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A taxonomic revision of South American species of the genus *Stenostomum* O. Schmidt (Platyhelminthes: Catenulida) based on morphological characters

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This paper revises the genus *Stenostomum* based on a rich collection of species from Argentina and on a review of bibliographical resources of all known South American species. The description of South American species is standardized. The new genus ***Anokkostenostomum*** is established and several species of *Stenostomum* are transferred to it based on the absence of light-refracting bodies and the presence of a metameric anterior brain lobe. We report five *Stenostomum* species and three *Anokkostenostomum* species new to Argentina and present an identification key for South American species. Finally, all the world species are compiled, with an overview of their distribution. © 2005 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2005, **144**, 37–58.

ADDITIONAL KEYWORDS: genus revision – Neotropical region – species redescription – *Stenostomum* sp. – 'Turbellaria'.

INTRODUCTION

Studies based on morphology (Ehlers, 1985, 1986; Ax, 1987) and on molecular data (Rohde *et al*., 1993; Campos *et al*., 1998) confirm the Catenulida as a basal clade within the Platyhelminthes. The family Stenostomidae, the most diverse within the Catenulida, comprises mainly freshwater ubiquitous organisms. The family Stenostomidae was created by Vejdovsky in 1880 with only one genus: *Stenostomum* O. Schmidt, 1848, but it was not considered valid (Bresslau, 1933; Nuttycombe & Waters, 1938) until 1945, when Marcus added the genus *Rhynchoscolex* Leidy, 1851. Later, Luther (1960) added the genus *Myostenostomum* Luther, 1960. The last genus to be included in the family was *Xenostenostomum* Reisinger, 1976. At present the family Stenostomidae comprises these four genera (Cannon, 1986).

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Whereas *Myostenostomum*, *Xenostenostomum* and *Rhynchoscolex* contain few species and have prominent morphological characters, *Stenostomum* includes approximately 50 species with a wide range of morphological characteristics.

Schmidt (1848) divided the species previously included in the genus *Derostoma* Dugès, 1828, into two new genera: *Stenostomum* O. Schmidt, 1848 and *Microstomum* O. Schmidt, 1848. He defined the genus *Stenostomum* as catenulids without statocyst, without preoral ciliated furrow, with paired ciliated pits and unpigmented light-refracting bodies. Later, many species without light-refracting bodies were included in the genus (Kepner & Carter, 1931).

The genus *Stenostomum* is cosmopolitan and has attracted widespread interest: Nuttycombe & Waters (1938), Marcus (1945a, b), Luther (1960), Young & Kolasa (1974a, b). These authors concur that the species have similar morphology allowing easy generic recognition, but the specific identification is generally problematic. They are simple forms, extremely fragile,

without specializations and sexually mature individuals are rarely encountered; hard structures are lacking and many characters (e.g. shape, size, colour) show high variability. The criteria followed by different authors for species identification have varied, giving unequal weight to the diagnostic morphological characters.

Of the approximately 50 species included in the genus *Stenostomum*, 25 are either endemic or have been cited for South America. Most of these species were described by Marcus (1945a, b, 1949) for Brazil, but there have been also records in Surinam (Van der Land, 1970) and Argentina (Noreña-Janssen, 1995).

The species richness of the genus *Stenostomum* in South America, the degree of endemism and the ambiguity of the morphological characters used in most descriptions stimulated the present revision. This paper focuses on South American *Stenostomum* species. Genera belonging to the Stenostomidae are presented, diagnostic morphological characters for *Stenostomum* species are analysed, the validity of the South American *Stenostomum* species is verified, and the descriptions of all South American species are updated. Some descriptions were based on specimens captured recently in freshwater environments within the Río de la Plata basin (Buenos Aires, Argentina), whereas others were made after a revision of bibliographical resources. The validity of one of the most problematic and cosmopolitan species of this genus, *Stenostomum leucops* (Dugès, 1828) O. Schmidt, is verified.

MATERIAL AND METHODS

Monthly samples were taken in various artificial lentic environments associated with the Río de la Plata basin (24°53′S, 57°50′W; Los Talas, Berisso, Buenos Aires Province, Argentina) from September 1998 to May 2000. Material was collected from vegetated areas, especially among floating vegetation (e.g. *Pistia striatiotes* L., Lemnaceae, *Spirodella intermedia* W. Koch and *Azolla filiculoides* Lam.) with a 40-μm mesh size net. The species found were studied and characterized *in vivo* under an optical microscope. Drawings of live specimens were made. Some specimens were fixed in Bouin, embedded in Paraplast, cut into a series of 4-μm-thick sagittal sections and stained with AZAN. Some were stored in the Helminthological Collection of the Museo de La Plata, Argentina (CHMLP).

In addition to the above mentioned collections from the wild, the species descriptions are also based on exhaustive bibliographical revisions: Schmidt (1848), Child (1902), Luther (1908), Martin (1908), Graff (1913), Gieysztor (1931), Kepner & Carter (1931), Nuttycombe (1931, 1932a, b), Jones (1932), Kepner, Carter & Hess (1933), Nuttycombe & Waters (1935, 1938), Marcus (1945a, b, 1949), Luther (1960), Borkott (1970), Van der Land (1970), Kolasa & Young (1974a, b), Young & Kolasa (1974a, b), Kolasa, Strayer & Bannon-O'Donnel (1987) and Noreña-Janssen (1995).

RESULTS

MORPHOLOGY AND ANATOMY

The following characters have been revised for the study and diagnosis of South American species.

Body shape

The body is cylindrical, somewhat flattened ventrally, 0.25–2 mm long. They form chains of up to nine individuals. Both body ends are pointed. The gut fills the entire body.

The intestine may extend into the caudal end, or there may be an intestine-lacking tail region. In this case, the posterior end may become thinner in the shape of a simple (e.g. Fig. 1B) or double tail, which looks like an accessory appendage (e.g. Figs 1C, 3A).

Epidermal cilia and rhabdites

A simple ciliated epithelium homogeneously lines the body surface. Apart from this uniform cover, several species have longer conspicuous cilia (heterogeneous ciliation).

The family Stenostomidae lacks laminar rhabdites. They have rhabdites of a compact nature, namely rhabdoids ('rod-shaped rhabdites' after Nuttycombe & Waters, 1938; 'false rhabdites or rhabdoides' after Marcus, 1945a; Kolasa, 1981; Rieger *et al*., 1991). Some species lack rhabdoids. When rhabdoids are present, they are found in the epidermal cells. Their arrangement may be homogeneous or heterogeneous with particular distribution patterns (absent in some regions and very abundant in others).

Ciliated pits

The ciliated pits are paired depressions seen in the antero-lateral body wall in live specimens. They are rounded or elongated, densely ciliated, small or large and extended. The epidermis of the pits is connected to the latero-basal region of the anterior brain lobes.

Cerebral ganglia

Brain morphology is variable within the order Catenulida, ranging from a cephalic mass without differentiation between anterior and posterior lobes, to paired anterior and posterior lobes.

The typical morphology of the cerebral ganglia ('brain') consists of two anterior lobes and two posterior lobes. The anterior lobes may have a smooth appearance (e.g. Fig. 3E) or be deeply dentate on their internal surface (e.g. Fig. 1A–D), or form small separate lobes, parallel to one another, with 'metameric' aspect (e.g. Fig. 4A, B). In the latero-basal region they join the epidermis of the ciliated pits. A transverse commissure relates the anterior ganglia by their proximal portion. The posterior lobes are placed behind the anterior lobes and are connected to them. In many species, light-refracting bodies are connected to the cerebral ganglia, especially with the posterior lobes. Nerve cords originating from each of these lobes innervate the epidermis. Marcus (1945a) describes the presence of a third pair of lobes, which he designates 'internal', related to the posterior lobes in some species.

Light-refracting bodies

Unpigmented refracting bodies are found in species of the genera studied here. Nuttycombe & Waters (1938) place great weight on their structure and arrangement for specific identification. These bodies are formed by a variable number of spherical granules; some species have fewer than five and others more than 15. The light-refracting bodies are frequently associated with the posterior cerebral lobes, or sometimes with the anterior lobes. Generally only one pair is found (e.g. Figs 1A, 2C–E, 3B–F), although, in some cases, more pairs are present (e.g. Figs 1B, C, 3A).

Graff (1913) divides the light-refracting bodies into three different types: type 1, disc-shaped with a large number (more than ten) of small spheres associated with a vesicle; type 2, bowl-shaped, formed by 1–5 spheres associated with a vesicle; and type 3, lenticular bodies with a single sphere. Type 1 light-refracting bodies are the most frequent. This distinction was taken up by Kepner & Carter (1931) and Nuttycombe & Waters (1938).

Pharyngeal glands and excretophores

Pharyngeal glands are usually present, but some species lack them. There exists a great variety in number, type and arrangement of pharyngeal glands.

Two types of glands are recognized; type a, small rounded glands; and type b, elongated club-shaped glands. In some species both types are present. The arrangement of the glands along the pharynx is variable. They can open onto the junction between the mouth and pharynx, or they may be uniformly distributed in the whole pharynx. Sometimes they are found only in the first two-thirds of the pharynx (e.g. Fig. 2B), in the posterior two-thirds or in lateral clusters along the pharynx (e.g. Figs 1A, 4A). Both the type and the arrangement of glands are useful features for species identification.

Nuttycombe & Waters (1938) mention the arrangement of pharyngeal glands as a relevant feature. Luther (1960) states that the number and arrangement of the glands is variable within a species. By contrast, Marcus (1945b) gives specific diagnostic relevance to the pharyngeal glands. According to our observations, these features are constant in the specimens obtained from natural environments.

Cells associated with the intestinal glands are described for several species (e.g. Figs 1A, 2D, 3B–F, 4B, C). Marcus (1945a) refers to them as excretophores (immobile cells), with excretory function, and he considers them to be equivalent to the 'granular gland cells of the enteric epithelium' of Nuttycombe & Waters (1938). These authors remark on the importance of these cells in specific identification.

Protonephridium

An unpaired protonephridial system is an autapomorphy of the Catenulida. It is formed by a duct with ascendant and descendant branches. The duct begins in the posterior region of the body and runs along the dorsal midline, curving around at the level of the cephalic commissure, directly below it (e.g. Figs 1A, 3D) (Kepner & Carter, 1931; Luther, 1960; Borkott, 1970). The two branches can run separately or together, and form evident sinuosities in several species (e.g. Fig. 3E). The nephridiopore is posterior, either terminal or subterminal.

TAXONOMY

Order Catenulida Meixner, 1924

Family Stenostomidae Vejdovsky, 1880

Diagnosis: Catenulida with lobulate preoral cerebral ganglia. Occasionally with ciliated pits. Asexual reproduction by paratomy. Brain formed by paired lobulate ganglia. Excretophores generally present. Male genital pore dorsal, at mouth level.

