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Smithsoniarhynches, a new genus of interstitial Gnathorhynchidae (Platyhelminthes: Kalyptorhynchia) from Mosquito Lagoon and Indian River Lagoon, Florida

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A new genus of marine, interstitial schizorhynch (Platyhelminthes: Kalyptorhynchia) is described from sediment collected in Mosquito Lagoon and Indian River Lagoon, Florida, USA. *Smithsoniarhynches* is characterized by the presence of proboscis hooks constructed of ten individual spine-like teeth that emerge separately from a basal plate. Histology and confocal laser scanning microscopy are used to reveal additional details of the proboscis musculature and reproductive anatomy. The type species, *Smithsoniarhynches sherryreedae* sp. nov., is characterized by well-developed proboscis pads, four pairs of proboscis retractor muscles, and a pharynx in the midbody region. The male reproductive system consists of an anterior testis, muscular seminal vesicle, copulatory bulb lined with spiral and circular muscles, and a sclerotic stylet. The female system consists of an unpaired vitellarium, ovary, uterus and bursa. The bursa tissue surrounds a muscular bursa seminalis with distinct sphincter muscles. The new genus is compared with the known 11 genera within the Gnathorhynchidae to establish a tentative hypothesis of relationships.

INTRODUCTION

Kalyptorhynchia is a species-rich taxon of microscopic, free-living platyhelminthes that occupy the sediments of salt marshes, sand flats and low- and high-energy beaches. Most species live within the interstitial pore spaces that characterize these sedimentary environments and are thus a general component of the meiofauna. Kalyptorhynchs can reach high abundances and species diversity in both temperate (Reise, 1988) and tropical sands (Dittmann, 1998).

As interstitial predators, kalyptorhynchs feed on other micrometazoa. Prey capture is a function of their terminal proboscis, an anterior, eversible muscular bulb that is anatomically separate from their mouth and pharynx but serves to hold and immobilize prey prior to ingestion. The structure of the proboscis has systematic value and can be used to differentiate between the two major clades of Kalyptorhynchia: Eukalyptorhynchia Meixner, 1928 and Schizorhynchia Meixner, 1928. In the eukalyptorhynchs, the muscular proboscis is a single cone-like organ, while in the schizorhynchs, the proboscis is dorsoventrally split into two equal halves or lips. In both groups, the proboscis may be naked (i.e. without any noticeable structures) or bear various papillae or hooks. Within the Eukalyptorhynchia, sclerotic elaborations such as proboscis hooks are produced as intracellular specializations within the proboscis epithelium, whereas in Schizorhynchia, sclerotic hooks are derivatives of the basal lamina (Rieger & Doe, 1975; Doe, 1976). In the eukalyptorhynch taxon, Gnathorhynchidae, the proboscis hooks come in a variety of shapes and sizes, but are generally present as spine-like teeth protruding from a single basal plate. The structure of the hooks is likely to reflect different prey specializations. At the taxonomic level, proboscis hooks are diagnostic of certain genera and species, and along with characters of the reproductive system, have been used to distinguish the currently recognized 11 genera and greater than 30 species within the family (Tyler & Bush, 2003). In this study, a new genus of Gnathorhynchidae is described from a tidal flat in Mosquito Lagoon and from dredged sediment in the Indian River Lagoon, Florida.

MATERIALS AND METHODS

Kalyptorhynchs were collected from 0.5 m depth in Mosquito Lagoon, eastern Florida (28°52′N 80°50′W) on 19 February, 2004. Sediment samples were collected by hand and placed into small containers. An additional specimen was found by dredge collection at 2.9 m depth at the 50′ mid-channel range marker of Fort Pierce Inlet (27°28.12′N 80°19.13′W) in the Indian River Lagoon, Florida on 10 March, 2004. Animals were extracted from the sediment using magnesium chloride isotonic to seawater. All animals were initially observed alive as wholemounts prior to histological and fluorescent analysis. For comparison, specimens of *Drepanorhynchides hastatus* were collected from Fort Meyers beach in western Florida on the Gulf of Mexico (26°27′N 82°0′W).

Specimens were processed for histology using the following protocol: fix in 2.5% glutaraldehyde in 0.1 M phosphate-buffered sodium (PBS) for 24 h, rinse in PBS for 1 h, postfix in 1% OsO_4 in 0.1 M PBS for 1 h, rinse 1 h in PBS, dehydrate in standard ethanol series, transfer through propylene oxide to a mixture of Epon–Araldite. Resin blocks were sectioned at 1.5 microns using glass knives, affixed to glass slides, and contrasted with Richardson's stain at 60°C.

