01 (0.07–0.11) [0.10], inserted dorsally (Figs. 1C, 2B).

Gubernaculum length 0.02 (n=8) [0.02] (Fig. 1C). Caudal mammilliform papillae distributed as follows: 1 pair precloacal, 1 pair paracloacal, and 1 pair basal to filament; apical region of papillae in rosette; 1 single postcloacal papilla with 2 nerve endings located on medium lobe of posterior lip (Fig. 2B). Anterior cloacal lip ornated with 6–8 irregular not well developed finger-like outgrowths, posterior cloacal lip divided into 3 inflated lobes, lateral simple lobes, medium lobe as described before (Fig. 2C). Phasmids on the base of the tail.

*Female (based on allotype and 11 paratypes):* Robust nematodes; tapering anteriorly to blunt point, posterior ending in median, stout spike (Fig. 1D). Body length (FBL) 2.50±0.28 (2.10–2.85) [2.76], maximum width at level of vulva 0.30±0.05 (0.22–0.37) (10.29–14.52% of FBL) [0.29, 10.54%]. Cuticle with transverse annulations. Esophagus length 0.40±0.03 (0.36–0.43) (13.68–17.13% of FBL) [0.41, 14.76%], width 0.04 (0.03–0.04) [0.04]; short isthmus; esophageal bulb length 0.10±0.01 (0.09–0.11) (3.43–4.47% of FBL) [0.10, 3.46%], width 0.11±0.01 (0.10–0.12) [0.11]. Nervous ring and excretory pore 0.10±0.01 (0.09–0.11) (3.27–4.96% of FBL) [0.11, 3.94%] and 0.59±0.10 (0.39–0.74) (19.12–28.05% of FBL) [0.56, 20.18%] from anterior end respectively. Vulva 1.26±0.15 (1.02–1.45) (49–57.76% of FBL) [1.31, 47.59% of FBL] from anterior end; vagina transversely directed flexing to posterior region of the body. Didelphic, prodelphic,

ovaries reaching level of esophageal isthmus; with several coils around corpus in larger individuals; not reaching esophageal bulb in nongravid females. Body terminates in stout spike tail,  $0.15\pm 0.02$  (0.11–0.20) [0.16] long (Fig. 2E). Phasmids basal to tail. Anus lateral,  $2.27\pm 0.26$  (1.86–2.6) (6.61–10.35% of FBL) [2.49, 9.64% of FBL] to posterior end. Eggs oval, analated, slightly flattened on 1 side,  $0.117\pm 0.005$  (0.098–0.128) (n=60) long by  $0.050\pm 0.004$  (0.035–0.062) (n=60) wide, shell punctuated with pores, thick in lateral view with transversal striations; operculum subpolar, containing embryo in early stages of cleavage (Figs. 1F, 2F).

### **Taxonomic summary**

*Type host:* *Diaglena spatulata* (Günther, 1882).

*Collecting date:* 21 July 2009.

*Type locality:* Chamela-Cuixmala Biosphere Reserve (19°30.032'N, 105°02.071'W, elevation 50 m a.s.l.), La Huerta, Jalisco, Mexico.

*Site of infection:* Large intestine.

*Type specimens:* Holotype, male, CNHE 8667. Allotype, female, CNHE 8668. Paratypes (11 males, 11 females), CNHE 8669.

*Etymology:* The species is named after the collecting site, Chamela Biological Station, Instituto de Biología, Universidad Nacional Autónoma de México, at the Chamela-Cuixmala Biosphere Reserve in the state of Jalisco, Mexico.

### **Remarks**

*Parapharyngodon chamelenesis* is diagnosed by the possession of a small spicule, equinate cloacal lip, presence of gubernaculum and caudal papillae consisting of 3 pairs plus a single papilla in males, and females with stout spike tail. Males of other 6 species of *Parapharyngodon* from Americas have been described as having 3 pairs plus 1 single



caudal papillae, namely *P. cubensis* (Baruš and Coy Otero, 1969), *P. binae* (Pereira, Sousa and de Souza Lima, 2011), *P. duniae* (Burse and Brooks, 2004), *P. langitor* (Alho and Rodrigues 1963), *P. riojensis* (Ramallo, Bursey and Goldberg, 2002) and *P. lamothei* (Jiménez, León-Règagnon and Pérez-Ramos, 2008). In every remaining species, the papillar pattern consist either 3 or 4 pairs (Table I). Of the species that share the papillar pattern with *P. chamelensis*, only *P. lamothei* shares the presence of gubernaculum, however, these 2 species differ in the majority of measurements, as is the spicule length, which is slightly larger in *P. lamothei* (64-66  $\mu\text{m}$ ) than in *P. chamelensis* (50-60  $\mu\text{m}$ ) and body size, which is larger in *P. lamothei* (2.10-2.25) than in *P. chamelensis* (1.31–1.78). Moreover, the structural differences include: the presence of the protuberance in the posterior cloacal lip in *P. chamelensis*, while *P. lamothei* lacks this structure, and the extension of the lateral alae which in *P. lamothei* starts just anteriorly to the esophageal bulb, while in *P. chamelensis* starts at the excretory pore level. About the females, 2 of the main differences are the conical tail in *P. lamothei* while in *P. chamelensis* the tail is stout spike and the body length, which is larger in *P. lamothei* (3.48-5.30) than in *P. chamelensis* (2.10–2.85). This is the 48<sup>th</sup> properly described species in the world for this genus, the seventh recorded in a Mexican host, and the first for amphibians in Mexico.

***Parapharyngodon hylidae* n. sp.**

(Figs. 3A-F, 4A-H)

*General:* Robust and fusiform nematodes; evident sexual dimorphism in size. Prominent cuticular annulations beginning just behind cephalic extremity and continuing to base of tail in both sexes. Triangular oral opening surrounded by 3 lips; males with 1 pedunculate amphid and 1 round papillae on each ventrolateral lip, 2 papillae on dorsal lip (Figs. 3A, 4A); females with 3 lips separated into 6 parts, single papillae on each part,

amphids opening in ventrolateral lips (Figs. 3E, 4D). Lateral alae present in males, females without alae with transversal and lateral thick striations on lateral flanks (Fig. 3E).

Excretory pore posterior to esophageal bulb. Caudal filament subterminal, directed dorsally in males (Fig. 3C), stout spike tail in females. Females with vulva approximately in mid-body; eggs analated with subterminal operculum (Figs. 3F, 4F).

*Male (based on holotype and 12 paratypes):* Small nematodes; blunt anterior end, distinctly truncate posterior end (Fig. 3A). Body length (MBL)  $2.01 \pm 0.37$  (1.47–3.04) [1.66]; maximum width at level of excretory pore  $0.14 \pm 0.05$  (0.05–0.2) (2.26–9.89% of MBL) [0.11, 6.87% of MBL]. Cuticle with wide annulations. Lateral alae arising at midlevel of esophageal corpus and extending approximately  $0.17 \pm 0.05$  (0.10–0.22) (6–14.18% of MBL) (n=8) [0.19, 11.16% of MBL] from posterior end of body, length  $1.46 \pm 0.37$  (1.06–2.59) (62.59–85.31% of MBL) (Fig. 3A). Esophageal corpus  $0.35 \pm 0.07$  (0.23–0.44) (13.04 – 21.43% of MBL) [0.27, 16.09% of MBL] long, by  $0.03$  (0.02–0.04) [0.03] wide; short isthmus; esophageal bulb  $0.08 \pm 0.01$  (0.07–0.09) (3.29–4.66% of MBL) [0.07, 4.29% of MBL] long by  $0.08 \pm 0.01$  (0.06–0.10) [0.06] wide. Nervous ring and excretory pore  $0.13 \pm 0.02$  (0.10–0.16) (4.94–9.23% of MBL) (n=11) [0.15, 9.23% of MBL] and  $0.64 \pm 0.14$  (0.44–0.84) (22.04–41.11% of MBL) (n=12) [0.49, 29.18% of MBL] from anterior end respectively. Testis extending anteriorly from mid-body region, flexing posteriorly behind excretory pore; vas deferens not observed. Spicule length  $0.06 \pm 0.01$  (0.05–0.07) (n=10) [0.07], spindle form (Fig. 3C). Cloaca opens terminally. Tail length  $0.09 \pm 0.01$  (0.07–0.11) [0.09]; tail filament  $0.06 \pm 0.01$  (0.04–0.10) [0.10] long, inserted dorsally. Gubernaculum length 0.01–0.02 (n=8) [0.02] (Fig. 3C). Caudal mammilliform papillae as follows: 1 lateral pair of precloacal papillae, 1 pair paracloacal, 1 caudal pair close to base of tail filament (Fig. 4B). Phasmids at the base of the tail. Anterior cloacal lip

echinate, with 9-11 irregular not well developed finger-like outgrowths; posterior cloacal lip divided in 3 lobes, 2 lateral lobes slightly inflated and central elongated lobe, triangular, with apical ornamentation: 2 lateral little papillae and 2 central plates (Fig. 4B).