Type genus: *Stenostomum* O. Schmidt, 1848

Genus *Stenostomum* O. Schmidt, 1848

Diagnosis: Catenulida without either statocyst or preoral ciliated furrow. Large brain formed by a pair of anterior lobes, connected to each other by means of a transverse commissure in their posterior region, and a pair of posterior lobes. Paired ciliated pits associated with the anterior cerebral lobes. Light-refracting bodies present; number, composition and arrangement variable; frequently associated with the posterior cere-

Table 1. List of valid species of ***Anokkostenostomum* gen. nov.** and Stenostomum O. Schmidt, 1848 (recorded outside South America) and their distribution. *Abbreviations*: AFR (Africa), AS (Asia), BAL (Baltic), CAM (Central America), EU (Europe), MI (the Mediterranean), NAM (North America)

Species	Distribution
***Anokkostenostomum* gen. nov.**	
A. anops (Nuttycombe & Waters, 1938) **comb. nov.**	NAM, EU
A. brevipharyngium (Kepner & Carter, 1931) **comb. nov.** (syn. *S. incaudatum* Sonnerborn 1930)	NAM
A. corderoi poznanensis (Kolasa & Young, 1974) **comb. nov.**	EU
A. gigerium (Kepner & Carter, 1931) **comb. nov.**	NAM
A. grabbskogense (Luther, 1960) **comb. nov.**	EU
A. karlingi (Luther, 1960) **comb. nov.**	BAL
A. mandibulatum (Kepner & Carter, 1931) **comb. nov.**	NAM
A. predatorium (Kepner & Carter, 1931) **comb. nov.**	NAM
A. pseudoacetabulum (Nuttycombe & Waters, 1935) **comb. nov.** (syn. *S. stuhlmanni* Böhmig, 1897)	NAM, AFR
A. romanae (Kolasa, 1981) **comb. nov.**	EU
Stenostomum O. Schmidt, 1848	
S. anophtalmum An der Lan, 1955	EU
S. arevaloi franconia Bauchhenss, 1971	EU
S. beauchampi Papi, 1967	NAM
S. beryli Young & Kolasa, 1974	AFR
S. binum Schmarda, 1859	Australia
S. caudatum Marlow, 1904	EU (Russia)
S. constrictum Luther, 1960 (syn. *S. unicolor constrictum* Luther, 1960)	EU, USA
S. gilvum Böhmig, 1898	AFR
S. ignavum Vejdovski, 1879	EU
S. kepneri Nuttycombe & Waters, 1938	NAM
S. langi Keller, 1895	EU
S. leucops aquariorum Luther, 1960	EU
S. middendorffii Braun, 1885	EU
S. occultum Kolasa, 1971	NAM, EU
S. perforatum Becklemischev, 1921	EU (Russia)
S. sieboldi Graff, 1878	MI
S. sphaegnetorum Papi in Luther, 1960 (syn. *S. unicolor* Schmidt, 1848)	EU, AFR, AS, NAM
S. temporaneum Kolasa, 1980	EU, NAM

bral lobes. Epithelial rhabdites and excretophores present in numerous species. Asexual reproduction as the main reproductive mechanism. Gonads known only for some species; the single testis is antero-dorsal and the ovary mid-ventral.

Type species: *Stenostomum leucops* (Dugès, 1828) O. Schmidt, 1848.

Distribution: Cosmopolitan.

Valid species: See below for South American species, and Table 1 for species recorded only in other world regions.

Genus *Rhynchoscolex* Leidy, 1851

Diagnosis: Stenostomidae without ciliated pits. Anterior end very prolonged (proboscidean body prolongation). Nerve ganglia form 8–14 pairs of sensory plates at the anterior end. Two pairs of anterior longitudinal nerves and four pairs of posterior nerves. Excretophores frequently present. Presence of larval stage (Luther's larva), with statocyst and division by paratomy. Adult with or without statocyst and without paratomy.

Type species: *Rhynchoscolex simplex* Leidy, 1851.

Distribution: Europe, North and South America, Japan.

Valid species: *Rhynchoscolex diplolithicus* Reisinger, 1924; *R. evelinae* Marcus, 1945; *R. platypus* Marcus, 1945; *R. pusillus* Marcus, 1945; *R. nanus* Marcus, 1945; *R. remanei* Rixen, 1961.

Genus *Myostenostomum* Luther, 1960
Diagnosis: Stenostomidae with ciliated pits and muscular intestine. Asexual reproduction by paratomy. Chains of zooids present.

Type species: *Myostenostomum tauricum* (Nassonov, 1923) Luther, 1960.

Distribution: Europe, North America and South America.

Valid species: *Myostenostomum bulbocaudatum* Luther, 1960.

Genus *Xenostenostomum* Reisinger, 1976
Diagnosis: Stenostomidae without preoral ciliated furrow. With very specialized evaginable paired ciliated pits. Light-refracting bodies present. Spots of reddish pigment in the region of the ciliated pits. Well-developed brain ganglia in direct contact with the ciliated pits. With only a single pair of longitudinal ventro-lateral nerves. Simple pharynx, with a dorsal band of pharyngeal glands. Without cyrtocites. Asexual reproduction by paratomy. Presence of chains of zooids (generally no more than two).

Type species: *Xenostenostomum microstomoides* Reisinger, 1976

Distribution: South America, South and Equatorial Africa; Madagascar.

Genus ***Anokkostenostomum* gen. nov.**
Diagnosis: Stenostomidae without light-refracting bodies. Developed anterior brain lobe with 'metamerically' arranged ganglia. Posterior brain lobe simple, or poorly developed. Ciliated pits present, associated with the anterior brain lobe. Pharyngeal glands generally arranged homogeneously along the whole of the pharynx. Epithelial rhabdites present. Sensory cilia or bristles present. Excretophores present. Asexual reproduction by paratomy.

Type species: *Anokkostenostomum anatirostrum* (Marcus, 1945) **comb. nov.**

Distribution: Brazil, Surinam, Kenya, England, Finland, France, Poland, Italy, USA.

Valid species: See below for South American species and Table 1 for species recorded only in other world regions.

South American species of *Stenostomum*

Stenostomum amphotum Marcus, 1945 (Fig. 1A)
Description: Isolated specimens up to 0.7 mm long. Chains of up to nine zooids, with different degree of development. Elongated body, with dorso-lateral ciliated pits, anterior end slightly tapering. With constriction at the level of the oral pore. Posterior end with intestine-lacking region. Homogeneous ciliated epithelium without longer sensory cilia. Sparse small rhabdites on the ventral surface. Colour in life whitish.

Cerebral ganglia with deeply dentate anterior brain lobes and a pair of internal lobes associated with the posterior ones (trilobate brain after Marcus, 1945a). Two light-refracting bodies, with more than ten spherical corpuscles (type 1), associated with the posterior lobes.

Oral pore oval. Pharynx large (greater than 1/5 of the body length). Two types of pharyngeal glands: (1) antero-ventral rounded glands (type a) and (2) groups of elongated club-shaped glands (type b) laterally in the posterior half of the pharynx. Transition between pharynx and intestine regulated by a muscular sphincter. Intestine with excretophores. Nephridiopore opens at the posterior intestine-lacking region.

Distribution: São Paulo and interior of São Paulo State, Brazil (Marcus, 1945b). Los Talas, Berisso, Buenos Aires, Argentina, September 1998, December 1998 to January 1999, April 1999 to July 1999, December 1999 to February 2000 and May 2000. This species has not been previously recorded in Argentina.

Stored material: Ten sagittally sectioned specimens in the CHMLP. No. 5303.

Discussion: *S. amphotum* was synonymized to *S. leucops* (de Beauchamp, 1948; Luther, 1960), owing to the difficulty in recognizing differences in the arrangement of the pharyngeal glands. The type and arrangement of the pharyngeal glands and the layout of the rhabdites, the number of brain lobes, and the sphincter between pharynx and intestine, are enough to separate both species. On the other hand, a cladistic analysis (our unpubl. data) confirms the independence of *S. amphotum* and *S. leucops*.

Stenostomum arevaloi Gieysztor, 1931 (Fig. 1B)
Stenostomum rachiocaudatum Nuttycombe, 1932

Description: Solitary individuals 0.6–0.8 mm long (minimum 0.35 mm long), diameter 0.13 mm. Chains of two zooids (1–1.5 mm) up to seven zooids (2.5 mm). Body cylindrical, slightly flattened ventrally. With post-pharyngeal constriction. Posterior end tapering, with intestine-lacking region, ending in a very long tail. Its proximal region is adhesive, and the posterior end bends upward (Nuttycombe & Waters, 1938; Marcus, 1945a). Ciliated pits anterior, long and deep. Epidermal cilia longer than the thickness of the epidermis. Caudal region with long semi-rigid sensory cilia. Rod-shaped rhabdites. The epidermal cells with refractory inclusions (other than rhabdites) of several (up to six) corpuscles. White colour in life.