The structure of the proboscis and positions of muscular reproductive organs were determined by whole-mount muscle staining with Alexa Fluor 488 phalloidin

(Molecular Probes, Eugene, OR, USA). Kalyptorhynchs were first relaxed for 10 min in 7.5% magnesium chloride solution prior to fixation in 5% formaldehyde in 0.1 M PBS (1 h). Kalyptorhynchs were next rinsed in 0.1 M PBS for 1 h, permeabilized for 1 h in 0.2% Triton X-100 in PBS, stained 1 h with Alexa Fluor 488 phalloidin and rinsed in PBS before mounting with Gel/Mount (Biomeda Corp.). Specimens were examined using a CLSM on a Nikon Eclipse E800 compound microscope equipped with a Biorad Radiance 2000 laser system. Series of 0.05 μm optical z-projections were made using Confocal Assistant version 4.02.

Type and voucher specimens of all examined species are deposited in the National Museum of Natural History, Smithsonian Institution.

SYSTEMATICS

KALYPTORHYNCHIA Graff, 1905
EUKALYPTORHYNCHIA Meixner, 1928
GNATHORHYNCHIDAE Meixner, 1929
Genus *Smithsoniarhynches* gen. nov.

Type species

Smithsoniarhynches sherryreedae sp. nov.

Etymology

The generic name is constructed from *Smithsonia*, a dedication to the research staff at the Smithsonian Marine Station at Fort Pierce, combined with the Greek suffix *rhynches* (*rhynchus*=snout), used in reference to the everscible proboscis. The gender is feminine.

Description

Gnathorhynchidae with paired proboscis hooks consisting of ten individual spine-like teeth protruding from a single basal plate with lateral flanges. Anterior tegumentary retractors and four pairs of proboscis retractors present. Paired pigmented eyespots. Pharynx rosulatus at approximately 60% body length. No adhesive girdles.

Male reproductive system consists of an unpaired, anterior testis and single large seminal vesicle in posterior body region. Seminal vesicle lined with longitudinal muscles only. Muscular copulatory bulb containing prostatic fascicles and surrounded by two muscle coats, inner circular muscles and outer spiral muscles. A muscular ductus ejaculatorius proceeds axially through the copulatory bulb. A funnel-shaped sclerotic stylet is present. Genital pore is ventral and subterminal. Female system consists of a muscular female genital canal (ductus uterocommunis) that gives rise to a short uterus and elongate bursa seminalis. Uterus and bursa are lined with longitudinal muscles. Unpaired vitellarium and ovary present.

Smithsoniarhynches sherryreedae sp. nov.
Figures 1–6

Material examined

Twelve specimens examined in total from Mosquito Lagoon, FL (28°52′N 80°50′W): six specimens examined alive as wholemounts, four specimens examined as fluorescent wholemounts stained for F-actin, and two specimens sectioned. One live specimen examined from Fort Pierce Inlet in the Indian River Lagoon, FL (27°28.12′N 80°19.13′W). Holotype is a wholemount mature specimen from Mosquito Lagoon, mounted in resin on a glass slide (USNM 1026575). Two paratypes are mature wholemount specimens in resin on glass slides; one from Mosquito Lagoon (USNM 1026575) and one from Indian River Lagoon (USNM 1026577). A fourth paratype of a Mosquito Lagoon specimen is sectioned parasagittally (USNM 1026578).