*Female (based on allotype and 8 paratypes):* Small nematodes, tapering anteriorly to blunt point, posterior ending in stout spike (Fig. 3D). Body length (FBL)  $3.65 \pm 1.22$  (2.18–5.55) [2.44]; maximum width at vulva  $0.37 \pm 0.12$  (0.22–0.58) (6.27–15.35% of FBL) [0.22, 9.22% of FBL]. Cuticle with wide annulations, transversal thick striations in flanks of body joining 3–5 ventral and dorsal annulations (Fig. 4E). Esophageal corpus length  $0.59 \pm 0.11$  (0.46–0.72) (10.44–21.24% of FBL) [0.50, 20.64% of FBL] by width  $0.05 \pm 0.01$  (0.04–0.06) [0.04]; short isthmus; esophageal bulb length  $0.12 \pm 0.02$  (0.10–0.14) (2.51–4.58% of FBL) [0.10, 3.95% of FBL], width  $0.13 \pm 0.01$  (0.11–0.14) [0.11]. Nervous ring and excretory pore from anterior end,  $0.12 \pm 0.01$  (0.11–0.14) (2.57–5.07% of FBL) [0.12, 4.83% of FBL] and  $0.87 \pm 0.17$  (0.56–1.03) (18.54–32.06% of FBL) [0.78, 32.06% of FBL], respectively. Vulva  $1.69 \pm 0.4$  (1.07–1.97) (48.86 – 50.66% of FBL) [1.29, 52.86% of FBL] from anterior end; vagina transversally located, flexing to posterior region of body. Didelphic, prodelphic, ovaries distributed mainly anterior to vulva, extending to level of esophageal isthmus only in gravid females, in larger specimens may form several coils around esophageal corpus. Body terminates in stout tail spike  $0.42 \pm 0.13$  (0.25–0.53) [0.27] long. Anus  $3.10 \pm 0.91$  (1.93–4.35) (78.33 – 88.4% of FBL) [2.17, 88.87% of FBL] to anterior region. Eggs oval, analated, slightly flattened on one side,  $0.126 \pm 0.019$  (0.082–0.153) (n=35) long,  $0.045 \pm 0.011$  (0.025–0.064) (n=35) wide; surface of the shell punctate with pores, thick in lateral view with transversal striations, operculum subpolar with a top surrounded by a thin shell, eggs containing embryo in early stages of cleavage (Figs. 3F, 4F).

## **Taxonomic summary**

*Type host:* *Tripurion petasatus* (Cope, 1865).

*Collecting date:* May 2005.

*Type locality:* Rancho Hobonil, Yucatán, Mexico (20°00'06"N, 89°02'30"W, elevation 80 m a.s.l.).

*Site of infection:* Large intestine.

*Other records:* *T. typhoni* (Linnaeus, 1758) – Yucatán, Mexico: Xcanatún (February, 2001; 20°59'42.92"N, 89°38'06.11"W; elevation 11 m a.s.l.); Rancho Xkante, Buctzots (March, 2003; 21°12'03.17"N, 88°46'29"W; elevation 6 m a.s.l.); Celestún (May and September, 2006; 20°45'N, 90°15'W). *Diaglena spatulata* (Günther, 1882) – Jalisco, Mexico: Tapalcatepec-Jilotlan Road (19°13'57"N, 102°51'52"W, elevation 538 m a.s.l.).

*Type specimens:* Holotype, male, CNHE 8670. Allotype, female, CNHE 8671. Paratypes (12 males, 8 females), CNHE 8672.

*Etymology:* The species is named after its host family.

## **Remarks**

*Parapharyngodon hylidae* shares the condition of having lateral alae starting at midlevel of esophageal corpus in males with *P. adramitana* (Adamson and Nasher, 1984b), *P. alvarengai* (Freitas, 1957a), *P. cubensis* (Baruš and Coy Otero, 1969), and *P. verrucosus* (Freitas and Dobbin, 1959); however, in these species alae extend to the level of cloaca, and in the new species lateral alae end far anterior to cloaca; additionally, those species are distributed in Saharo-Arabian, Panamanian and Neotropical (Central and South America) realms. *Parapharyngodon hylidae* belongs to the group of *Parapharyngodon* species with short spicule (0.05-0.07) (see Bursey and Goldberg, 2007; Table I); but is different from them in the length of the lateral alae in males and, mainly, for the presence of a

conspicuous gubernaculum. The other species featuring this accessory piece is *P. lamothei* (Jiménez et al., 2008). *Parapharyngodon hylidae* and *P. lamothei*, both from Mexico, are similar in the following male characteristics: the spicule length (0.05–0.07 and 0.064–0.066, respectively), ending of lateral alae and length of total tail (including filament tail), 0.07–0.11 and 0.076–0.084, respectively. However, the clearest difference between males of these species is the position of the single medial papilla and the structure of the anterior cloacal lip: in *P. lamothei* the single medial papilla is postcloacal and the anterior lip shows short blunt projections, whereas in *P. hylidae* the single medial papilla is absent and the anterior cloacal lip is echinate, with 9-11 irregular finger-like outgrowths. Other feature that characterizes *P. hylidae* is the structure of the posterior cloacal lip, which is divided in 3 lobes with a central elongated, ornamented lobe. Another evident difference is the host of each species: *P. lamothei* was recorded as parasite of a reptile, *Bipes canaliculatus* Latreille in Sonnini and Latreille, 1801, and *P. hylidae* is parasitizing 3 species of amphibians. About female characteristics, *Parapharyngodon hylidae* resembles *P. chamelensis* on the cephalic region of both sexes, the spicule shape and length (0.05-0.07 and 0.05-0.06 respectively), the presence of gubernaculum of similar length (0.01-0.02 and 0.02 respectively), vulva transversally located, stout spike tail and oval eggs with subpolar operculum. However, there are many differences between both species: males and females of *P. hylidae* are larger (1.47-3.04 and 2.18-5.55 respectively) than those of *P. chamelensis* (1.31-1.78 and 2.10-2.85 respectively); the lateral alae start at the esophageal corpus level in *P. hylidae* while in *P. chamelensis* they start at the excretory pore level; the single medial papilla is postcloacal in males of *P. chamelensis*, while it is absent in males of *P. hylidae*; the ornamentation of the apical region of the posterior cloacal lip in *P. hylidae* consists of 2 lateral little papillae and 2 central plates while in *P. chamelensis* there is only a single

papillae with 2 nervous endings; also *P. hylidae* differs by featuring transversal and lateral cuticular striations joining dorsal and ventral cuticular annulations. *Parapharyngodon hylidae* is the 49<sup>th</sup> properly described species in the world for this genus and the eighth recorded in Mexico. *Parapharyngodon chamelensis* and *P. hylidae* are the third and fourth species registered for hylid frogs and the sixth and seventh for amphibians in the world respectively.

Up to date, 77 species have been assigned to the genus *Parapharyngodon* worldwide. However, only 46 can be considered valid species because they have been properly described, clearly schematized, with both male and female morphometric characteristics recorded; of these, 30 were nominally described. Seventeen are considered *species inquirenda*, 12 species are considered as members of the genus *Thelandros*, one to *Skrjabinodon*, and one as a junior synonym (Table II).

In this paper, we additionally propose the following changes: *Parapharyngodon arequipensis* should be *species inquirenda* because of the lack of information about females; we also consider *P. hemidactylii* under this status because the position of the egg operculum, as well as the presence or absence of lateral alae were not described. On the other hand, we transfer *P. moqueguensis* to *Thelandros* because of the presence of genital cone and the polar position of the egg operculum; *P. yurensis* is also considered as member of this genus because the polar operculum in the eggs.

## **DISCUSSION**

According to Bursey et al. (2013), the most relevant character for the differentiation of species in *Parapharyngodon* and species in the very similar genus *Thelandros* is the egg morphology. *Parapharyngodon* spp. eggs show a subterminal operculum and are in early

stages of cleavage at deposition, whereas in *Thelandros* spp. the eggs operculum is terminal and are completely embryonated when released. Other differences between species of both genera include a narrow, elongated papillated genital cone, and tail in a terminal position in *Thelandros* spp., while males of *Parapharyngodon* spp. lack a genital cone, papillae are situated around the cloaca, and the dorsally curved tail is subterminal. Based on the morphology of the eggs and male characteristics, the specimens described here are assigned to the genus *Parapharyngodon*.

According to Burseý and Goldberg (2005), Burseý et al. (2007) and Jiménez et al. (2008), species of *Parapharyngodon* are distinguished based on the pattern of caudal papillae, morphology of the anterior cloacal lip, location of the ovary, traits of the tail of females, size of spicule, egg morphology and geographical distribution. Additionally, we recommend the length of lateral alae as another important character in the taxonomy of this genus. Description of lips and papillae surrounding oral opening has been rarely detailed for both males and females in previous descriptions, although at least in some species of this genus, the arrangement of these structures is different in males and females. We strongly recommend their detailed description in specimens of both sexes in future morphological studies of species of *Parapharyngodon*. A molecular approach is highly recommended to test the monophyly of this genus and *Thelandros* as suggested by Chaudhary et al. (2014).

Regarding the biogeographic distribution of valid species of *Parapharyngodon*, the biological realm with more described species is the Panamanian with 8 valid species, followed by Oriental and Palearctic with 7 each; the Neotropical has 6; Afrotropical, Nearctic and Arabic have 5 records; and the Australian, Sino-Japanese and Madagascan have only 1 record.

The reptilian suborder Lacertilia is the most frequently parasitized group of vertebrates and the less parasitized are Amphisbaenia, Testudinae, Amphibia and Monotremata. However, considering that many species of these groups of vertebrates remain to be studied from the parasitological point of view, and that several of the newly described *Parapharyngodon* species have been described from these group of hosts, it is possible that there are still many new species to be discovered.

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Figure 1. *Parapharyngodon chamelensis* n. sp. (A) Male, entire, lateral view. (B) Male, apical view. (C) Male, lateral view of caudal region. (D) Female, entire, lateral view. (E) Female, apical region. (F) Egg. Scale bars = (A) 0.25 mm, (B) 0.01 mm, (C) 0.05 mm, (D) 0.5 mm, (E) 0.01 mm, (F) 0.05 mm.

Figure 2. *Parapharyngodon chamelensis* n. sp. (A) SEM of male, apical view of cephalic end. (B) SEM of male, ventral view of posterior region. (C) SEM of male, ventral view of posterior end showing cloaca. (D) SEM of female, apical view of cephalic region. (E) SEM of female, ventral posterior extremity showing phasmids. (F) SEM of egg, detail of subpolar plug.