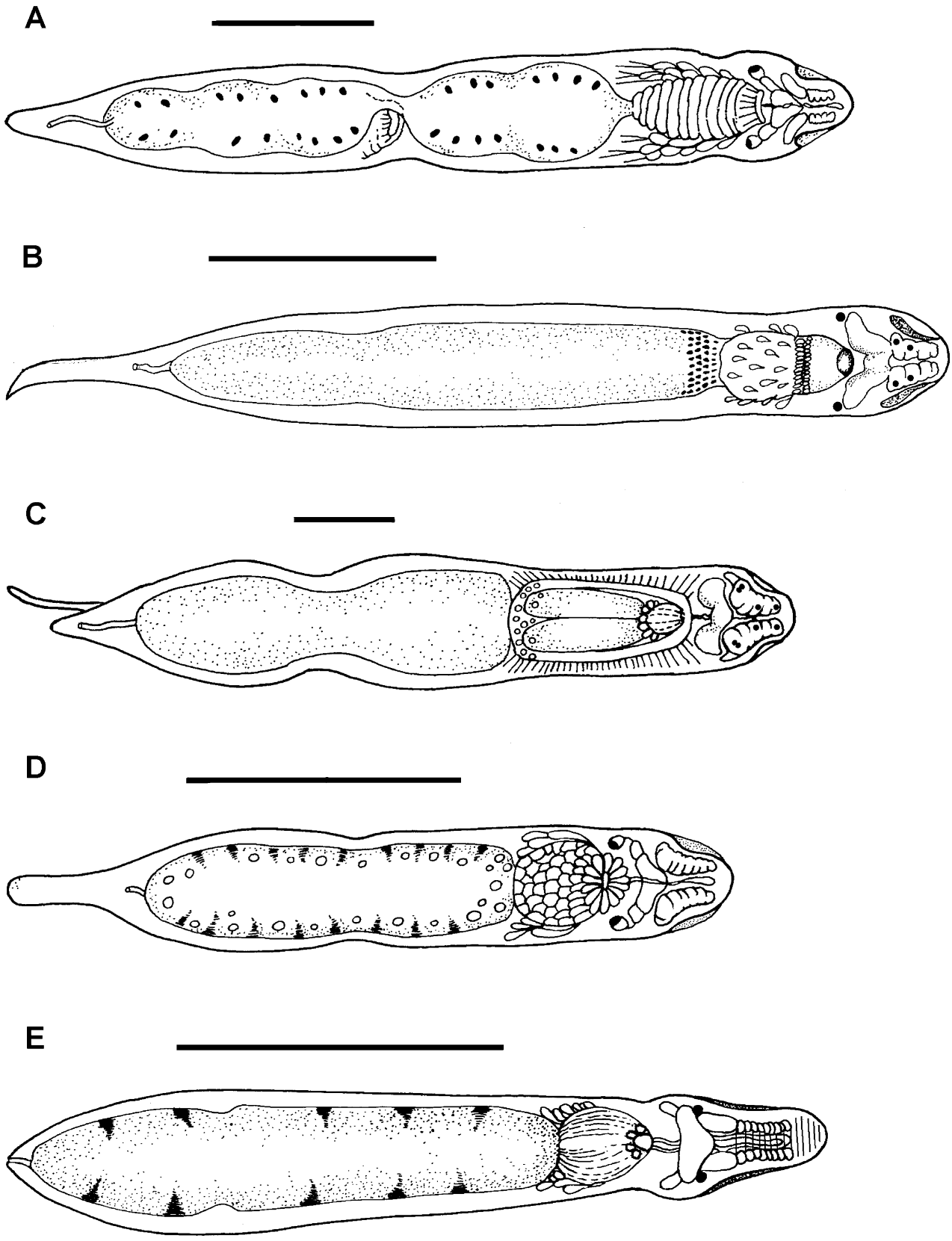

Figure 1. A, *Stenostomum amphotum*. B, *S. arevaloi*. C, *S. bicaudatum*. D, *S. ciliatum*. E, *S. cryptops*. Scale bars = 200 μm.

Anterior brain lobes deeply dentate. Three pairs of subepidermal light-refracting bodies. The first pair, simple and small, located before the anterior brain lobe. The second pair, simple, at the level of the ciliated pits, above the anterior lobes. The third pair at oral pore level, above the posterior lobes; this pair is frequently the largest and formed by two spheres (type 2).

Oral pore rounded, opening between the posterior brain lobes. Muscular pharynx. Pharyngeal glands (type a) opening onto the last two-thirds. A transverse line of cells can be seen ventrally to the pharynx. Conspicuous pharyngeal muscular sphincter. Intestine with a smooth outline ending at the base of the tail. The anterior intestinal region frequently with fine, dark granules. Dorsal excretory pore in the intestine-lacking region.

Distribution: Valencia, Spain (Gieysztor, 1931); Virginia (Nuttycombe, 1932b; Nuttycombe & Waters, 1938); Georgia (Nuttycombe & Waters, 1938; Kolasa, 1991), USA; São Paulo and interior of São Paulo State, Brazil (Marcus, 1945b); Poznan, Poland (Kolasa, 1973); Kenya (Young & Kolasa, 1974b); Italy, France and Germany (Lanfranchi & Papi, 1978).

Discussion: Gieysztor (1931) mentions the occasional presence of a terminal excretory vesicle in the region of the excretory pore. The former has not been observed in the South American specimens.

Marcus (1945b) stated that the pharyngeal glands open only onto the posterior pharyngeal region, while Nuttycombe & Waters (1938) mention that the pharyngeal glands open onto the whole pharyngeal length. The transverse line of cells exhibited ventrally to the pharynx is similar to that described for *S. paraguayense* (Martin, 1908) Luther, 1908.

Stenostomum bicaudatum Kennel, 1889 (Fig. 1C)
Stenostoma bicaudatum Kennel, 1889

Description: Solitary individuals, 1–1.5 mm long. Chains of usually two zooids, 2.5 mm long. Body digitiform, ventrally flattened. Anterior end rounded, with a short mid-dorsal groove. Posterior end with intestine-lacking region, and forming a tail with two appendages (one dorsal, short and thick and one ventral thin, and longer). Front lateral semi-spherical ciliated pits. Homogeneous ciliated epithelium with refractive inclusions. Rhabdites abundant, uniformly distributed, except for two dorsal tracts lacking rhabdites on both sides of the dorsal mid-line.

Anterior brain lobes deeply dentate. Three pairs of light-refracting bodies (type 2) anterior and overlapping the sensory cells of the ciliated pits. The two first pairs are formed by a single sphere and the third pair by two or three spheres (rarely four).

Oral pore rounded. The pharynx is long, occupying almost half the body. It bears longitudinal creases giving it the appearance of two 'oblong sacs'. Well-developed circular, dorsal and diagonal musculature. The claw-organ is found on the dorsal wall of the pharynx, behind the oral pore. It comprises six tentacles covered with an adhesive substance and associated with unicellular glands, and is characteristic of this species. The pharyngeal glands (type a) open onto the posterior portion of the pharynx. Presence of a muscular sphincter between the pharynx and the intestine. No excretophores present. The intestine narrows caudally. The dorsal excretory pore opens anteriorly to the dorsal appendage.

Distribution: Trinidad (Kennel, 1889); near Paramaribo, Brazil (Marcus, 1945b); Surinam (Van der Land, 1970); Paraná River, Argentina (Noreña-Janssen, 1995).

Discussion: There are several differences between the specimens described by Nuttycombe & Waters (1938) and the South American specimens. These authors mention the presence of chains of up to nine zooids 7 mm long, while in South America only two specimens were found with zooid chains. They also mention the absence of pharyngeal glands. However, Marcus (1945b) mentions small pharyngeal glands associated with the posterior region of this organ.

Marcus (1945b) describes the body as dorsally flattened and ventrally convex and he states that animals swim with their ventral surface upwards, in disparity with the descriptions of Nuttycombe & Waters (1938) and Noreña-Janssen (1995). Marcus (1945b) does not mention the heterogeneous arrangement pattern of the rhabdites described for the specimens in North America (Nuttycombe & Water, 1938).

Stenostomum ciliatum Kepner & Carter, 1931 (Fig. 1D)
Stenostomum agile Silliman, 1885

Description: Solitary individuals, 1 mm or less long. Chains with two zooids. Body robust, anterior end blunt. Ciliated pits lateral and superficial. Tapering posterior end with intestine-lacking region. Small epidermal cilia, uniformly distributed, longer at the posterior end. Rod-like rhabdites throughout the entire epidermis.

Anterior brain lobes deeply dentate. A pair of light-refracting bodies associated with the posterior brain lobes; each one formed by one, two or three spheres, included in a colourless vesicle (type 2).

Oral pore oval, transversal and surrounded by glands. Wide pharynx. The glands on both sides of the pharynx (type b) open onto the anterior end, and smaller ones (type a) open onto the whole surface. Conspicuous pharyngeal sphincter. Intestinal wall with

irregularly distributed excretophores. Nephridiopore ventral, subterminal and posterior to the intestine.

Distribution: Virginia, USA (Kepner & Carter, 1931; Kolasa, 1991); São Paulo and Paraná State, Brazil (Marcus, 1945b).

Discussion: Kepner & Carter (1931) described the ciliated pits as relatively small for the specimens from Virginia and Marcus (1945b) described them as long and extensive. This author states that this difference would not suffice to separate the species, because they share the rest of the diagnostic characters.

Stenostomum cryptops Nuttycombe & Waters, 1935 (Fig. 1E)

Description: Isolated specimens, 0.4–0.5 mm long. Chains of up to six zooids (3 mm long). Anterior end blunt. Body constriction behind the ciliated pits. Tapering posterior end. Large, deep dorso-lateral ciliated pits. Uniformly ciliated epithelium. Scarce semi-rigid sensory cilia. Rhabdites uniformly distributed. Colour in life white.

Brain large and elongated. Anterior brain lobes divided into small independent masses ('metamerics'). A pair of light-refracting bodies formed of small spheres included in a vesicle (type 2) associated with the anterior brain lobes.

U-shaped oral pore. Short muscular pharynx. Small pharyngeal glands (type a) in the anterior region, elongated glands (type b) in the posterior region. Well-developed pharyngeal sphincter. An intestinal caecum with granulose epithelium, dorsal to the pharynx. High intestinal epithelium. Excretophores laterally placed. Nephridiopore terminal or subterminal.

Distribution: Georgia, USA (Nuttycombe & Waters, 1935; Kolasa, 1991); São Paulo, Brazil (Marcus, 1945b).

Discussion: At variance with the single pair of light-refracting bodies described by Marcus (1945b), Nuttycombe & Waters (1935, 1938) describe a second pair, associated with the posterior lobes and larger than the first pair.

Stenostomum glandulosum Kepner & Carter, 1931 (Fig. 2A)

Description: Isolated specimens 0.6–0.8 mm long. Chains of up to 16 zooids which may reach 12 mm long. Anterior end very mobile and retractile. Large, superficial lateral ciliated pits. Presence of ciliated channels or grooves, dorsal or ventral, intimately connected to the brain ganglia. Rosette-shaped gland cells in the epidermis at the anterior end. Each rosette is formed by 2–4 refractive, toxic vesicles (Kepner & Carter, 1931). Posterior end truncate. No rhabdites. Colour in life whitish.

Anterior lobes of the brain divided into small independent masses ('metamerics'). One to three pairs of light-refracting bodies, formed by one or two spheres associated with the anterior brain lobes (type 2).

Oral pore very dilatable and surrounded by a layer of muscle. Long muscular pharynx. Numerous club-shaped glands (type b) open onto the pharynx and the oral pore. Intestine extended up to the caudal end. Intestinal epithelium folded, with excretophores. Nephridiopore terminal or subterminal.

Benthic species, either predatory (Marcus, 1945b) or scavenger (Kepner & Carter, 1931); mainly feeds on *Stenostomum* sp., rotifers, oligochaetes, etc.

Distribution: Virginia (Kepner & Carter, 1931; Nuttycombe & Waters, 1938), North Carolina and Georgia (Nuttycombe & Waters, 1938; Kolasa, 1991), USA; São Paulo, Brazil (Marcus, 1945b); near Onverwacht, Surinam (Van der Land, 1970); Poznan, Poland (Kolasa, 1973); North of Europe, in laboratory aquaria (Lanfranchi & Papi, 1978).

Discussion: Several features relevant for specific identification vary according to different authors. The absence of rhabdites was mentioned by Kepner & Carter (1931) and by Marcus (1945b). Nuttycombe & Waters (1938) mention the presence of relatively numerous fragile rhabdites in the anterior region and in lesser number in the rest of the body.

Kepner & Carter (1931) describe four pairs of light-refracting bodies associated with the anterior brain lobes. Nuttycombe & Waters (1938) state that the number and position of the light-refracting bodies is variable and each one may be formed by two spheres. Marcus (1945b) found two or three pairs in the Brazilian specimens.