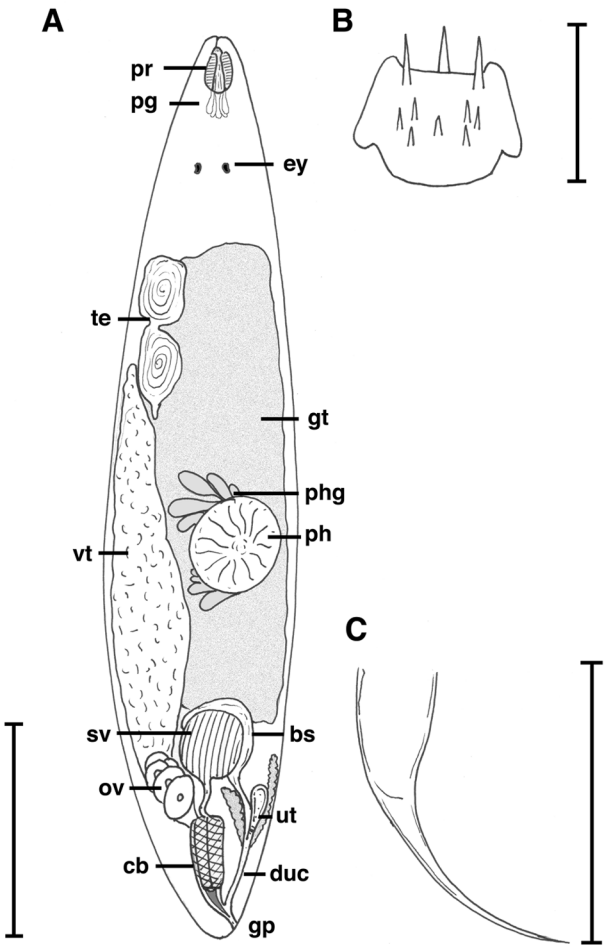

Figure 1. *Smithsoniarhynches sherryreedae* sp. nov., holotype. (A) General organization; (B) copulatory hook; (C) copulatory stylet. bs, bursa seminalis; cb, copulatory bulb; duc, ductus uterocommunis; ey, eyes; gp, common gonopore; gt, gut; ov, ovary; ph, pharynx; phg, pharyngeal glands; pg, proboscis glands; pr, proboscis; sv, seminal vesicle; ut, uterus; vt, vitellarium. Scale bars: A, 250 μm; B, 12 μm; C, 60 μm.

Etymology

The specific epithet, *sherryreedae*, is dedicated to Sherry Reed, Research Assistant at the Smithsonian Marine Station at Fort Pierce, for her gracious assistance in collecting the specimens. The gender is feminine.

Description

Specimens are translucent, slender in outline and range from 700 μm to 960 μm long and 95 μm to 130 μm wide. A pair of large, pigmented eyes, to 10 μm long, is positioned approximately 200 μm from the tip of the head (Figure 1A). Pharynx rosulatus is positioned at approximately 60

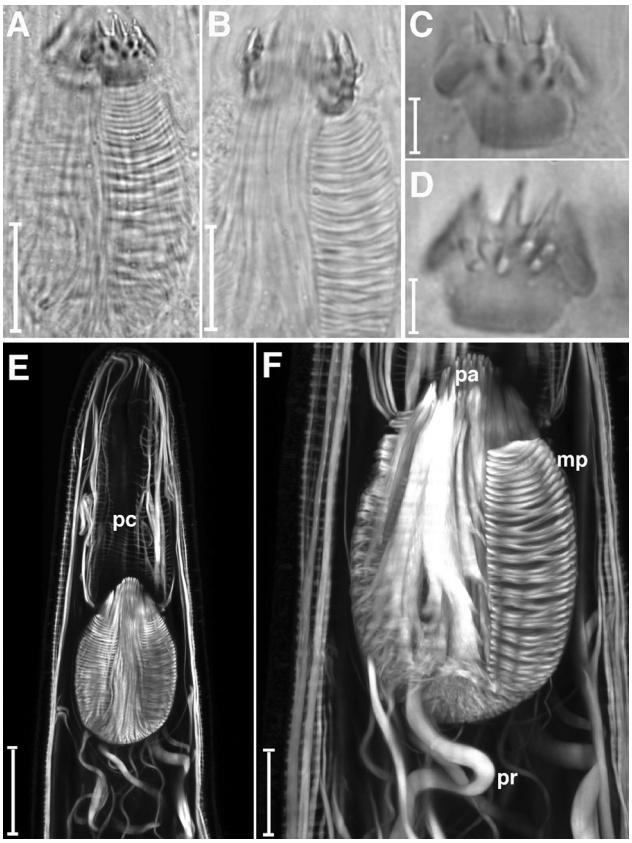

Figure 2. *Smithsoniarhynches sherryreedae* sp. nov. (A) Proboscis of holotype; (B) proboscis of paratype; (C) proboscis hooks of holotype, terminal spines in focus; (D) proboscis hooks of holotype, subterminal spines in focus; (E) z-projection of f-actin stained specimen, anterior end; (F) z-projection of f-actin stained specimen, close-up of proboscis musculature. pa, terminal apex of proboscis; pc, proboscis cavity; pr, proboscis retractor muscles. Scale bars: A,B, 25 μm; C,D, 5 μm; E, 40 μm; F, 15 μm.

per cent body length and up to 75 μm in diameter. Several pharyngeal glands are present. The body wall epidermis is completely ciliated and up to 3 μm high. Cilia are 4–6 μm long. No adhesive girdles are present.