Figure 3. *Parapharyngodon hylidae* n. sp. (A) Male, entire, lateral view. (B) Male, apical view. (C) Male, lateral view of caudal region. (D) Nongravid female, entire, lateral view. (E) Female, apical region. (F) Egg. Scale bars = (A) 0.25 mm, (B) 0.01 mm, (C) 0.05 mm, (D) 0.5 mm. (E) 0.01 mm, (F) 0.05 mm.

Figure 4. *Parapharyngodon hylidae* n. sp. (A) SEM of male, apical view of cephalic end. (B) SEM of male, ventral view of posterior extremity showing cloaca, precloacal and paracloacal papillae; postcloacal lip with elongated central lobe, detail of apical ornamentation. (C) SEM of male, base of tail filament, showing postcloacal pair of papillae. (D) SEM of female, apical view of cephalic end. (E) Photomicrograph of female, lateral cuticular ornamentation Scale bar = 0.5 mm. (F) SEM of egg, detail of subpolar operculum.

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Figure 1  
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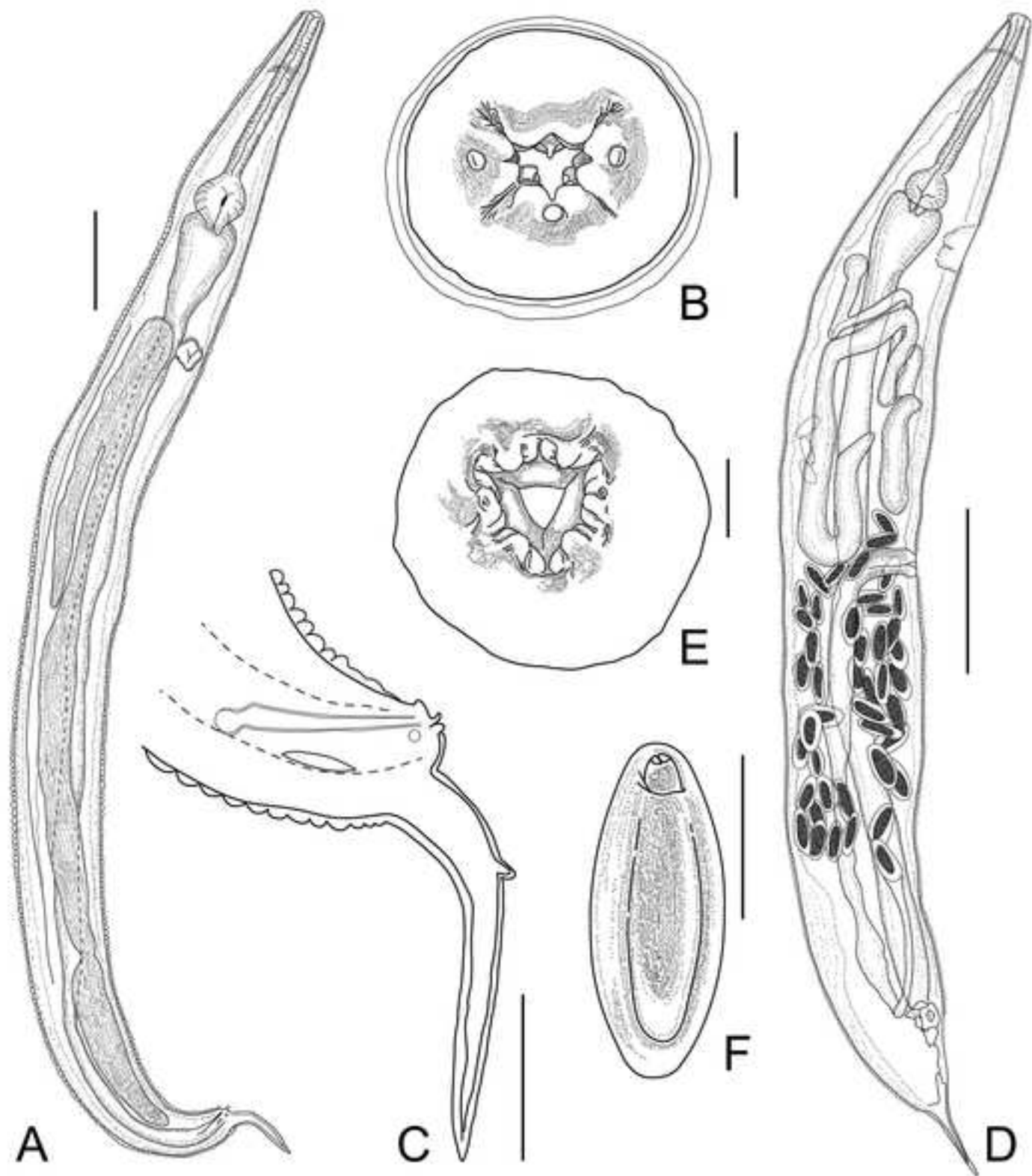


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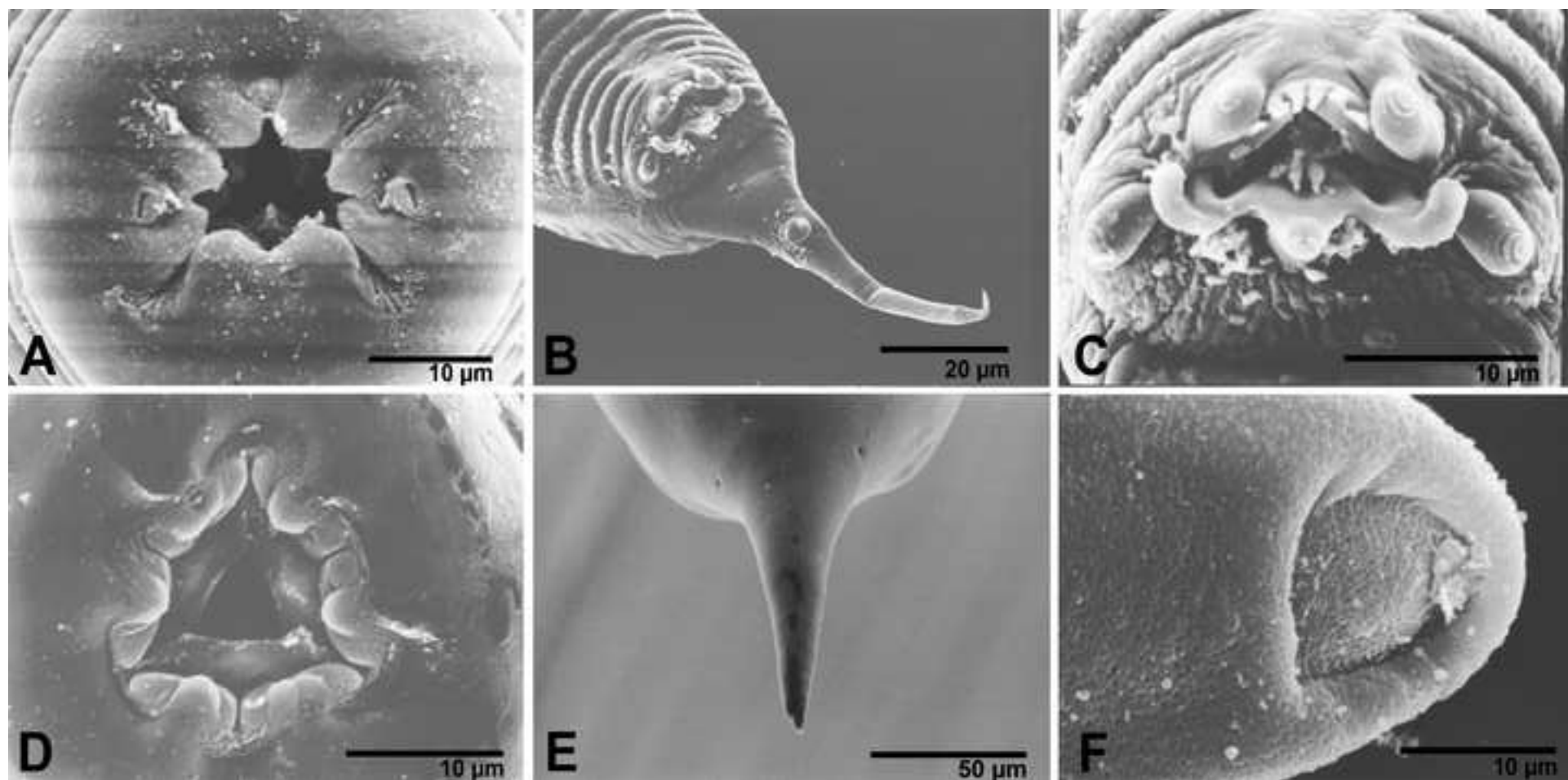