Stenostomum grande Child, 1902 (Fig. 2B)

Stenostomum oesophagium Kepner & Carter, 1931

Description: Single specimens 1–2 mm long, two- to six-zooid chains up to 6 mm long. Body cylindrical, anteriorly rounded. Dorso-lateral ciliated pits longitudinally elongated. Constriction at the level of the oral pore. Posterior end with an intestine-lacking region. Heterogeneous ciliated epithelium, with scarce semi-rigid sensory cilia. Dorsal epidermis with rhabdites arranged perpendicularly in rosettes. The rhabdites are parallel to the surface in the ventral epidermis, where three longitudinal lines without rhabdites can be seen. Colour in life whitish. From the apical end to the brain, the epidermis bears compact rhabdites giving it a darker colour.

Anterior brain lobes deeply dentate. A pair of light-refracting bodies type 1 associated with the posterior lobes.

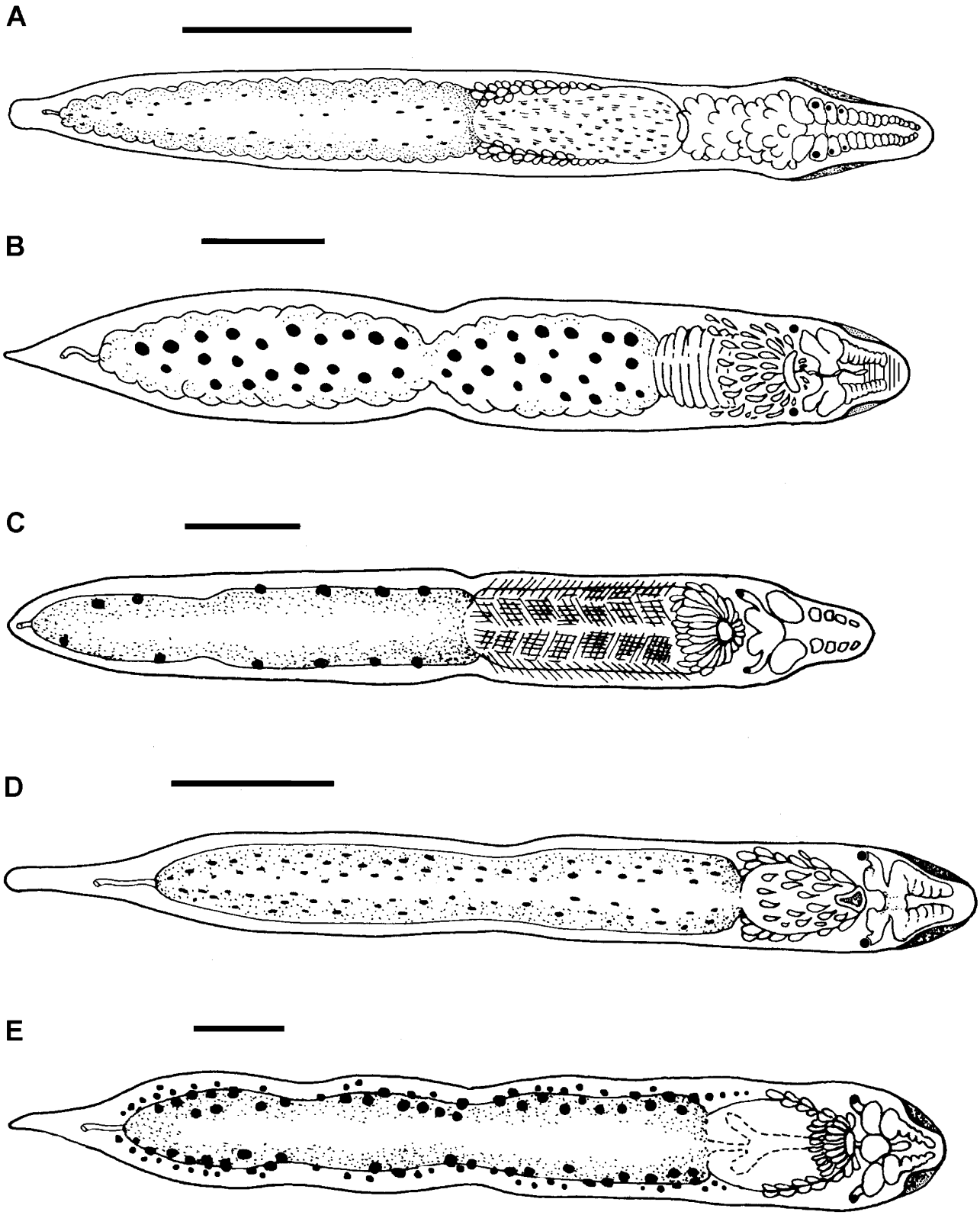

Figure 2. A, *Stenostomum glandulosum*. B, *S. grande*. C, *S. hemisphericum*. D, *S. leucops*. E, *S. matarazzoi*. Scale bars = 200 μm.

Dilatable, semicircular oral pore. Pharynx occupying 1/5–1/6 of body length. Pharyngeal glands (type a) in the anterior half. Transition between pharynx and intestine with a narrow sphincter. Excretophores irregularly distributed along the intestine. Nephridiopore proximal to the terminal end.

Distribution: Chicago (Child, 1902), Illinois and New York (Graff, 1913), Pennsylvania (Kepner & Carter, 1931), and Virginia (Nuttycombe & Waters, 1938; Kolasa, 1991), USA; southern Finland (Nassonov, 1924); Kola Peninsula (Nassonov, 1925); St Petersburg (Leningrad) (Nassonov, 1926); São Paulo and Paraná State, Brazil (Marcus, 1945b); near Onverwacht, Surinam (Van der Land, 1970); Konin Lakes, Poland (Kolasa, 1977). Los Talas, Berisso, Buenos Aires, Argentina, October 1998 to April 1999 and March 2000. This species has not been previously recorded in Argentina.

Stored material: Ten sagittally sectioned specimens in the CHMLP. No. 5304.

Discussion: Marcus (1945a) indicates two forms: 'typica' which corresponds to Child's (1902) description and 'megista' for the specimens coming from Tieté River, São Paulo, Brazil. The difference between these forms is based on body size, brain development, arrangement of the rhabdites and colouring of the pharynx. The specimens from Berisso, Buenos Aires, correspond to the form 'typica'.

Mature forms of this species have been recognized. Nuttycombe & Waters (1938) and Marcus (1945b) observed specimens with an unpaired testis at the level of the pharynx and Kepner *et al*. (1933) found mature female gonads.

Stenostomum hemisphericum Nassonov, 1924 (Fig. 2C)

Description: Adult specimens 1–2 mm long. Four- to five-zooid chains, 18 mm long. Body cylindrical. Anterior end blunt. Lateral and reduced ciliated pits. A slight body constriction between the pharynx and the intestine. Rounded posterior end, without intestine-lacking region. Abundant semi-rigid cilia in the anterior and posterior regions. Rhabdites grouped in bundles vertically arranged in the epidermis. Colourless in life.

Anterior brain lobes separated into small independent masses ('metamerics'). Posterior brain lobes enclosing an internal lobe (trilobate brain). A pair of light-refracting bodies, comprising a pear-shaped vesicle (0.01 mm in diameter) and a spherical element, refractory in its inner part (type 2) associated with the posterior lobe.

Oral pore rounded. Pharynx very long and provided with lateral, circular, oblique and longitudinal muscular fibres, especially developed on the anterior dorsal region. Finger-shaped glands surround the oral pore. Conspicuous pharyngeal sphincter. Excretophores regularly arranged in the anterior intestinal region; irregular on the rest of the body. Nephridiopore subterminal.

Distribution: Ukraine, Crimea (Nassonov, 1924); São Paulo, Brazil, in aquaria (Marcus, 1945a); margins of the Suriname River, near Paramaribo, Surinam (Van der Land, 1970).

Discussion: The description given is based on Marcus's (1945a) description for the Brazilian specimens with some differences with the Russian specimens described by Nassonov (1924): the Brazilian specimens have glands only surrounding the oral pore. This feature contrast with the Nassonov description. Nevertheless, these glands are not clear in the original drawings. The posterior brain lobes are larger in the Brazilian specimens and the light-refracting bodies more concave in the Russian specimens. These differences would not suffice to separate them because of other similarities: the proportions of the pharynx and intestine; the space taken up by the intestine; the ciliated pits; the shape of the oral pore; the musculature and the glands surrounding the oral pore (Marcus, 1945a).

Stenostomum leucops (Dugès, 1828) O. Schmidt, 1848 (Fig. 2D)

Fasciola composita Schrank, 1776
Derostoma leucops Dugès, 1828
Stylacium isabellinum Corda, 1838
Microstomum leucops Ørsted, 1844
Stenostomum torneense Schmidt, 1852
S. neoborecense Girard, 1893
S. tenuicaudatum Nuttycombe & Waters, 1938
S. sthenum Borkott, 1970
S. platycaudatum Borkott, 1970
S. plebejum Borkott, 1970

Description: Length variable. Two-zooid chain 1–1.75 mm. Cylindrical body. Rounded or pointed anterior end. Posterior end of the body with intestine-lacking region forming a tail. Ciliated epithelium with small rhabdites. Epidermic cilia with rigid sensitive cilia at anterior and occasionally at the posterior end. Colour in life yellowish white.

Anterior brain lobes deeply dentate. A pair of type 1 light-refracting bodies associated with the posterior brain lobes.

Oral pore shape variable, rounded, triangular or elongated. Simple muscular pharynx. Two types of pharyngeal glands: type a, abundant at the distal end, opening onto the posterior region of the pharynx; and type b, arranged in bunches lateral to the pharynx, opening onto the anterior end. Excretophores present.

Nephridiopore subterminal, in the intestine-lacking region.

Distribution: Cosmopolitan. In South America, margins of the Surinam River, near Paramaribo, Surinam (Van der Land, 1970); Paraná River, Argentina (Noreña-Janssen, 1995).

Discussion: Nuttycombe & Waters (1938) consider the validity of this species questionable. This criterion has been followed by Marcus (1945b). These authors consider that the descriptions of this species are so broad and ambiguous as to make its recognition difficult. By contrast, Borkott (1970) in an exhaustive study of *Stenostomum leucops* subdivides this species into three new species: *S. sthenum, S. platycaudatum* and *S. plebejum*. The results of this research did not confirm the existence of these species in South America (Noreña-Janssen, 1995). Young & Kolasa (1974b) identified specimens from Africa as *S. leucops leucops*, on the basis of Luther's (1960) description, ascribing the differences described by Borkott (1970) to those originated in the cultures or not visible in animals captured in natural environments.

In the 1990s, Reuter (Reuter, 1988, 1991, 1994; Reuter & Palmberg, 1990; Reuter & Eriksson, 1991; Reuter & Kuusisto, 1992; Reuter, Joffe & Palmberg, 1993; Reuter *et al*., 1995) as well as Wikgren & Thorndyke (1990), Lindroos & Reuter (1991), Palmberg & Reuter (1992) and Grahn *et al*. (1995) carried out ultrastructural studies of stenostomids, mainly *S. leucops*. *S. sthenum* was not mentioned in any of them.