The terminal proboscis cavity, lined with thin circular and longitudinal muscles, is up to 65 μm long and leads posteriorly to an unsplit proboscis (Figure 2E). The proboscis is up to 65 μm long and consists of a terminal apex and sclerotic hooks on paired muscular cones ('Muskelwülste of Meixner' (1929)). The apex and central region of the proboscis consists of longitudinal muscles, some as cone retractors and some as cone protractors (Figure 2F). Longitudinal muscles of the proboscis cavity insert on the proboscis cone musculature. Tegumentary retractors are present. On either side of the terminal apex are circular muscle cells that appear as distinct columns ('bourrelets musculaires de la trompe' of L'Hardy (1966)). At the anterior end of each column is a single sclerotic hook. Each hook consists of a basal plate with lateral flanges and ten individual teeth (Figure 2A–D). In the holotype, the plate is 11 μm long and 15 μm wide, with lateral flanges to 8 μm long, and an 8 μm wide base that contacts the proboscis column (Figure 2A,C,D). Ten teeth protrude from the basal plate. The teeth are present in three sizes with the largest three teeth positioned terminally; the central tooth is 4.5 μm long and flanked by a tooth on either side to 3.5 μm long. Seven smaller teeth, all approximately 2 μm long, are positioned more centrally on the plate body, with two bilateral groups of three teeth surrounding a single tooth. Four pairs of longitudinal retractor muscles attach to the base of the proboscis (Figure 2E,F). Three to five proboscis glands, approximately 30 μm to 40 μm long, are present at the base of the proboscis.

The reproductive system consists of a ventral, subterminal common gonopore that leads into a muscular genital atrium (Figures 3 & 4B). The female reproductive system

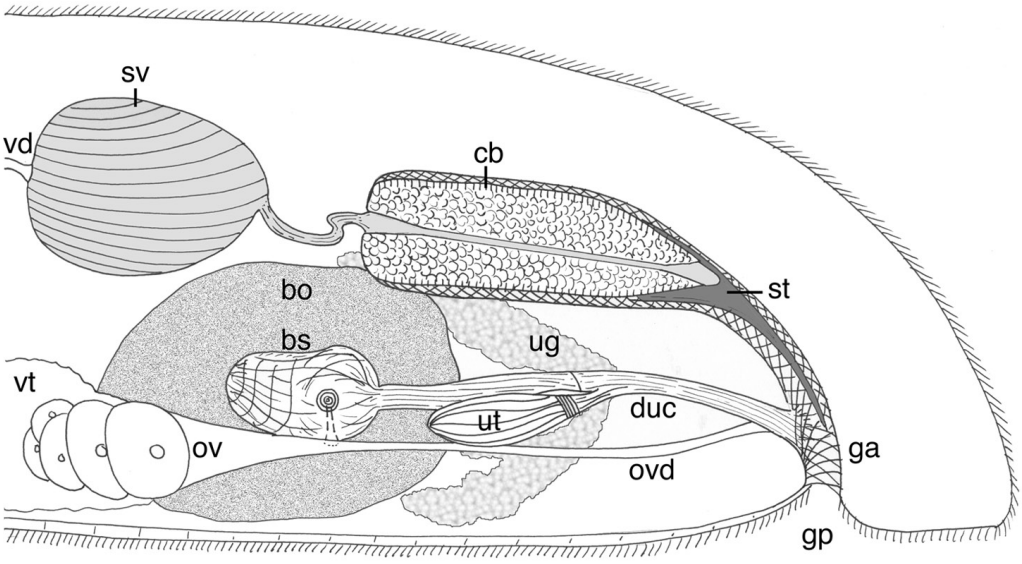

Figure 3. *Smithsoniarhynches sherryreedae* sp. nov., schematic of posterior reproductive organs observed in lateral view. bo, bursal organ tissue; bs, muscular bursa seminalis; cb, copulatory bulb; duc, ductus uterocommunis; ga, genital atrium; gp, common gonopore; ov, ovary; ovd, ovovitelline duct; st, copulatory stylet; sv, seminal vesicle; ug, uterine glands; ut, uterus; vd, vas deferens; vt, vitellarium.