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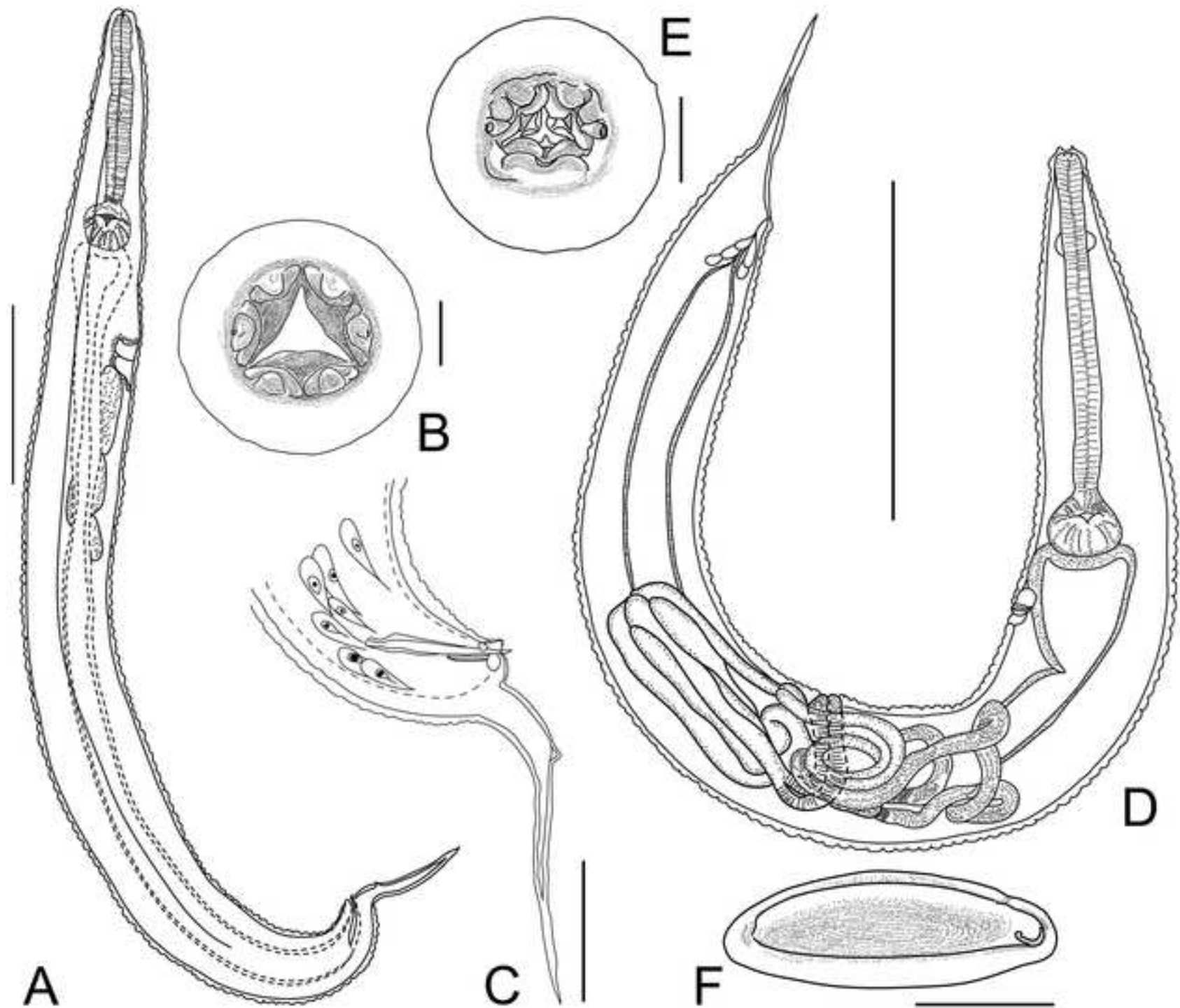




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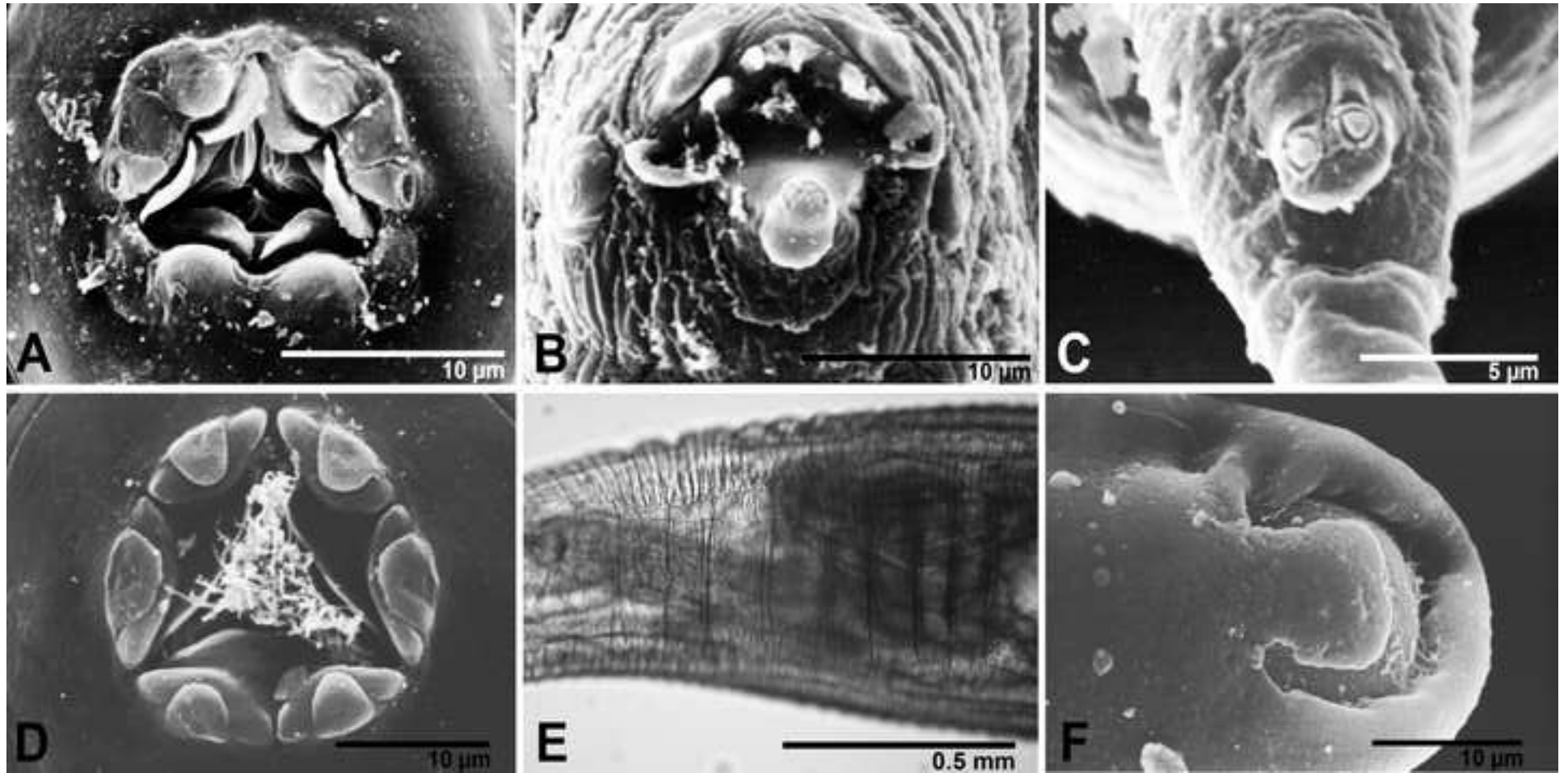


Table 1

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Table I. Selected characters of species assigned to *Parapharyngodon* from the Americas. Measurements in micrometers; species recorded in Mexico in bold; \*species parasitizing hylidae; E = esophageal; ND = not described; Pr= pair.

Biogeographical realm/ species	Males				Females				Reference
	Papillae	Spicule	Extension of lateral alae	Cloacal lip	Ovary location	Tail shape	Ornaments	Eggs Long/wide	
Nearctic									
<b><i>P. californiensis</i></b>	4 pr	53-76	Absent	ND	Prebulbar	Spike stout	Shell punctate; analate	90-110/48-52	Read and Amrein, 1952
<b><i>P. chamelensis</i></b> *	3 pr + 1	50-60	Excretory pore extending 69-96 long	Echinate	Prebulbar	Spike stout	Shell punctate; analate	98-128/35-62	This study
<b><i>P. grimeri</i></b>	3 pr	116-128	1,785-2,040 from lip to 85-116 from rear	Echinate	Prebulbar	Spike stout	Shell punctate; alate	79-88/46-52	Burseay and Goldberg, 2007a

<i>P. iguanae</i>	3 pr	30-60	From nearly midbody to anal region	Echinate	Prebulbar	ND	Shell punctate; ND	85-98/43-53	Telford Jr., 1965
<i>P. ocalaensis</i>	3 pr	46-55	From nerve ring to just anterior of cloaca	Smooth	Prebulbar	Spike stout	Shell punctate; ND	88-93/40-43	Burseley and Telford Jr., 2002
Neotropical									
<i>P. alvarengai</i>	3 pr	80-100	Mid-E to near cloaca	Smooth	Prebulbar	Spike stout	Shell smooth; ND	78-87/39-52	Freitas, 1957a
<i>P. bainaie</i>	3 pr + 1	100-140	320-380 from lip to 320-436 from rear	Echinate	Prebulbar	Spike stout	Shell punctate; ND	81-95/ 49-60	Pereira et al., 2011
<i>P. grenadaensis</i>	4 pr	67-104	Nerve ring to precloacal	Echinate	Prebulbar	Conical, no spike	Shell punctate;	67-73/31-37	Burseley et al., 2013

			papillae				Analate		
<i>P. largitor</i>	3 pr + 1	54-68	Present not described	Smooth	Prebulbar	Spike stout	Shell smooth; analate	72-82/32-33	Baruš and Coy-Otero, 1969; Bursey and Goldberg, 2005
<i>P. riojensis</i>	3 pr + 1	90-110	E-isthmus to 48 from cloaca	Echinate	Prebulbar	Spike stout	Shell punctate; ND	110-130/ 60-80	Ramallo et al., 2002
<i>P. sceleratus</i>	4 pr + 1	80-109	300 from lip to 120 from rear	Smooth	Prebulbar	Spike stout	Analate	-	Bursey and Goldberg, 2005, 2007b
<i>P. verrucosus</i>	3 pr	55-63	E region to cloaca	Echinate	Prebulbar	Spike stout	Analate	-	Bursey and Goldberg, 2005, 2007b
Panamanian									
<i>P. colonensis</i>	4 pr	61-67	202-244 from	Echinate	Prebulbar	Conical,	Shell	70-76/40-44	Bursey et al.,