Stenostomum matarazzoi Marcus, 1949 (Fig. 2E)

Description: Solitary specimens 1–1.5 mm long. Chains of four zooids, 2.5 mm long. Chains of six zooids, 3 mm long. Anterior end blunt. Posterior end with an intestine-lacking region. Apical ciliated pits. Constriction of the body at the level of the mouth. Live specimens are vermilion red, owing to the secretions of the glandular epidermal cells. These secretions appear as irregular spots on the surface. Body surface homogeneously covered by cilia that are longer on the mid-ventral line. Semi-rigid sensory cilia, more abundant at both body ends. The rhabdites are placed in the cells among the glands. The rhabdites and the glands are absent on the mid-ventral line and around the ciliated pits.

Anterior brain lobes deeply dentate. Posterior brain lobes with developed internal lobe (trilobate brain after Marcus, 1945a). A pair of light-refracting bodies formed by numerous spheres, type 1, associated with the posterior brain lobes.

Oral pore triangular. Short bag-like pharynx, a constriction dividing it into two parts: a rostral one with thick epithelium, short cilia and cyanophilic glands; and a caudal one with long cilia and no glands. Circular musculature present. Intestine with Minot's club-shaped cells, but without excretophores. Nephridiopore subterminal, ventral.

Distribution: Periodic pools near the Pirajussara River (tributary to the Pinheiros River), São Paulo, Brazil (Marcus, 1949).

Stenostomum paraguayense (Martin, 1908) Luther, 1908 (Fig. 3A)

Weldonia parayguensis Martin, 1908

Description: Solitary specimens up to 0.8 mm long. Chains with 2–3 zooids with different degrees of development. Oval body, blunt anterior end, with a constriction behind the mouth. Extended lateral ciliated pits. Posterior end with an intestine-lacking region, with two caudal finger-like extensions, a long ventral one and a short dorsal one. Homogeneous ciliated epithelium. Small rhabdites, scarce on a mid-dorsal line from the postoral constriction to the caudal extension. Colour in life light brown.

Anterior brain lobes deeply dentate. Three pairs of type 2 light-refracting bodies. The first two pairs are formed by one sphere and are placed subcutaneously over the sensory cells of the ciliated pits. The third pair is formed by two spheres, also superficial and associated with the posterior brain lobes.

Oral pore triangular. Pear-shaped pharynx. Pharyngeal glands (type a) arranged in the posterior half. A row of glandular cells in the ventral region of the pharynx (area of insertion for the musculature of the buccal lower lip). Fifteen to 25 cells with refringent granules form a 'transverse' row in the first third of the intestine. Nephridiopore opening between the caudal appendages.

Distribution: Paraguay (Martin, 1908); São Paulo and interior of São Paulo State, Brazil (Marcus, 1945b); Onverdacht, Surinam (Van der Land, 1970); Los Talas, Berisso, Buenos Aires, Argentina, September 1998 to July 1999, December 1999 to February 2000. This species has not been previously recorded in Argentina.

Stored material: Four sagittally sectioned specimens in the CHMLP. No. 5305.

Discussion: This species was described by Martin (1908) as *W. parayguensis*. Because this material came from Paraguay (South America), the original spelling was corrected by Marcus (1945b) (article 32.5 in the ICZN, 2000).

S. paraguayense was placed in the genus *Stenostomum* by Luther (1908) and it was considered as a synonym of *Stenostomum bicaudatum* Kennel, 1889 by Nuttycombe & Waters (1938). This criterion was followed by Noreña-Janssen (1995). However, Marcus (1945b) and Van der Land (1970) recognize the validity of both species.

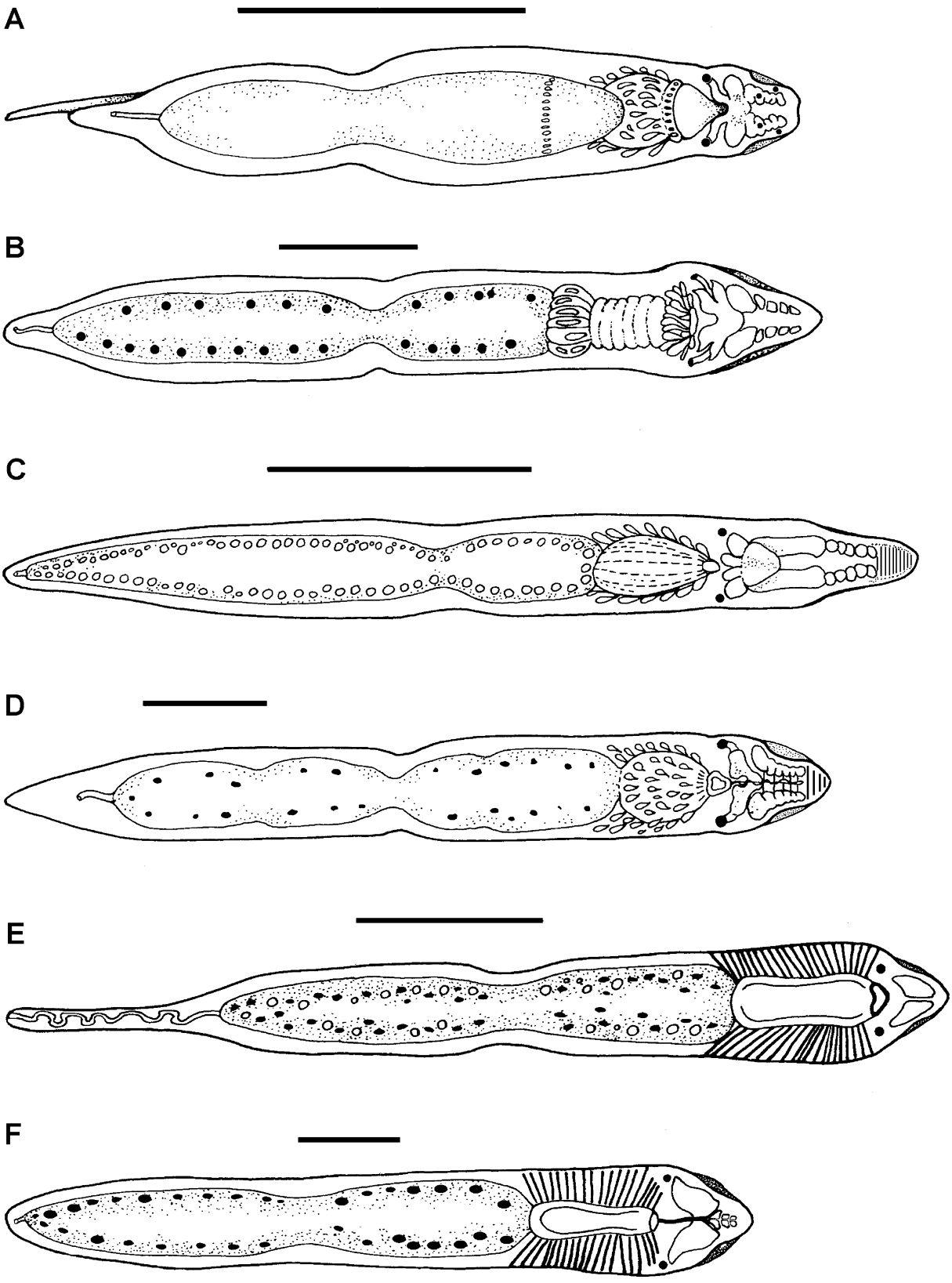

Figure 3. A, *Stenostomum paraguayense*. B, *S. rosulatum*. C, *S. simplex*. D, *S. tenuicauda*. E, *S. uronephrium*. F, *S. virginianum*. Scale bars = 200 μm.

Marcus (1945b) mentions that the dorsal caudal appendage may be reduced or absent in some specimens.

Stenostomum rosulatum Marcus, 1945 (Fig. 3B)
Description: Simple individuals 0.5–0.9 mm long. Two-zooid chains 1.2 mm long. Anterior end blunt. Small lateral ciliated pits. Body broader at mouth level. Body constriction between pharynx and intestine. Intestine-lacking region at posterior end. Body covered with cilia. Presence of semi-rigid sensory cilia, more abundant at both body ends. Rhabdites parallel to the axial axis. Colourless in life.

Anterior brain lobes deeply dentate, internal brain lobes associated with posterior lobes (Marcus, 1945a); posterior lobes slender. One pair of light-refracting bodies with a single refractory element (type 2), associated with the posterior brain lobes.

Oral pore circular. Long sacciform pharynx with internal cilia and strong pharyngeal muscles. Club-shaped glands (type b) open between mouth and pharynx. Well-developed circular musculature can be observed in the posterior pharyngeal region. With muscles extending from pharynx to body wall. First region of the intestine with high, vacuolated cells, with contractile activity independent from the rest of the intestine, and separated from the posterior intestinal region by a marked constriction (Marcus, 1945a). The rest of the intestine is homogeneous with irregularly arranged excretophores. The protonephridium becomes sinuous at the posterior end. Nephridiopore terminal.

Distribution: Tieté River, São Paulo, Brazil (Marcus, 1945a).

Stenostomum simplex Kepner & Carter, 1931 (Fig. 3C)
Description: Individuals with 2–4 zooids, 0.7–0.8 mm long. Body cylindrical. Anterior end tapering. Presence of lateral constrictions in the ciliated pit regions, and at the caudal edge of the posterior lobes. Small lateral ciliated pits. Rounded posterior end, without an intestine-lacking region. Ciliated epithelium frequently with sparse longer sensory cilia. Homogeneous rhabdites.

Anterior brain lobes separated into small independent masses ('metamerics'). A pair of internal lobes associated with the posterior lobes (trilobate brain after Marcus, 1945a). Spherical nerve commissure. A pair of light-refracting bodies formed by a single naked sphere, with no vesicle (type 3), associated with the posterior brain lobes.

Small, axially elongated oral pore. Type a pharyngeal glands. No excretophores. Nephridiopore terminal.

Distribution: Virginia, USA (Kepner & Carter, 1931; Kolasa, 1991); São Paulo, Brazil (Marcus, 1945b); Finland? (Lanfranchi & Papi, 1978).

Stenostomum tenuicauda Graff, 1911 (Fig. 3D)
Description: Chains of up to eight zooids up to 5 mm long. Body cylindrical, slightly flattened ventrally. Anterior end blunt. Deep dorso-lateral ciliated pits. Body constriction at the level of the oral pore. Elongated intestine-lacking region at the posterior end (up to one-third of the body length). Caudal portion ventrally adhesive. Long, thin and dense epithelial cilia. Presence of long semi-rigid sensory cilia. Rhabdites grouped in packets placed vertically to the epidermis. Colour in life white.

Anterior brain lobe deeply dentate. Internal brain lobes associated with posterior lobes (Marcus, 1945a). A pair of type 1 light-refracting bodies formed by numerous spheres (about 50) included into a large vesicle and associated with the posterior ganglia.