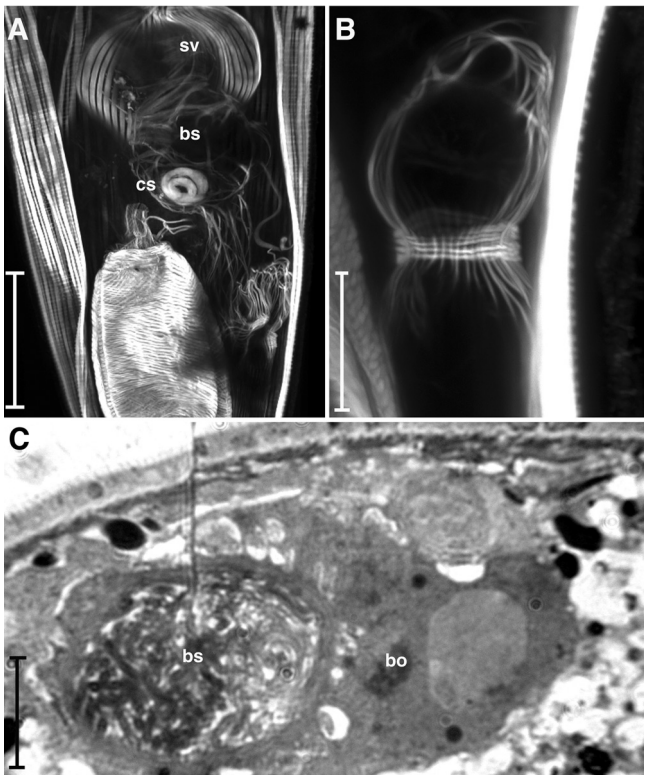

Figure 4. *Smithsoniarhynches sherryreedae* sp. nov., female reproductive system. (A) Z-projection of female reproductive system; (B) z-projection of uterus and sphincter muscles; (C) longitudinal section of bursal organ. bo, bursal organ tissue; bs, muscular bursa seminalis; cs, concentric sphincter muscles of bursal organ.

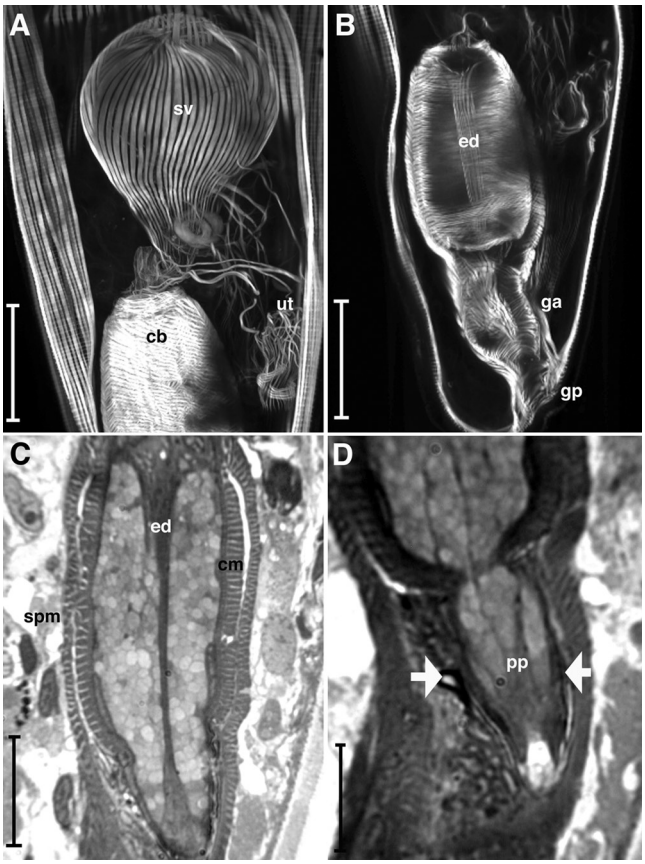

Figure 5. *Smithsoniarhynches sherryreedae* sp. nov., views of male reproductive system. (A) Z-projection of region around seminal vesicle; (B) z-projection of copulatory bulb; (C) longitudinal section of copulatory bulb; (D) longitudinal section of penis papilla projecting into the copulatory stylet. cb, copulatory bulb; cm, inner circular muscle layer of copulatory bulb; ed, ejactulatory duct; ga, genital atrium; gp, genital pore; pp, penis papilla; spm, spiral muscle coat; sv, seminal vesicle; ut, uterus; arrow heads, walls of sclerotic stylet. Scale bars: A, 25 μm; B, 20 μm; C, 10 μm; D, 5 μm.

branches off the base of the atrium as a long female genital canal (ductus utero-communis *sensu* Den Hartog 1968), is 75 μm to 100 μm long, and leads anteriorly to an uterus and bursa seminalis (Figure 3). Both uterus and bursa seminalis are lined with longitudinal muscles (Figure 4A,B). The uterus is a small bag-like structure approximately 18 μm long and demarcated from the female genital canal by five to six sphincter muscles (Figure 4B). No eggs were present in the uterus of any examined individuals. Several glands emanate from the base of the uterus and extend anteriorly (Figures 1A, 3 & 6C). A bursa seminalis branches off the ductus uterocommunis just prior to the uterine sphincters. A single sphincter is present at its base. The bursa is an expansive organ that consists of weakly staining bursal tissue surrounding a muscular extension of the bursal canal (bursa seminalis *sensu stricto*) (Figure 4A,C). The bursa seminalis is a loosely defined muscular bag lined with thin longitudinal muscles and containing sperm (Figure 4A); sperm were present within the bursal tissue outside of the bursa seminalis. A pair of concentric sphincter muscles is present on the lateral side of the bursa seminalis where it approaches the ovovitelline duct (Figure 4A). These muscles were not located in histological sections, but based on location, they appear to demarcate the bursa seminalis from the ovovitelline duct; a short non-muscular canal probably connects the bursa to the ovovitelline duct. Anteriorly, the ovovitelline duct leads to a short ovary and elongate vitellarium, and posteriorly to the genital canal.