			lip to caudal			no spike	punctate;		2007
			papillae				analate		
<i>P. cubensis</i>	3 pr + 1	77	E-bulb to 400- 500 from rear	ND	Prebulbar	Spike stout	Shell punctated;	82-90/ 49-57	Baruš and Coy- Otero, 1969
							ND		
<i>P. duniae</i> *	3 pr + 1	40-49	320-380 from lip to 320-436 from rear	Echinate	Prebulbar	Conical	Shell punctated;	110-122/ 36-49	Burseý and Brooks, 2004
							ND		
<i>P. hylidae</i> *	3 pr	50-70	Mid-E to 100- 220 from rear	Echinate	Prebulbar	Spike stout	Shell punctate;	98-128/ 35-62	This study
							analate		
<i>P. lamothei</i>	3 pr + 1	64-66	E-bulb to near end of body, total length 1479-1781	Echinate	Prebulbar	Conical	Shell punctated;	92-119/ 34-44	Jiménez et al., 2008
							ND		
<i>P. maestro</i>	3 pr	62-70	E-bulb to near	Smooth	Prebulbar	Conical	Shell	88-109/ 27-36	Jiménez et al.,

			of tail				smooth;		2008
							ND		
<i>P. osteopili*</i>	4 pr	53-61	Absent	Echinate	Bulbar	Conical, no spike	Shell smooth; alate	110-129/47-61	Adamson, 1981

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Table II. Revision of species historically included in the genus *Parapharyngodon* Chatterji, 1933.

Biogeographical realm /	Type host (family)	Type locality	Taxonomical status	Taxonomical comments
Species				
Afrotropical realm				
<i>P. awokoyai</i> Babero and Okpala, 1962	<i>Agama agama</i> (Linnaeus) (= <i>Agama colonarum</i> Daudin) (Agamidae)	Lagos, Nigeria	Valid species of <i>Thelandros</i>	Described as <i>P. awokoyai</i> (Babero and Okpala, 1962); transferred to <i>Thelandros</i> by Adamson (1981). Considered as <i>Parapharyngodon</i> : Adamson and Nasher (1984a); Bursey and Goldberg (2005, 2007a); Bursey et al. (2013); Mašová et al. (2008); Rahimian et al. (2014). Considered as <i>Thelandros</i> : Bursey and Goldberg (1999); Rizvi and Bursey (2013). Species epithet misspelled as “ <i>awakoyai</i> ” by Bursey and Goldberg (1999; 2005); Bursey et al. (2013), Mašová et al. (2008); Rizvi and Bursey

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(2013); Rahimian et al. (2014).

<i>P. baueri</i> Bursey and Goldberg, 2007	<i>Acontias kgalagadi</i> (Lamb, Biswas and Bauer) (= <i>Typhlosaurus lineatus</i> Fitzsimons and Brain) (Scincidae)	Southern Africa	Valid species of <i>Parapharyngodon</i>	Nominally described (Bursey and Goldberg, 2007b).
<i>P. gerrhosauri</i> Hering-Hagenbeck, 2001	<i>Gerrhosaurus flavigularis</i> (Wiegmann) (Gerrhosauridae)	Timbavati Private Game Reserve, South Africa	Valid species of <i>Parapharyngodon</i>	Nominally described. Redescription by Hering-Hagenbeck et al. (2002).
<i>P. kenyaensis</i> Bursey and Goldberg, 2005	<i>Agama caudospinosa</i> (Meek) (= <i>Agama caudospina</i> ) (Agamidae)	Maralal, Samburu District, Kenya	Valid species of <i>Parapharyngodon</i>	Nominally described (Bursey and Goldberg, 2005).
<i>P. margaritifera</i> Hering-Hagenbeck, 2001	<i>Trachylepis margaritifera</i> (Peters) (= <i>Mabuya margaritifera</i> ) (Scincidae)	Klaserie Private Game Reserve, South Africa	Valid species of <i>Parapharyngodon</i>	Nominally described. Redescription by Hering-Hagenbeck et al. (2002).

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<i>P. rotundus</i> (Malan, 1939) Freitas, 1957	<i>Agama atra</i> (Daudin) (Agamidae), <i>Pseudocordylus microlepidotus</i> (Cuvier) (Cordylidae) (type host not designated)	South Africa	Valid species of <i>Parapharyngodon</i>	Transferred from <i>Thelandros</i> to <i>Parapharyngodon</i> by Freitas (1957a). Specific epithet misspelled as “ <i>rotundatus</i> ” (Burse and Goldberg, 1999, 2005, 2007a; Rahimian et al., 2014).
<i>P. seurati</i> (Sandground, 1936) Freitas, 1957	<i>Acontias percivali</i> (Loveridge) (Scincidae)	Taita, Kenya Colony	<i>Species inquirenda</i> (Adamson, 1981; inadequately described)	Described as <i>Thelandros</i> (Sandground, 1936); transferred to <i>Parapharyngodon</i> by Freitas (1957a).
<i>P. sexlabiata</i> (Ortlepp, 1933) Freitas, 1957	<i>Psammobates tentorius verroxii</i> (Smith) (= <i>Testudo tentoria verreauxi</i> ) (Testudinidae)	Niekerk's Hope, South Africa	Valid species of <i>Thelandros</i>	Described as <i>Thelandros</i> , transferred to <i>Parapharyngodon</i> by Freitas (1957a), returned to <i>Thelandros</i> by Adamson (1981).
Australian realm				
<i>P. anomalus</i> Hobbs,	<i>Tachyglossus aculeatus</i>	Lesmurdie,	Valid species of	Nominally described. Hobbs (1996) describes

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1996	(Shaw) (Monotremata: Tachyglossidae)	Western Australia	<i>Parapharyngodon</i>	a prominent genital cone in males, (as in <i>Thelandros</i> spp.), but subpolar egg operculum and shape of the tail of females (as in <i>Parapharyngodon</i> spp.), suggesting this species to be close to the ancestor of both genera.
<i>P. fitzroyi</i> Jones, 1992	<i>Tiliqua multifasciata</i> (Sternfeld) (Scincidae)	0.5 km W. of Fitzroy Crossing, W Australia	Valid species of <i>Thelandros</i>	Assigned to <i>Parapharyngodon</i> (Jones, 1992), but considering limits between <i>Thelandros</i> and <i>Parapharyngodon</i> unresolved. Shares with <i>Parapharyngodon</i> the subpolar operculum, the lateral alae in males and shape of the female's tail; and with <i>Thelandros</i> the presence of prominent genital cone. Hobbs (1996) transferred it to <i>Thelandros</i> after revising the type material. Considered as <i>Parapharyngodon</i> by Bursey and Goldberg

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				(1999, 2005, 2007a); Bursey et al. (2013); Rahimian et al. (2014), ignoring Hobbs’ observations.
<i>P. kartana</i> (Johnston and Mawson, 1941) Mawson, 1971	<i>Hemiergis peronii</i> (Gray) (Scincidae)	Kangaroo Island, South Australia	<i>Species inquirenda</i> (egg morphology not described properly)	Transferred from <i>Thelandros</i> to <i>Parapharyngodon</i> by Mawson (1971). Considered as <i>Thelandros</i> : Adamson (1981). Considered as <i>Parapharyngodon</i> : Bursey and Goldberg (1999). Johnston and Mawson (1941) described two species with the same epithet: <i>Pharyngodon kartana</i> and <i>Thelandros kartana</i> . Anderson (1981) misspelled specific epithet as “ <i>khartana</i> ”.
<i>P. trachysauri</i> (Johnston and Mawson, 1947) Adamson, 1981	<i>Tiliqua rugosa</i> (Gray) (= <i>Trachysaurus rugosus</i> ) (Scincidae)	Adelaide, South Australia	Valid species of <i>Thelandros</i>	Described as <i>Thelandros</i> (Johnston and Mawson, 1947). Considered as <i>Thelandros</i> : Jones (1992); Hobbs (1996), based on observation of type specimens (prominent

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genital cone, supported by a V-shaped sclerotized accessory piece, eggs with terminal opercula). Considered as *Parapharyngodon*: Adamson (1981) in the abstract, but as *Thelandros* in the text; Rahimian et al. (2014) based on original description, ignoring Hobbs (1996). Species not mentioned in compilations of *Thelandros* or *Parapharyngodon* by Adamson and Nasher (1984a; 1984b).

Madagascan realm

<p><i>P. cinctus</i> (Linstow, 1897) Freitas, 1957</p>	<p><i>Stellagama stellio</i> (Linnaeus) (=Agama <i>stellio</i>). According to Adamson (1981) this species does not occur in</p>	<p>Madagascar</p>	<p><i>Species inquirenda</i> (Adamson, 1981; males unknown)</p>	<p>Described as <i>Oxyuris cincta</i> based exclusively on females from a Madagascar lizard. Baylis (1923) provided a male description based on samples from <i>Stellagama stellio</i> (=Agama <i>stellio</i>) from Egypt and transferred the species</p>
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	Madagascar, reason why type host should be considered as an unidentified lizard			to <i>Thelandros</i> . Considered as <i>Parapharyngodon</i> by Freitas (1957a).
<i>P. maculatus</i> (Caballero, 1968) Adamson, 1981	<i>Geckolepis maculata</i> (Peters) (= <i>Geckolepis</i> <i>maculatus</i> ) (Gekkonidae)	Nossi-be, Madagascar	Valid species of <i>Thelandros</i>	Described as <i>Thelandros maculatus</i> . Recognized as <i>Thelandros</i> by Bursey and Goldberg (1999) because of polar operculum of eggs; Rizvi and Bursey (2013) considered it as <i>Thelandros</i> in their discussion, although kept as <i>Parapharyngodon</i> in their list of species. Considered as <i>Parapharyngodon</i> : Adamson (1981); Bursey and Goldberg (2005; 2007a); Mašová et al. (2008); Pereira et al. (2011); Rahimian et al. (2014). Pereira et al. (2011) misspelled the species epithet as “ <i>macullatus</i> ”.