Oral pore semi-lunar, surrounded by longitudinal pharyngeal muscles. Pharynx almost as wide as it is long, with little circular musculature. Presence of radial muscles between the pharynx and the body wall. Regularly arranged glands (type a) along the entire pharynx. Intestinal walls smooth. Excretophores irregularly arranged, not very conspicuous. Nephridiopore ventrally placed in the intestine-lacking region (subterminal).

Distribution: New York and Massachusetts (Graff, 1911), Virginia (Nuttycombe, 1932a; Nuttycombe & Waters, 1938), North Carolina, South Carolina, Tennessee and Georgia (Nuttycombe & Waters, 1938), USA; São Paulo, Brazil (Marcus, 1945b); Russia (Beklemichev, 1917, 1921; Nassonov, 1926); Finland (Nassonov, 1924); temporary pond near Zapata Stream and Route 11, Buenos Aires, Argentina, November 1999. This species has not been previously recorded in Argentina.

Stored material: Four sagittally sectioned specimens in the CHMLP. No. 5306.

Discussion: *S. tenuicauda* was synonymized with *S. leucops* (Luther, 1960). However, the differences found not only in the material studied here, but also in the specimens described by Marcus, support the validity of at least the South American populations as a species distinct from *S. leucops*.

Stenostomum uronephrium Nuttycombe, 1931 (Fig. 3E)
Description: Individuals of 1–4 zooids. Two-zooid chains 0.8–0.9 mm long, up to 1.8 mm in the Brazilian forms. Body cylindrical, ventrally flattened, gradually tapering. Anterior end blunt. Small, rounded, antero-lateral ciliated pits. Posterior end with a long

intestine-lacking tail (1/3–1/2 of the total body length). Long, semi-rigid cilia concentrated at both ends of the body. Vacuolar epidermal cells, with rhabdites. Colour in life whitish. Some of the studied individuals with anastomosed pigment accumulations.

Anterior brain lobes smooth. A pair of light-refracting bodies at mouth level, with few spheres in a vesicle (type 2), associated with the posterior brain lobes.

Subapical oral pore, generally with circular outline. Tubular pharynx, with small glands (type a) uniformly distributed on the pharynx. Sphincter between the pharynx and intestine. Presence of excretophores. The protonephridium becomes sinuous at the caudal end. Nephridiopore terminal.

Distribution: Georgia, USA (Nuttycombe, 1931; Kolasa, 1991); São Paulo and São Paulo State, Brazil (Marcus, 1945b); Poland (Kolasa, 1977); Finland, Russia, Germany (Lanfranchi & Papi, 1978); Paraná River, Argentina (Noreña-Janssen, 1995); Los Talas, Berisso, Buenos Aires, Argentina, April 1999, January and February 2000.

Discussion: In contrast to the observations for South American specimens, Nuttycombe (1931) does not mention the presence of a sphincter between the pharynx and the intestine.

Stenostomum virginianum Nuttycombe, 1931 (Fig. 3F)
Stenostomum carnivorum Jones, 1932

Description: Individuals with 1–4 zooids up to 5 mm long, solitary individuals 0.4–1 mm long. Mobile tapering anterior end. Small, rounded ciliated pits lateral or latero-ventrally placed. Truncate caudal end without intestine-lacking region. Vacuolar epidermic cells and short rhabdites. Long semi-rigid cilia concentrated in the anterior and posterior ends of the body. Vacuolar epidermal cells. Colour in life whitish.

Anterior brain lobes forming small independent masses ('metameric'). A pair of light-refracting bodies, with fewer than ten spheres (type 2), associated with an extension of the posterior brain lobes.

Small rounded oral pore. Long tubular pharynx (1/4 body length) with isolated pharyngeal glands (type a) distributed along the entire pharynx. Excretophores regularly arranged in two lateral bands, or irregularly in the North American specimens. Nephridiopore subterminal.

Distribution: Virginia (Nuttycombe, 1931; Nuttycombe & Waters, 1938), Georgia, North Carolina (Nuttycombe & Waters, 1938; Kolasa, 1991), USA; Nova Scotia, Canada (Jones, 1932); São Paulo State and Paraná State, Brazil (Marcus, 1945b); Los Talas, Berisso, Buenos Aires, Argentina, July 1999. This species has not been previously recorded in Argentina.

Stored material: One sagittally sectioned specimen in the CHMLP No. 5307.

Discussion: Marcus (1945b) and Luther (1960) refer to the similarity between this species and *Stenostomum unicolor* O. Schmidt, 1848.

The largest sized specimens correspond to those mentioned by Marcus (1945b).

South American species of *Anokkostenostomum* gen. nov.

Anokkostenostomum anatirostrum (Marcus, 1945) **comb. nov.** (Fig. 4A)
Stenostomum anatirostrum Marcus, 1945
Stenostomum bryophilum Luther, 1960

Description: Adult specimens 0.2–0.75 mm long. Chains with two zooids (0.5–1 mm) or six zooids (2.5 mm). Anterior end generally rounded, spatulate or sharply arched with 'anatiform' aspect. Constriction before the pharynx. Posterior end rounded. The intestine reaches the caudal body region. Epithelium with short uniform cilia and rigid sensory cilia scattered on the body surface, more numerous in the anterior region. Rhabdites regularly distributed in the adult specimens; but in immature individuals only visible in the ciliated pits. Lateral and broad ciliated pits. Colour in life whitish.

Anterior brain lobes formed by small independent masses ('metamerics'). No light-refracting bodies.

Oral pore oval, frequently surrounded by radial or longitudinal muscular bundles. Pharynx 1.5–2 times longer than it is wide. Presence of conspicuous transverse muscular bundles. Elongated pharyngeal glands (type b) placed on both sides of the pharynx, grouped in clusters and opening into a simple duct. Immature individuals without pharyngeal glands. Presence of excretophores. Protonephridium slightly sinuous, nephridiopore terminal.

Distribution: São Paulo, Brazil (Marcus, 1945b); Tvaerminne, Finland (Luther, 1960); Sabakoekreek, Surinam (Van der Land, 1970); Cheshire and Yorkshire, England; near Poznan, Poland, and south of Mombasa, Kenya (Kolasa & Young, 1974a); France (Lanfranchi & Papi, 1978); Fosso Contesora, Italy (Kolasa, 1983); south-eastern New York State, USA (Kolasa *et al*., 1987; Kolasa, 1991).

Anokkostenostomum corderoi (Marcus, 1945) **comb. nov.** (Fig. 4B)
Stenostomum corderoi Marcus, 1945

Description: Solitary individuals, 0.4–0.8 mm long. Two-zooid chains (1.2 mm) to four-zooid chains (2 mm). Body cylindrical, anterior end blunt. Body

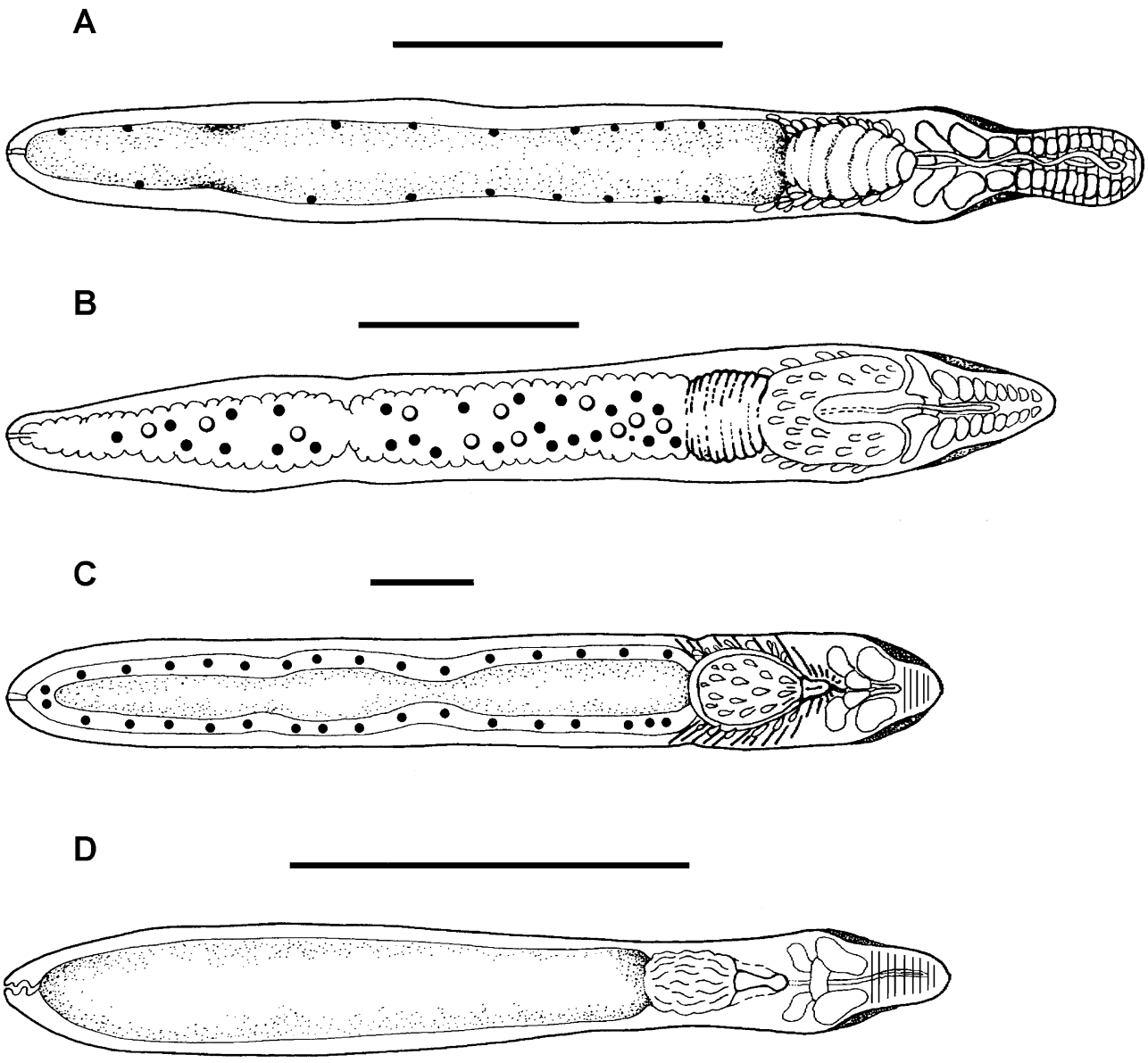

Figure 4. A, *Anokkostenostomum anatirostrum*. B, *A. corderoi*. C, *A. eveline*. D, *A. membrenosum*. Scale bars = 200 μm.

widening at the level of the oral pore; post-buccal narrowing. Posterior end rounded. The intestine reaches the caudal body region. Small, dorso-lateral ciliated pits; occasionally with creases which make them appear larger. Ciliated epithelium with long semi-rigid sensory cilia, concentrated especially on the anterior body. The rhabdites are arranged in longitudinal grooves. Live specimens transparent.