The male reproductive system consists of a single, anterior testis that often appears as a pair of testis follicles because of a slight median constriction (Figure 1A). A vas deferens leads posteriorly to an ovoid seminal vesicle, 50 μm to 83 μm in diameter, lined with longitudinal muscles only (Figure 5A). In section, the seminal vesicle was filled with sperm. From the base of the seminal vesicle is a single, muscular spermatic duct that connects to the male copulatory bulb. The copulatory bulb is 58 μm to 73 μm long and 28 μm to 43 μm wide. The bulb is wrapped in an outer coat of crossed spiral muscles that are continuous with most of the genital atrium (Figure 5B,C). Inside the spiral muscle coat is a layer of circular muscles that encloses only the bulb itself. Together, both layers of muscle are approximately 7–9 μm thick. The copulatory bulb is thick-walled and filled with compact spherical tissue (1–2 μm diameter) that stains regularly but poorly (Figure 5C). In some longitudinal sections, the tissue appears to be divided, indicating fascicles (Figure 5D). A straight canal, the ductus ejaculatorius, penetrates the copulatory bulb and connects the spermatic duct to the proximal opening of the copulatory stylet (Figure 5B,C).

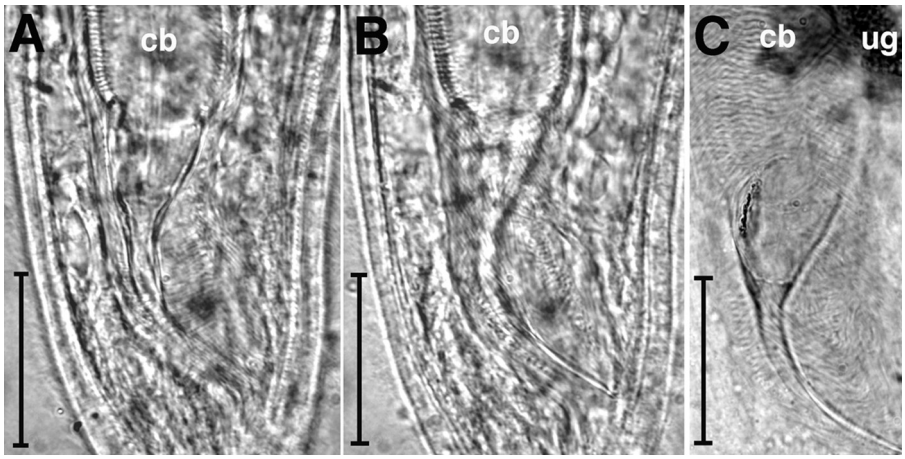

Figure 6. *Smithsoniarhynches sherryreedae* sp. nov., light micrographs of stylets viewable in mounted type specimens. (A) Focus on proximal region of stylet in holotype; (B) focus on distal region of stylet in holotype; (C) stylet of paratype. cb, copulatory bulb; ug, uterine glands. Scale bars: A,B, 30 μm; C, 40 μm.