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<i>P. meridionalis</i> (Chabaud and Brygoo, 1962) Adamson, 1981	<i>Oplurus</i> sp. (Opluridae)	Route Tulear, P.K. 556, Madagascar	Valid species of <i>Parapharyngodon</i>	Transferred from <i>Thelandros</i> to <i>Parapharyngodon</i> by Adamson (1981).
Nearctic realm				
<i>P. californiensis</i> (Read and Amrein, 1952) Adamson, 1981	<i>Xantusia vigilis</i> (Baird) (Xantusiidae)	Palmdale, Los Angeles, California, USA	Valid species of <i>Parapharyngodon</i>	Described as <i>Thelandros</i> (Read and Amrein, 1952). Transferred to <i>Parapharyngodon</i> by Adamson (1981).
<i>P. bicaudatus</i> Read and Amrein, 1952	<i>Xantusia riversiana</i> <i>riversiana</i> (Cope) (Xantusiidae)	San Nicolas Island, California, USA	Valid Species of <i>Thelandros</i>	Described as <i>Thelandros</i> , transferred to <i>Parapharyngodon</i> by Adamson and Nasher (1984a). Returned to <i>Thelandros</i> by Bursey and Goldberg (1999) because the operculum of the egg is terminal. Accepted as member of <i>Parapharyngodon</i> by Pereira et al. (2011).
<i>P. chamelensis</i> n. sp.	<i>Diaglena spatulata</i>	Chamela-	Valid species of	Nominally described (this paper).

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Velarde-Aguilar, Mata- López, Guillén- Hernández and León- Règagnon	(Günther) (Hylidae)	Cuixmala, Jalisco, Mexico	<i>Parapharyngodon</i>	
<i>P. grismeri</i> Bursey and Goldberg, 2007	<i>Petrosaurus repens</i> (Van Denburgh) (Phrynosomatidae)	San José de Comondú, Baja California Sur, Mexico	Valid species of <i>Parapharyngodon</i>	Nominally described (Bursey and Goldberg, 2007a).
<i>P. iguanae</i> (Telford, 1965) Adamson, 1981	<i>Sceloporus orcutti</i> (Stejneger) (= <i>Sceloporus</i> <i>orcutti orcutti</i> ) (Phrynosomatidae)	California, Riverside, San Jacinto Moun., Pinyon Flats, USA	Valid species of <i>Parapharyngodon</i>	Described as <i>Thelandros</i> (Telford, 1965); transferred to <i>Parapharyngodon</i> by Adamson (1981) on the basis of male and female caudal morphology and egg structure.
<i>P. ocalaensis</i> Bursey and Telford, 2002	<i>Plestiodon reynoldsi</i> (Stejneger) (= <i>Neoseps</i> <i>reynoldsi</i> ) (Scincidae)	Ocala Nal. Forest, Marion, Florida, USA	Valid species of <i>Parapharyngodon</i>	Nominally described (Bursey and Telford, 2002).

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<i>P. pseudothaparius</i> (Lucker, 1951) Freitas, 1957	<i>Xantusia riversiana</i> <i>reticulata</i> (Smith) (Xantusiidae)	San Clemente Island, California, USA	Valid species of <i>Thelandros</i>	Described as <i>Thelandros</i> (Lucker, 1951). Transferred to <i>Parapharyngodon</i> by Freitas (1957a). Considered as <i>Thelandros</i> : Adamson (1981) (epithet misspelled as “ <i>psuedothaparius</i> ”); Bursey and Goldberg (1999) based on polar operculum of eggs. Considered as <i>Parapharyngodon</i> : Adamson and Nasher (1984a).
<i>P. waltoni</i> (Read and Amrein, 1952) Adamson, 1981	<i>Anniella pulchra</i> (Gray) (Anniellidae), (Type host not designated)	California, USA	<i>Species inquirenda</i> (Adamson, 1981; male unknown)	Described as <i>Thelandros</i> (Read and Amrein, 1952). Transferred to <i>Parapharyngodon</i> by Adamson (1981) and declared <i>species</i> <i>inquirenda</i> ; followed by Bursey and Goldberg (1999).
<i>P. xantusi</i> (Lucker, 1951) Adamson and Nasher, 1984	<i>Xantusia riversiana</i> <i>reticulata</i> (Smith) (Xantusiidae)	San Clemente Island, California,	Valid species of <i>Thelandros</i>	Described as <i>Thelandros xantusi</i> ; transferred to <i>Parapharyngodon</i> by Adamson and Nasher (1984a). Considered as species of <i>Thelandros</i>

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		USA		by Bursey and Goldberg (1999) because the operculum of the egg is polar.
Neotropical realm				
<i>P. alvarengai</i> Freitas, 1957	<i>Trachylepis maculata</i> (Gray) (= <i>Mabuya maculata</i> Mausfeld and Vrcibradic) (Scincidae)	Ilha Fernando do Noronha, Brazil	Valid species of <i>Parapharyngodon</i>	Nominally described (Freitas, 1957a).
<i>P. arequipensis</i> Calisaya and Córdova, 1997	<i>Microlophus peruvianus</i> (Lesson) (Tropiduridae)	Omate, Moquegua, Peru	<i>Species inquirenda</i> (description lacking information about females)	Original description (Calisaya and Córdova, 1997) overlooked by many authors (i. e. Ramallo et al., 2002; Bursey and Goldberg, 1999, 2005, 2007a).
<i>P. binae</i> Pereira, Sousa and de Souza Lima, 2011	<i>Tropidurus torquatus</i> (Wied-Neuwied) (Tropiduridae)	Toledos, Juiz de Fora, state of Minas Gerais, Brazil	Valid species of <i>Parapharyngodon</i>	Nominally described (Pereira et al., 2011).
<i>P. largitor</i> Alho and	<i>Hemidactylus mabouia</i>	Guanabara	Valid species of	Nominally described.

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Rodrigues, 1963	(Moreau de Jonnés)	State, Brazil	<i>Parapharyngodon</i>	
	(Gekkonidae)			
<i>P. moqueguensis</i>	<i>Microlophus peruvianus</i>	Moquegua,	Valid species of	Described as <i>Parapharyngodon</i> , but males
Calisaya and Córdova,	(Lesson) (Tropiduridae)	Moquegua,	<i>Thelandros</i>	have genital cone, pedunculate caudal papillae
1997		Peru		and eggs with polar operculum (Calisaya and
				Córdova, 1997), characteristics of <i>Thelandros</i>
				spp.; no figures of female were presented.
				Species name was misspelled as <i>P.</i>
				<i>mosqueguensis</i> in the figure legend of
				description. Species overlooked by many
				authors (i. e. Ramallo et al., 2002; Bursey and
				Goldberg, 1999, 2005, 2007a).
<i>P. riojensis</i> Ramallo,	<i>Phymaturus punae</i> (Cei,	Quebrada del	Valid species of	Nominally described (Ramallo et al., 2002).
Bursey and Goldberg,	Etheridge and Videla)	leoncito, Depto	<i>Parapharyngodon</i>	
2002	(Liolaemidae)	General		
		Sarmiento, La		

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		Rioja, Argentina		
<i>P. sceleratus</i> (Travassos, 1923) Freitas, 1957	<i>Tropidurus torquatus</i> (Wied-Neuwied) (Tropiduridae)	Manguinhos, Brazil	Valid species of <i>Parapharyngodon</i>	Described as <i>Thelandros</i> , transferred to <i>Parapharyngodon</i> by Freitas (1957a). Widely misspelled as <i>P. "sceleratus"</i> . According to Ávila and Silva (2010), who reviewed the original description and redescription, the correct epithet is " <i>sceleratus</i> ".
<i>P. senisfaciecaudus</i> Freitas, 1957	<i>Liolaemus signifer</i> (Duméril and Bibron) (= <i>Liolaemus lenzi</i> ) (Liolaemidae)	La Paz, Bolivia	Valid species of <i>Thelandros</i>	Described as <i>Parapharyngodon</i> , transferred to <i>Thelandros</i> by Bursey and Goldberg (1999) because the operculum of the egg is terminal. Considered as <i>Parapharyngodon</i> : Adamson (1981); Ramallo et al. (2002); Bursey and Goldberg (2005); Jiménez et al. (2008); Ávila and Silva (2010); Rahimian et al. (2014).
<i>P. verrucosus</i> Freitas and	<i>Diploglossus lessonae</i>	João Alfredo	Valid species of	Nominally described (Freitas and Dobbin

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Dobbin, 1959	(Peracca) (Diploglossidae)	Municipality, Pernambuco State, Brazil	<i>Parapharyngodon</i>	1959). Misspelled as “ <i>verrucossus</i> ” by some authors (Adamson, 1981; Bursey and Goldberg, 2005, 2007a; Rizvi and Bursey, 2013; Rahimian et al., 2014).
<i>P. yurensis</i> Calisaya and Córdova, 1997	<i>Microlophus peruvianus</i> (Lesson) (Tropiduridae)	Yura, Arequipa, Peru	Valid species of <i>Thelandros</i>	Males described as presenting all features characterizing <i>Parapharyngodon</i> , except for the eggs, showing a polar operculum (Calisaya and Córdova, 1997), criterion used by Bursey and Goldberg (1999) to transfer the species to <i>Thelandros</i> . Description overlooked by many authors (i. e. Ramallo et al., 2002; Bursey and Goldberg, 2005, 2007a).
Oriental realm				
<i>P. acanthura</i> (Linstow, 1904) Adamson and Nasher, 1984	<i>Calotes versicolor</i> (Daudin) (Agamidae)	Colombo, Sri Lanka	<i>Species inquirenda</i> (Adamson and Nasher, 1984)	Described as <i>Oxyuris acanthura</i> by Linstow in 1904; considered synonymous of <i>P. micipsae</i> by Seurat in 1917 (Adamson and Nasher,