Large brain ganglia. Anterior brain lobes separated into small independent masses ('metamerics'). Posterior lobes with pharyngeal internal and external nerves. No light-refracting bodies.

Oral pore wide, V-shaped, extending to the middle of the pharynx. Pharynx very voluminous (1/3–1/2 of the body length), differentiated into oral (2/3 of its length) and oesophageal regions. A strong sphincter separating the oesophageal region from the intestine. Oral region of the pharynx with scattered large glands (type a) on the musculature. The pharynx is covered by a refringent membrane that broadens at the edges of the mouth. The inner pharyngeal membrane is folded in a zigzag manner in the posterior third of the pharynx (oesophageal region). Intestine with a numerous lateral excretophores, regularly arranged. Nephridiopore terminal.

Distribution: São Paulo, Brazil (Marcus, 1945b); France (de Beauchamp 1948).

Anokkostenostomum evelinae (Marcus, 1945) **comb. nov.** (Fig. 4C)

Stenostomum evelinae Marcus, 1945

Description: Length of simple specimens, 1.2 mm. Two-zooid chains 2 mm long. Body compact, dorsoventrally flattened. Anterior end rounded. Short lateral ciliated pits placed near the apical end of the body. Posterior end gradually tapering. Ciliated epithelium with long sensory cilia, concentrated mainly in the anterior and posterior ends. Small rhabdites. Colour white, with yellow intestine in live specimens.

Short, compact brain ganglia. Solid anterior lobes and reduced posterior lobes. No light-refracting bodies.

Small oral pore, longer than it is wide, its posterior end widening. Presence of radial musculature. Large, wide pharynx. Well-developed circular and parietal pharyngeal musculature. Strong pharyngeal sphincter. Well-developed pharyngeal glands (type a) in the anterior region. Presence of a caecum dorsal to the pharynx. Lateral excretophores, irregularly arranged in the anterior region, and posteriorly regular. Nephridiopore terminal.

Distribution: São Paulo, Brazil (Marcus, 1945b); near Paramaibo, Surinam (Van der Land, 1970).

Anokkostenostomum membranosum (Kepner & Carter, 1931) **comb. nov.** (Fig. 4D)

Stenostomum membranosum Kepner & Carter, 1931

Description: Solitary individuals, 0.5 mm long. Two-zooid chains. Fusiform body with tapering ends. The intestine reaches the caudal region of the body. Reduced lateral ciliated pits. No rhabdites. Homogeneous ciliated epithelium, without sensory cilia. Well-developed cilia in the ciliated pits. Specimens colourless in life.

Anterior brain lobes larger than the posterior lobes. No light-refracting bodies.

Oral pore axially elongated. Fibrous pharynx. Conspicuous lip sphincter. No pharyngeal glands. No excretophores. Nephridiopore terminal.

Distribution: Virginia, USA (Kepner & Carter, 1931); São Paulo, Brazil (Marcus, 1945b).

Anokkostenostomum pegephilum (Nuttycombe & Waters, 1938) **comb. nov.** (Fig. 5A)

Stenostomum pegephilum Nuttycombe & Waters, 1938

Description: Solitary specimens: 0.26 mm long. Chains with two zooids (0.8 mm) up to 5–6 zooids (2 mm). Slight ventral flattening. Anterior end narrowing abruptly. Apical zone blunt. Long ciliated pits. Intestine-lacking region at the posterior end. Conspicuous ciliated epithelium. Irregularly arranged sensory cilia, more abundant in the anterior end. Epidermis with small rhabdites. Colour in life whitish.

The anterior brain lobes form independent masses ('metameric'). No light-refracting bodies.

Oral pore transverse. Pharynx short, with radial musculature and small rounded glands (type a), which open onto its entire surface. A muscular sphincter separating the pharynx from the intestine. Irregularly arranged excretophores. Conspicuous sinuous protonephridium. Nephridiopore terminal.

Distribution: Mountain Lake, Virginia, USA (Nuttycombe & Waters, 1938); Tieté River, São Paulo, Brazil (Marcus, 1945b); Germany, Poland (Lanfranchi & Papi, 1978); Fosso Contesora, Italy (Kolasa, 1983); south of New York State, USA (Kolasa *et al*., 1987; Kolasa, 1991).

Anokkostenostomum pseudoacetabulum (Nuttycombe & Waters, 1935) **comb. nov.** (Fig. 5B)

Stenostomum stuhlmanni Böhmig, 1897

S. pseudoacetabulum Nuttycombe & Waters, 1935

Description: Adult individuals 0.75–2.5 mm long. Two- to eight-zooid chains. Anterior region elongated. Reduced lateral ciliated pits. Body cylindrical, with a constriction before the mouth and sometimes another constriction at the level of the pharyngeal sphincter. Body tapering caudally. Intestine-lacking region at the posterior end that becomes thinner, forming a typical dorsal appendage. The ciliated epidermis forms a regular cover, except at the posterior end where cilia are scarce. Longer sensory cilia in the posterior region. Epidermis with regular vacuoles and short rhabdites. Colour in life yellowish-white.

The anterior brain lobes differentiate into small independent masses ('metameric'). No light-refracting bodies.

Oral pore and pharynx resemble a trematode acetabulum, appearing as a body projection in lateral view. The pharynx is posteriorly expanded and forms a cup onto the apical end of the intestine. The mouth and first third of the pharynx can be invaginated, proboscis-like. The pharyngeal glands are uniform (type a) in the whole pharynx. A sphincter between pharynx and intestine. No excretophores. Nephridiopore at the base of the caudal appendage.

Distribution: Georgia, USA (Nuttycombe & Waters, 1935, 1938; Kolasa, 1991); São Paulo and Paraná State, Brazil (Marcus, 1945b); near Paramaribo, Surinam (Van Der Land, 1970); Konin Lakes, Poland (Kolasa, 1977); Germany (Lanfranchi & Papi, 1978); Los Talas, Berisso, Buenos Aires, Argentina, February 1999 and February 2000. This species has not been previously recorded in Argentina.

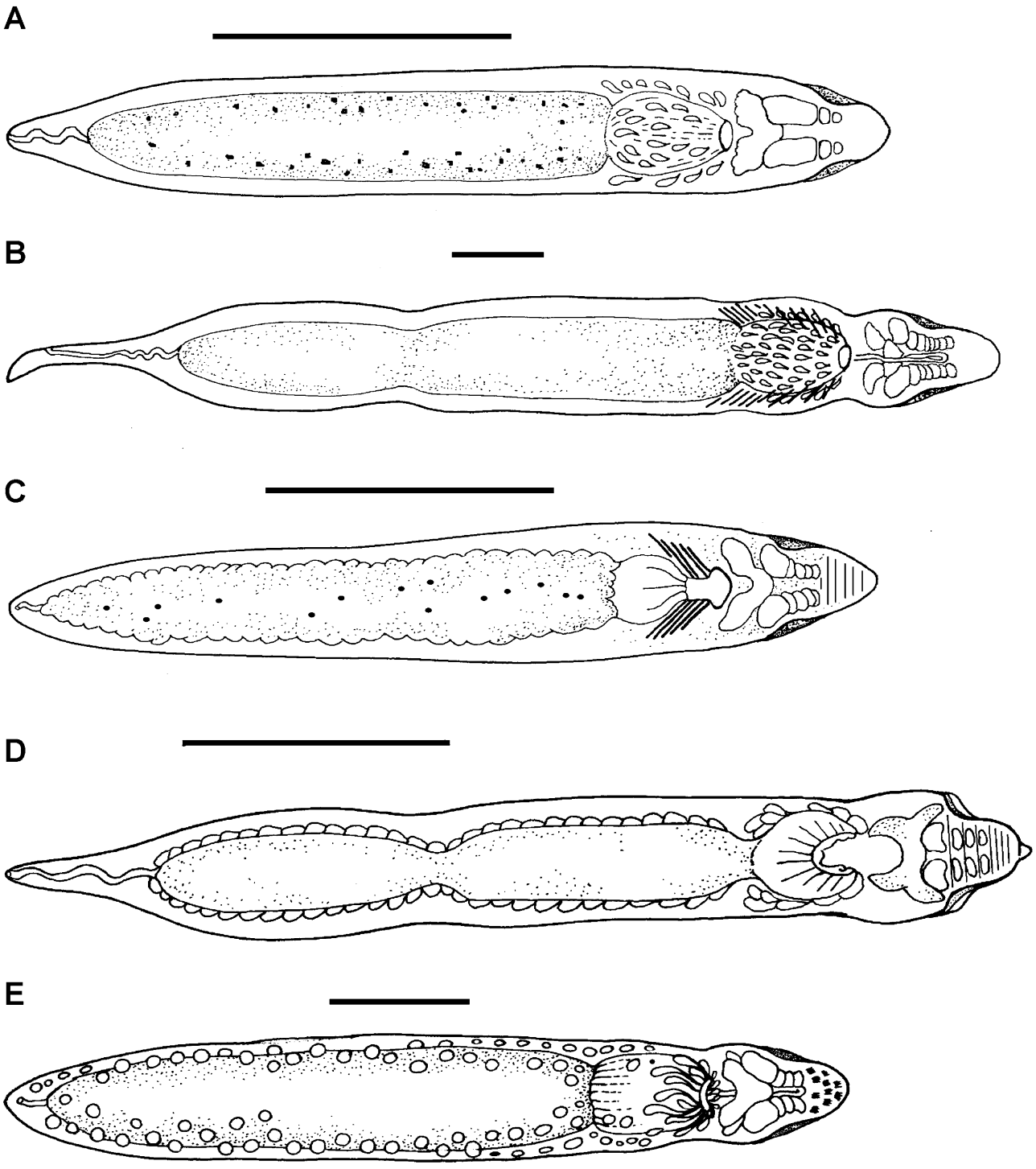

Figure 5. A, *Anokkostenostomum pegephilum*. B, *A. pseudoacetabulum*. C, *A. saliens*. D, *A. tuberculosum*. E, *A. ventronephrium*. Scale bars = 100 μm.

Anokkostenostomum saliens (Kepner & Carter, 1931) **comb. nov.** (Fig. 5C)

Stenostomum saltatum Kepner & Carter, 1931
S. saliens Kepner & Carter, 1931

Description: Solitary individuals 0.15–0.62 mm long. Two- (0.29 mm) or three- (0.54 mm) zooid chains. Anterior and posterior ends noticeably tapering. The intestine reaches the posterior end of body. Small, lateral ciliated pits. Dense ciliated epidermis, long cilia. Thin and rigid longer sensory cilia, irregularly arranged on the whole body. Uniform rhabdites. Yellowish-white colour in life.

Elongated anterior brain lobes, differentiated into small independent masses ('metameric'); posterior ones voluminous. No light-refracting bodies.

Oral pore large. Two mobile projections at the posterior region of the oral pore. Pharynx somewhat longer than the mouth. Intestine with lobulated edges, ending near the posterior end. No pharyngeal glands. No excretophores. Nephridiopore ventral and terminal.