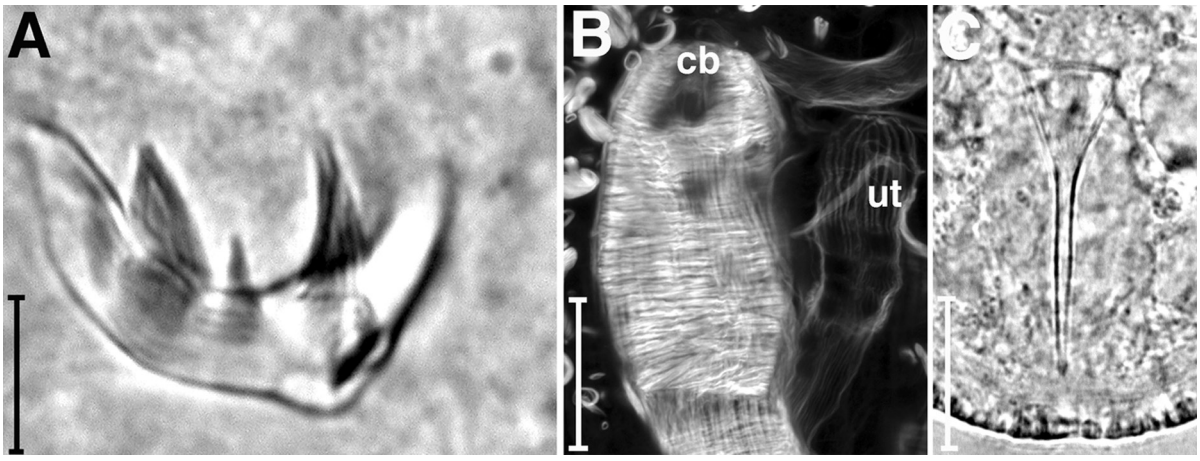

Figure 7. *Drepanorhynchides hastatus* from Fort Pierce, FL, USA. (A) Light micrograph of proboscis hooks showing three terminal spines or teeth; (B) z-projection of f-actin stained specimen, distal portion of copulatory bulb revealing inner circular muscles of bulb and outer longitudinal muscles; (C) copulatory stylet. cb, copulatory bulb; ut, uterus. Scale bars: A, 10 μm; B, 20 μm; C, 25 μm.

Approximately ten longitudinal muscle fibres are present within the canal (Figure 5B). The canal is wide at the proximal end of the bulb, narrows at its centre, and widens again as it approaches the distal end of the bulb where a penis papilla projects into the proximal aperture of a sclerotic stylet (Figure 5D). The stylet is funnel-shaped, to 60 μm long, has a gradual dorsal–ventral curvature, and a proximal opening of 15 μm to 22 μm wide that tapers to 1 μm at its distal tip (Figures 1C & 6A–C). Prostatic secretions, presumably originating from the walls of the copulatory bulb, are present within the proximal opening of the stylet of one individual. There are no prostatic glands outside of the copulatory bulb.

Ecology

Twelve specimens of the new species were collected from a tidal flat in Mosquito Lagoon. The sediment was mixed with coarse and fine sand grains covered with a layer of silt. Fauna included: Oligochaeta and Polychaeta (Annelida), Copepoda and Ostracoda (Arthropoda), *Macrodasys* sp. and *Urodasys* sp. (Gastrotricha), Acoela, Macrostomida and Proseriata (Platyhelminthes), and Nematoda. Various molluscan and crustacean larvae were also present. A single specimen of the new species was collected from Indian River Lagoon. Sediment was mixed with fine silt. Fauna included: Copepoda and Ostracoda (Arthropoda), *Macrodasys* sp. and *Tetranchyroderma* sp. (Gastrotricha), Acoela and Proseriata (Platyhelminthes), Nematoda, and Polychaeta (Annelida).

DISCUSSION

The family Gnathorhynchidae was erected in 1929 by Meixner to unite species of Eukalyptorhynchia with sclerotic hooks on their proboscis. Several species of Schizorhynchia also possess sclerotic hooks, namely species of Karkinorhynchidae and some species of Schizorhynchidae, but the ultrastructural origin of hooks in these species is different from those of Gnathorhynchidae, at least in the few species that have been examined

(Rieger & Doe, 1975; Doe, 1976). To date, there are 11 genera and greater than 30 species of gnathorhynchs known worldwide, though only a few novel species have been described from North America (Ax & Armonies, 1987, 1990; Karling, 1995; Ax, 1997).

Den Hartog (1968) reviewed the characters of Gnathorhynchidae with a particular emphasis on the structure of the proboscis, proboscis hooks and reproductive anatomy, and concluded that considerable variation in characters (e.g. organ topology, hook structure) made it difficult to establish generic relationships, though individual genera are easily defined taxonomically. The new genus, *Smithsoniarhynches*, is distinguished from other gnathorhynchs primarily by the structure of the proboscis hooks. As opposed to the sclerotic hooks of other species, where a single or occasionally two to three spines (e.g. *Orbiculorhynchus luebbeni* Noldt, 1989) emerge from a basal plate, the hooks of *S. sherryreedae* sp. nov. bear ten individual spines that originate separately from the basal plate. The three terminal spines are arranged in a similar fashion to those of *Orbiculorhynchus luebbeni* and might in fact represent the plesiomorphic, multispined condition; three terminal spines are a common condition in species of *Drepanorhynchides* (see Figure 7A), *Odontorhynchus*, and *Prognathorhynchus*. However, the straight, thin shape of the spines differentiates those of *Smithsoniarhynches* gen. nov. from the more broad, curved appearance of most sclerotic teeth in other species. Additional differences exist in the structure of the basal plate. The plate appears flat in several wholemount specimens, but is distinctly arched in live animals, similar to the condition in *Psittacorhynchus verweyi* Den Hartog, 1968. The plate is also rounded-square in shape, with lateral flanges different from the lateral outgrowths of the basal plate in other species.

Four pairs of proboscis retractors arise off the plate-like muscular pads ('Muskelwülste') of *Smithsoniarhynches* gen. nov., a condition present in most other genera including *Ancistrorhynchus*, *Odontorhynchus*, *Orbiculorhynchus*, *Neognathorhynchus*, *Prognathorhynchus* and *Uncinorhynchus*. Tegumentary retractors are also present in most of the these species with the exception of *Ancistrorhynchus*.