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				1984a). Adamson and Nasher (1984a)
				reinstate <i>P. acanthura</i> as a distinct species,
				but as <i>species inquirenda</i> .
<i>P. adamsoni</i> Cruzs and Daundasekera, 1988	<i>Chalcidoseps thwaitesi</i> (Günther) (Scincidae)	Sri Lanka (=Ceylon).	Valid species of <i>Parapharyngodon</i>	Nominally described.
<i>P. almoriensis</i> (Karve, 1949) Freitas, 1957	<i>Laudakia tuberculata</i> (Gray) (=Agama <i>tuberculata</i> ) (Agamidae)	Almora, Kumaon District, India	Valid species of <i>Parapharyngodon</i>	Described as <i>Thelandros</i> ; transferred to <i>Parapharyngodon</i> by Freitas (1957a). Considered as <i>Thelandros</i> by Adamson (1981). Considered as <i>Parapharyngodon</i> by Adamson and Nasher (1984a).
<i>P. aspiculus</i> (Khera, 1961) Adamson, 1981	<i>Calotes versicolor</i> (Daudin) (Agamidae)	Gorakhpur, India	<i>Species inquirenda</i> (Adamson, 1981; inadequately described)	Described as <i>Thelandros</i> (Khera, 1961); transferred to <i>Parapharyngodon</i> and declared <i>species inquirenda</i> by Adamson (1981); followed by Bursey and Goldberg (1999).
<i>P. calotis</i> (Johnson,	<i>Calotes versicolor</i> (Daudin)	Jodhpur, India	Valid species of	Described as <i>Thelandros</i> (Johnson, 1966);

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1966) Adamson, 1981	(Agamidae)		<i>Parapharyngodon</i>	transferred to <i>Parapharyngodon</i> by Adamson (1981), who mistakenly referred the date of description as 1967.
<i>P. evaginatus</i> Fotedar, 1974	<i>Calotes versicolor</i> (Daudin) (Agamidae)	Jammu Kashmir, India	<i>Species inquirenda</i> (Burse and Goldberg, 1999; inadequately described)	Description published in a congress abstract; Adamson (1981) did not include it in his revision.
<i>P. fotedari</i> Nanda and Malhotra, 1989	<i>Hemidactylus flaviviridis</i> (Rüppell) (Gekkonidae)	Allahabad, India	<i>Species inquirenda</i> (Burse and Goldberg, 1999; inadequately described)	Described as subspecies of <i>Thelandros</i> (Nanda and Malhotra, 1989).
<i>P. hemidactylus</i> (Patwardhan, 1935) Freitas, 1957	<i>Hemidactylus flaviviridis</i> (Rüppell) (Gekkonidae)	Nagpur, India	Synonym of <i>P. maplestoni</i>	Described as <i>Thelandros</i> (Patwardhan, 1935); Karve (1938) synonymized it with <i>P. maplestoni</i> based on study of types and

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				material from <i>H. flavoviridis</i> , and proposed that <i>P. maplestoni</i> should be placed in <i>Thelandros</i> . Transferred to <i>Parapharyngodon</i> by Freitas (1957a) as <i>P. maplestoni</i> . Adamson (1981) shared this view.
<i>P. hemidactylii</i> Gupta, Bhaskar and Gupta, 2009	<i>Hemidactylus flaviviridis</i> (Rüppell) (Gekkonidae)	Bareilly Uttar Pradesh, India	<i>Species inquirenda</i> (egg operculum and lateral alae not described)	Assigned to <i>Thelandros</i> and to <i>Parapharyngodon</i> in the same paper (Gupta et al., 2009); these authors considered <i>Parapharyngodon</i> as an invalid genus.
<i>P. jairajpurii</i> Rizvi and Bursey, 2013	<i>Hemidactylus flaviviridis</i> (Rüppell) (Gekkonidae)	Dehradun, Uttarakhand, India	Valid species of <i>Parapharyngodon</i>	Nominally described. Although the egg operculum is schematized, it is not described.
<i>P. kasauli</i> (Chatterji, 1935) Freitas, 1957	<i>Saara hardwickii</i> (Gray) (Agamidae)	India	Valid species of <i>Parapharyngodon</i>	Described as <i>Thelandros</i> ; transferred to <i>Parapharyngodon</i> by Freitas (1957a). Considered as <i>Thelandros</i> by Adamson (1981); transferred back to <i>Parapharyngodon</i>

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				by Adamson and Nasher (1984a).
<i>P. mabouia</i> (Rao and Hiregaudar, 1962) Adamson, 1981	<i>Eutropis carinata</i> (Schneider) (= <i>Mabuya carinata</i> Smith) (Scincidae), <i>Hemidactylus leschenaultii</i> Duméril and Bibron (Gekkonidae) (type host not designated)	Bombay, India	<i>Species inquirenda</i> (Burseay and Goldberg, 1999; egg morphology not described)	Transferred from <i>Thelandros</i> to <i>Parapharyngodon</i> by Adamson (1981). Rizvi and Bursey (2013) consider this a valid species without justification, and misspelled epithet as “ <i>mabuaiae</i> ”.
<i>P. macrocerca</i> Fotedar, 1974	<i>Laudakia tuberculata</i> (Gray) (Agamidae)	Khashmir, India	<i>Species inquirenda</i> (Burseay and Goldberg, 1999; inadequately described)	Described in a congress (Fotedar, 1974); species not mentioned by Adamson (1981).
<i>P. maplestoni</i> Chatterji, 1933	<i>Calotes versicolor</i> (Daudin) (Agamidae)	Yangon, Myanmar (=Rangoon,	Valid species of <i>Parapharyngodon</i>	Nominally described; type species of the genus. Name of type host was misspelled as “ <i>versicolor</i> ” in the original description

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		Burma)		(Chatterji, 1933). Name of the species misspelled by some authors as “ <i>P. maplestonei</i> ” (Bursey and Goldberg, 1999, 2005, 2007a).
<i>P. megaloon</i> (Linstow, 1906) Adamson, 1981	<i>Hemidactylus leschenaultii</i> (Duméril and Bibron) (Gekkonidae)	Mamadu, Sri Lanka	<i>Species inquirenda</i> (Adamson, 1981; males unknown)	Transferred to <i>Parapharyngodon</i> and declared <i>species inquirenda</i> by Adamson (1981); followed by Bursey and Goldberg (1999).
<i>P. striatus</i> Singh and Malhotra, 1986	<i>Hemidactylus flaviviridis</i> (Rüppell) (Gekkonidae)	Srinagar, Uttarakhand, India	Valid species of <i>Parapharyngodon</i>	Nominally described (Singh and Malhotra, 1986).
<i>P. taylori</i> (Chatterji, 1935) Skrjabin, Schikhobalova and Lagodovskaya, 1960 Palearctic realm	<i>Saara hardwickii</i> (Gray) (Agamidae)	India	Valid species of <i>Thelandros</i>	Transferred from <i>Thelandros</i> to <i>Parapharyngodon</i> by Skrjabin et al. in 1960 (Adamson, 1981). Adamson (1981) considered it as <i>Thelandros</i> .
<i>P. brevicaudatus</i>	<i>Paralaudakia lehmanni</i>	Turkestan	Valid species of	Synonym of <i>T. kasauli</i> according to Adamson

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Bogdanov and Markov, 1955	(Nikolsky) (Agamidae)		<i>Parapharyngodon</i>	(1981). Considered a valid species by Bursey and Goldberg (2005; 2007a) and Pereira et al. (2011).
<i>P. dolgieli</i> (Markov and Bogdanov, 1965) Adamson and Nasher, 1984	<i>Paralaudakia himalayana</i> (Steindachner) (= <i>Agama himalayana</i> ) (Agamidae)	Goluboe Lake, Kugitang Mountain Range, Russia (=USSR)	Valid species of <i>Parapharyngodon</i>	Transferred from <i>Thelandros</i> to <i>Parapharyngodon</i> by Adamson and Nasher (1984a). Misspelled as “ <i>dogieli</i> ” by many authors (Bursey and Goldberg, 1999, 2005, 2007a; Pereira et al., 2011; Bursey et al., 2013; Rizvi and Bursey, 2013; Rahimian et al., 2014).
<i>P. echinatus</i> (Rudolphi, 1819) Freitas, 1957	<i>Tarentola mauritanica</i> (Linnaeus) (Phyllodactylidae) (type host an unidentified gecko)	Algeciras, Spain	Valid species of <i>Parapharyngodon</i>	Described as <i>Ascaris echinatus</i> from fourth stage females. Seurat in 1917 found female and male oxyurids with similar larvae from <i>Tarentola mauritanica</i> in North Africa and assigned them to <i>Thelandros echinatus</i> (Mašová et al., 2008). Transferred to

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				<i>Parapharyngodon</i> by Freitas (1957a).
<i>P. lilfordi</i> Castaño-Fernández, Zapatero-Ramos, Solera-Puertas and Gonzalez-Santiago, 1987	<i>Podarcis lilfordi</i> (Günther) (Lacertidae)	Baleares Islands, Spain	Valid species of <i>Parapharyngodon</i>	Nominally described (Castaño-Fernández et al., 1987).
<i>P. pavlovskyi</i> Markov, Ataev and Bogdanov, 1968	<i>Eurylepis taeniolata</i> (Blyth) (Scincidae)	Central Asia	Valid species of <i>Parapharyngodon</i>	Nominally described; considered valid by Bursey and Goldberg (1999, 2005, 2007a).
<i>P. psammodromi</i> Roca and Lluch, 1986	<i>Psammodromus hispanicus</i> (Fitzinger) (Lacertidae)	Valencia, Spain	Valid species of <i>Parapharyngodon</i>	Nominally described (Roca and Lluch, 1986).
<i>P. skrzyabini</i> Vakker, 1969	<i>Pseudopus apodus</i> (Pallas) (= <i>Ophisaurus apodus</i> ) (Anguidae)	Republic of Kazakhstan (=Kazakhstan, USSR)	Valid species of <i>Parapharyngodon</i>	Nominally described.
<i>P. szczyrbaki</i> Radchenko	<i>Paralaudakia caucasia</i>	Turkestan and	<i>Species inquirenda</i>	Ikromov and Cho (2004) provided a