Distribution: Virginia (Kepner & Carter, 1931; Nuttycombe & Waters, 1938) and Georgia (Nuttycombe & Waters, 1938), USA; São Paulo, interior of São Paulo State and Paraná State, Brazil (Marcus, 1945b); near Paramaribo and near Zanderij, Surinam (Van Der Land, 1970); Poznan, Poland (Kolasa, 1973); Los Talas, Berisso, Buenos Aires, Argentina, October 1998, February to March and June to September 1999. This species has not been previously recorded in Argentina.

Discussion: The length of the solitary individuals found by Kepner & Carter (1931) in the USA (0.62 mm) is slightly greater than that recorded for the South American specimens (0.15–0.4 mm).

Anokkostenostomum tuberculosum (Nuttycombe & Waters, 1938) **comb. nov.** (Fig. 5D)

Stenostomum tuberculosum Nuttycombe & Waters, 1938

Description: Chains with two zooids 0.72 mm long. Neither solitary individuals nor longer chains were observed. Anterior end blunt. A small, apparently tactile, tubercle in the ventral cephalic end is characteristic of this species. Small, antero-dorsal ciliated pits. Constriction posterior to the ciliated pits. Intestine-lacking region at the posterior end. Densely ciliated ventral epithelium (long cilia). The cilia on the dorsal epithelium are inconspicuous. Semi-rigid sensory cilia irregularly arranged along body. Slender rhabdites. Live specimens yellowish-white, darker at the pharyngeal region because of the presence of glands and musculature. Anterior brain lobes divided into small independent masses ('metameric'). No light-refracting bodies.

Oral pore V-shaped. Short muscular pharynx associated with elongated unicellular glands (type b), which open onto the whole length of the pharynx. Pharynx with refractory corpuscles. Anterior end of the intestine overlying the posterior part of the pharynx. Intestinal wall dentate. No excretophores. Nephridiopore terminal.

Distribution: Virginia and Georgia, USA (Nuttycombe & Waters, 1938; Kolasa, 1991); São Paulo and interior of São Paulo State (Marcus, 1945b), Brazil; margins of the Suriname River near Paramaribo, Surinam (Van Der Land, 1970); Poznan, Poland (Kolasa, 1973); Germany, Finland (Lanfranchi & Papi, 1978); Los Talas, Berisso, Buenos Aires, Argentina, January and April 1999. This species has not been previously recorded in Argentina.

Discussion: Unlike the material found in Argentina, Marcus (1945b) describes chains of up to four zooids (1 mm) for Brazilian specimens. The South American specimens show refractory corpuscles in the pharynx. This feature was not mentioned by Nuttycombe & Waters (1938).

Anokkostenostomum ventronephrium (Nuttycombe, 1932) **comb. nov.** (Fig. 5E)

Stenostomum ventronephrium Nuttycombe, 1932

Description: Single individuals, 0.5–0.8 mm long. Three-zooid chains, 2 mm long. Anterior end spatulate. Long lateral ciliated pits. Posterior end without an intestine-lacking region, ending bluntly, no tail. Body uniformly covered with cilia. Semi-rigid cilia, more abundant at both body ends. With epidermal rhabdites. With groups of 10–15 conspicuous rhabdites at the anterior body end. These rhabdites are produced at glands situated latero-dorsally to the pharynx, which have four tracts (two dorsal and two lateral) through which the rhabdites migrate. Whitish, reddish or colourless in life. Brain ganglia with well-developed transverse commissure. No light-refracting bodies.

Oral pore circular, surrounded by muscles. Long, wide, muscular and densely ciliated pharynx. Granular pharyngeal glands (type b), placed mainly ventrally and opening at mouth level. Dorsal wall of the intestine overlying the pharynx. No excretophores. The protonephridium runs dorsal to the pharynx, loops towards the left and continues ventrally or ventro-laterally to the intestine. Nephridiopore subterminal.

Distribution: Virginia, USA (Nuttycombe, 1932b; Kolasa, 1991); Tieté River, São Paulo, Brazil (Marcus, 1945a); Italy (Kolasa, 1983).

Discussion: Differences between the South and North American specimens are: absence of tail and presence of rhabdite-forming glands in the South American specimens (Nuttycombe, 1932b; Marcus, 1945a).

KEY TO THE SOUTH AMERICAN SPECIES OF THE GENERA *STENOSTOMUM* AND ***ANOKKOSTENOSTOMUM***

1. With light-refracting bodies ..... Genus *Stenostomum* 2
   Without light-refracting bodies ..... Genus ***Anokkostenostomum*** 15
2. Light-refracting bodies type 1 (disc shaped with more than ten small spheres) 3
   Light-refracting bodies type 2 (bowl shaped with one to five spheres). 7
   Light-refracting bodies type 3 (single-granule bodies, with no vesicle) ..... *S. simplex*
3. Pharyngeal glands type a (small rounded glands) 4
   Pharyngeal glands types a and b (rounded and club shaped) 6
4. Pharyngeal glands uniformly arranged in the whole pharynx ..... *S. tenuicauda*
   Pharyngeal glands only in the anterior half of the pharynx 5
5. With sphincter between pharynx and intestine, oral pore circular ..... *S. grande*
   Without a sphincter between pharynx and intestine, oral pore triangular ..... *S. matarazzoi*
6. Without a sphincter between pharynx and intestine, opening of pharyngeal glands along the whole pharynx ..... *S. leucops*
   With a sphincter between pharynx and intestine, opening of the pharyngeal glands at the anterior half of the pharynx, internal cerebral lobes associated with the posterior cerebral lobes ..... *S. amphotum*
7. One pair of light-refracting bodies. No caecum dorsal to the pharynx 8
   More than one pair of light-refracting bodies. No caecum dorsal to the pharynx 12
   One or more pairs of light-refracting bodies. Intestinal caecum dorsal to the pharynx ..... *S. cryptops*
8. Posterior end with no intestine-lacking zone 9
   Posterior end with intestine-lacking zone 10
9. Pharyngeal glands type a (small rounded), opening uniformly onto the whole pharynx ..... *S. virginianum*
   Pharyngeal glands type b (club shaped), opening at the transition between mouth and pharynx ..... *S. hemisphericum*
10. Distal end of the protonephridium straight, and subterminal nephridiopore. ..... *S. ciliatum*
    Distal end of the protonephridium sinuous and terminal nephridiopore. 11
11. First part of the intestine with high vacuolated cells, separated from the gut by a strong constriction ..... *S. rosulatum*
    Without vacuolated cells in the gut, pharynx glands type b (club shaped) ..... *S. uronephrium*
12. Light-refracting bodies associated only with the anterior brain lobes 13
    Light-refracting bodies associated with both anterior and posterior brain lobes 14
13. Posterior end with intestine-lacking zone. Tail with two appendages. With tentacular pharyngeal organ ('claw-organ') ..... *S. bicaudatum*
    Posterior end with no intestine-lacking zone. Epidermis with groups of refractive corpuscles ..... *S. glandulosum*
14. Tail simple (one appendage) ..... *S. arevaloi*
    Tail double (two appendages) ..... *S. paraguayense*
15. Posterior end with intestine-lacking zone, with simple tail. 16
    Posterior end with no intestine-lacking zone 18
16. Tail very long forming a dorsal appendage. Nephridiopore subterminal ..... *A. pseudoacetabulum*
    Tail short. Nephridiopore terminal 17
17. Excretophores absent. Type b (club-shaped) pharyngeal glands No sphincter between pharynx and intestine ..... *A. tuberculosum*
    Excretophores present. Type a (rounded) pharyngeal glands. With sphincter between pharynx and intestine ..... *A. pegephilum*
18. With excretophores 19
    Without excretophores ..... *A. ventronephrium*
19. Smooth anterior cerebral lobe. Intestinal caecum dorsal to the pharynx ..... *A. evelinae*
    Anterior cerebral lobe with small independent masses 20
20. Anterior end 'anatiform' ..... *A. anatirostrum*
    Anterior end not 'anatiform'. Pharyngeal glands in the anterior region only ..... *A. corderoi*

DISCUSSION

The family Stenostomidae is characterized mainly by the presence of pre-oral rows of sensory cells and a ventro-lateral furrow anterior to the oral pore. In spite of the fact that this family includes morphologically simple catenulids, a great diversity of forms is recognized. The genera *Myostenostomum* and *Rhynchoscolex* include few easily identifiable species. Within the family Stenostomidae, only *Myostenostomum* presents a third muscular layer, which attaches the digestive tube to the body wall. This genus is also characterized by the presence of a strongly muscular intestinal region. *Rhynchoscolex* is characterized by the lack of ciliated pits and the typical anterior end with proboscidean aspect. The monotypic genus *Xenostenostomum* is recognized by the presence of a pair of evaginable and specialized ciliated pits. By contrast, *Stenostomum* includes numerous (approximately 50) species. In many cases, the lack of complete descriptions adds to the inherent simplicity of the species in this genus and hinders species recognition. However, a detailed analysis of the morphological characteristics allows species discrimination. A kinship analysis carried out on the 25 species of *Stenostomum* found in South America to date (our unpubl. data) has shown that there are two clearly delimited species groups within the genus *Stenostomum*. One group is characterized by the presence of light-refracting bodies and paired anterior brain lobes, with smooth or deeply dentate inner/interior surface, and the second group by the lack of light-refracting bodies and the possession of anterior brain lobes that form small separate masses, showing a 'metameric' aspect (with exceptions, e.g. *Anokkostenostomum evelinae*). This last characteristic is also present in species of genera *Rhynchoscolex* and *Myostenostomum*.

This situation, added to the unique combination of other morphological characters, leads us to propose the new genus *Anokkostenostomum* (type species *A. anatirostrum*). The group of *Stenostomum* species characterized by the presence of light-refracting bodies retains its generic assignation (type species *S. leucops*).

The presence and structure of the pharyngeal glands has been greatly discussed with regard to its taxonomic validity. Luther (1960) considers that the morphology of the glands depends of the degree of food ingestion of the specimens. However, from the material studied in the present work, it is considered that the pharyngeal glands of well-developed specimens are constant for each species, thus becoming a character of diagnostic importance. Most of the species of the genera *Stenostomum* and *Anokkostenostomum* have pharyngeal glands, and the type of the glands as well as their arrangement along the pharynx is characteristic for species identification.

Anokkostenostomum saliens and *A. membranosum* lack pharyngeal glands. These two species present few specializations and differ mainly by the presence of a post-ganglial constriction and radial musculature in the pharynx in *A. saliens*.

The genera belonging to the family Stenostomidae are closely related and share an exclusive combination of characters, including the presence of a brain formed by paired lobulated ganglia, the post-oral position of the genital pore and, generally, asexual reproduction by paratomy. *Anokkostenostomum* seems closely related to the genera *Myostenostomum* and *Rhynchoscolex*, with which it shares the absence of light-refracting bodies and the development of anterior brain lobes of the 'metameric' type. It is related to *Stenostomum* and *Xenostenostomum* mainly by the presence of ciliated pits.

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