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and Sharpilo, 1975	(Eichwald) (=Agama <i>caucasica</i> ) (Agamidae)	Caucasus, URSS	(Burseay and Goldberg, 1999; females undescribed)	redescription of this species giving a female description, but they did not include egg morphology, thus we retain it as <i>species</i> <i>inquirenda</i> . Misspelled as “szyczerbaki” by Rahimian et al. (2014).
Panamanian realm				
<i>P. colonensis</i> Bursey, Goldberg and Telford, 2007	<i>Lepidophyma</i> <i>flavimaculatum</i> (Duméril) (Xantusiidae)	Colón Province, Panama	Valid species of <i>Parapharyngodon</i>	Nominally described (Burseay et al., 2007). Name mistakenly written as <i>P. panamensis</i> in the figure legends of the original description. Misspelled as “ <i>coloensis</i> ” by Rahimian et al. (2014).
<i>P. cubensis</i> (Baruš and Coy-Otero, 1969) Baruš, 1973	<i>Anolis carolinensis</i> (Voigt) (Dactyloidae)	Marianao, Havana Province, Cuba	Valid species of <i>Parapharyngodon</i>	Described as subspecies of <i>P.</i> <i>senisfaciecaudus</i> (Baruš and Coy-Otero, 1969). Considered valid species by Baruš (1973).
<i>P. duniae</i> Bursey and	<i>Trachycephalus typhonius</i>	Area de	Valid species of	Nominally described (Burseay and Brooks,

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Brooks, 2004	(Linnaeus) (= <i>Phrynohyas</i> <i>venulosa</i> ) (Hylidae)	Conservación, Guanacaste, Costa Rica	<i>Parapharyngodon</i>	2004).
<i>P. garciai</i> (Schmidt and Whittaker, 1975)	<i>Eleutherodactylus</i> <i>portoricensis</i> (Schmidt)	Towers Road, E1 Yunque Mountain, Puerto Rico	<i>Species inquirenda</i> (Burse and Goldberg, 1999; description of egg morphology lacking)	Described as <i>Thelandros</i> (Schmidt and Whittaker, 1975); transferred to <i>Parapharyngodon</i> by Adamson (1981). Considered valid species by Ramallo et al. (2002); Bursey and Goldberg (2005; 2007a), Bursey et al. (2013). Description also lacking information on position of male lateral alae, description of anal papillae and female tail shape; thus, we retain it as <i>species inquirenda</i> . Species epithet misspelled as “ <i>garciae</i> ” by many authors (Adamson, 1981; Bursey and Goldberg 1999, 2005, 2007a; Bursey et al., 2013; Rizvi and Bursey, 2013; Rahimian et

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				al., 2014).
<i>P. grenadaensis</i> Bursey, Drake, Cole, Sterner, Pinckney and Zieger, 2013	<i>Rhinella marina</i> (Linnaeus) (Bufonidae)	St. George's Parish. Grenada	Valid species of <i>Parapharyngodon</i>	Nominally described (Bursey et al., 2013).
<i>P. hylidae</i> n. sp. Velarde-Aguilar, Mata- López, Guillén- Hernández and León- Règagnon	<i>Triprion petasatus</i> (Cope) (Hylidae)	Rancho Hobonil, Yucatan, Mexico	Valid species of <i>Parapharyngodon</i>	Nominally described (this paper). Distribution of this species also includes Jalisco State in Mexico, which is located in the Nearctic realm.
<i>P. lamothei</i> Jiménez, León-Règagnon and Pérez-Ramos, 2008	<i>Bipes canaliculatus</i> (Bonnaterre) (Bipedidae)	Cocula, Guerrero, Mexico	Valid species of <i>Parapharyngodon</i>	Nominally described (Jiménez et al., 2008).
<i>P. maestro</i> Jiménez, León-Règagnon and Pérez-Ramos, 2008	<i>Bipes tridactylus</i> (Dugés) (Bipedidae)	Tecpan de Galeana, Guerrero,	Valid species of <i>Parapharyngodon</i>	Nominally described (Jiménez et al., 2008).

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		Mexico		
<i>P. osteopili</i> Adamson, 1981	<i>Osteopilus septentrionalis</i> (Duméril and Bibron) (Hylidae)	Moncada, Pinar del Rio Province, Cuba	Valid species of <i>Parapharyngodon</i>	Nominally described (Adamson, 1981).
Saharo-Arabian realm				
<i>P. adramitana</i> Adamson and Nasher, 1984	<i>Acanthocercus adramitanus</i> (Anderson) (= <i>Agama</i> <i>adramitana</i> ) (Agamidae)	Al Gara, Saudi Arabia	Valid species of <i>Parapharyngodon</i>	Nominally described (Adamson and Nasher, 1984b).
<i>P. aegyptiacus</i> Moravec, Baruš and Ryšavý, 1987	<i>Chalcides ocellatus</i> (Forsk.) (Scincidae)	Abu Rawash, Egypt	Valid species of <i>Skrjabinodon</i>	Described as <i>Parapharyngodon</i> (Moravec et al., 1987); transferred to <i>Skrjabinodon</i> by Moravec and Baruš (1990).
<i>P. bulbosus</i> (Linstow, 1899) Freitas, 1957	<i>Stellagama stellio</i> (Linnaeus) (Agamidae)	Egypt	<i>Species inquirenda</i> (Bursey and Goldberg, 1999; description of egg	Linstow in 1899 described <i>Oxyuris bulbosa</i> and <i>Oxyuris annulata</i> ; both transferred to <i>Thelandros</i> ; considered both to be variants of the same species (Adamson, 1981). Freitas

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			lacking)	(1957a) synonymized <i>P. bulbosus</i> with <i>P. annulata</i> . Accepted as <i>Parapharyngodon</i> by (Adamson, 1981); Mašová et al. (2008); Rizvi and Bursey (2013); Rahimian et al. (2014).
<i>P. cameroni</i> (Belle, 1957) Freitas, 1957	<i>Chalcides sepsoides</i> (Audouin) (Scincidae)	Bergel Arab, Faiyam Province, Egypt	<i>Species inquirenda</i> (Adamson, 1981; inadequately described)	Described as species of <i>Thelandros</i> (Belle, 1957). Transferred to <i>Parapharyngodon</i> by Freitas (1957b). Considered <i>species inquirenda</i> by Adamson (1981); followed by Bursey and Goldberg (1999).
<i>P. micipsae</i> (Seurat, 1917) Freitas 1957	<i>Tarentola mauritanica</i> (Linnaeus) (Phyllodactylidae)	Algeria, North Africa	Valid species of <i>Parapharyngodon</i>	Described as <i>Thelandros</i> ; transferred to <i>Parapharyngadon</i> by Freitas (1957a). Synonymized with <i>P. echinatus</i> by Chabaud and Golvan, 1957 (Mašová et al., 2008) and resurrected by Adamson and Nasher (1984b); Ruiz-Sánchez (1996) found differences between both species using RAPDs.

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				Redescription of this species by Mašová et al. (2009).
<i>P. rousseti</i> (Tcheprakoff, 1966) Adamson and Nasher, 1984	<i>Agama impalearis</i> (Boettger) (= <i>Agama bibronii</i> ) (Agamidae)	In 'Ekker, région d'In 'Anguel Hoggar (Ahaggar in Algeria)	Valid species of <i>Parapharyngodon</i>	Transferred from <i>Thelandros</i> to <i>Parapharyngodon</i> (Adamson and Nasher, 1984a). Adamson (1981) referred this species to South Africa, but according to Hering-Hagenbeck et al. (2002) the type locality corresponds to Ahaggar in Algeria. Misspelled “ <i>rousseti</i> ” by Mašová et al. (2008).
<i>P. tyche</i> (Sulahian and Schacher, 1968) Adamson and Nasher, 1984	<i>Stellagama stellio</i> (Linnaeus) (= <i>Agama stellio</i> ) (Agamidae)	Kartaba, Nebi-Chite, Zaoutar and Beirut, Lebanon	Valid species of <i>Parapharyngodon</i>	Described as <i>Thelandros</i> ( <i>Parapharyngodon</i> ) <i>tyche</i> (Sulahian and Schacher, 1968). Considered as <i>Thelandros</i> by Adamson (1981). Transferred to <i>Parapharyngodon</i> by Adamson and Nasher (1984a).
<i>P. thulini</i> Rahimian, Pazoki and Habashi,	<i>Laudakia nupta nupta</i> (De Filippi) (Agamidae)	Near Dorreh village,	Valid species of <i>Parapharyngodon</i>	Nominally described (Rahimian et al., 2014).

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2014		Kashan, Iran		
Sino-Japanese realm				
<i>P. japonicus</i> Bursey and Goldberg, 1999	<i>Onychodactylus japonicus</i> (Houttuyn) (Caudata: Hynobiidae)	Hineomata, Fukushima Prefecture, Honshu Island, Japan	Valid species of <i>Parapharyngodon</i>	Nominally described (Bursey and Goldberg, 1999). Misspelled as “ <i>japonicaus</i> ” by Rahimian et al. (2014).

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