Den Hartog (1968) distinguished three general positions of the pharynx within the body of species of Gnathorhynchidae: anterior, middle and posterior. While the position of the pharynx is recognized to vary with body length, it is in general a good diagnostic character, and aligns *Smithsoniarhynches* gen. nov. more closely to species of *Neognathorhynchus* than perhaps any other genus.

The structure of the gnathorhynch reproductive system is relatively constant throughout the family though there is some variation in the structure and general topology of certain organ systems. Concerning the male reproductive system, *Smithsoniarhynches* gen. nov. possesses an anterior testis, similar to the condition in species of *Ancistrorhynchus* and *Drepanorhynchides*; however, as pointed out by Den Hartog (1968), many of these and others species of *Gnathorynchus*, *Uncinorhynchus*, and *Psittacorhynchus* possess a highly elongate testis that extends from in front of to well beyond the length of the pharynx. Posteriorly, a single vas deferens generally leads to a seminal vesicle ('spermaducal vesicle' of Den Hartog) lined with longitudinal muscles; a seminal vesicle is absent in *Psittacorhynchus*. The seminal vesicle of *Smithsoniarhynches* gen. nov. is large and oval, quite different in appearance from the more general elongate seminal vesicle present in most other species.

The structure of the copulatory bulb ('granular bulbus' of Den Hartog) displays some variation throughout the Gnathorhynchidae, in both histological organization and its surrounding musculature. *Smithsoniarhynches* gen. nov. is characterized by a copulatory bulb with an outer coat of spiral muscles that extends from the genital atrium, an inner layer of fine circular muscles restricted to the bulb itself, and an axial ejactulatory duct lined with longitudinal muscles. Interestingly, there do not appear to be any external prostatic glands, but the walls of the bulb may be divided into prostatic fascicles (see Figure 5D). Taken together, this condition appears unique within the family. A muscular coat of outer orthogonal muscles is characteristic of many species, while some species such as *Drepanorhynchides hastatus* (Meixner, 1929) appear to lack circular muscles in the outer layer (though present in the genital atrium, see Figure 7B); spiral muscle coats are also variously known throughout the family, most recently observed in *Oribiculorhynchus lubbeni* by Noldt (1989). Running axially through the copulatory bulb is an ejaculatory duct lined with longitudinal muscles. In several gnathorhynchs, the ejaculatory duct is lined with orthogonal musculature or no musculature at all, and the condition of many species remains undetermined, so the polarity of this character also remains unknown.

External prostatic glands that supply secretions to the copulatory bulb and stylet are well known from several species of Gnathorhynchidae, so it is surprising that similar glands were not present in *Smithsoniarhynches* gen. nov. In most gnathorhynchs, and other kalyptorhynchs, prostatic tissue is generally present as external prostatic glands and/or internal prostatic fascicles. In *S. sherryreedae* sp. nov., prostatic tissue appears to be restricted to internal longitudinal fascicles, though this was not evident in all sectioned material. Secretions were only observed in the stylet of a single live specimen and these were not characterized. Regarding the stylet, its funnel shape is not unique in the family, but similar in structure to species of *Drepanorhynchides* (Figure 7C) and *Neognathorhynchus*.

The female reproductive system of *Smithsoniarhynches* gen. nov. is characteristic of the Gnathorhynchidae, with an unpaired vitellarium, ovary, and uterus. In many gnathorhynchs including the new genus, a ductus uterocommunis (female genital canal) also exists, connecting the genital atrium to the uterus and ovovitelline duct. This duct is present in species with a bursa seminalis such as *Odontorhynchus aculeatus* and species without a bursa such as *Prognathorhynchus dubius* Meixner, 1929. Den Hartog (1968) correctly points out that this character is somewhat variable in distribution, but in general, the ductus uterocommunis is absent from species that lack a bursa seminalis. In *Smithsoniarhynches* gen. nov., the ductus uterocommunis presumably connects indirectly to the bursa seminalis by way of a short canal. The canal is cordoned off from the bursa seminalis by a pair of concentric sphincter muscles on the lateral wall of the bursa. These sphincters may function to control movement of allosperm into the ductus uterocommunis.

Despite a growing knowledge of anatomical characters on gnathorhynchs worldwide, phylogenetic relationships

within the family remain unknown, hindering attempts to define the systematic position of novel species such as *Smithsoniarhynches sherryreedae*. Schockaert (1977) warns that the use of reproductive characters alone to determine phylogenetic relationships may give erroneous results because of convergence in stylet and glandular structures, at least for the Polycystididae. A similar warning may be warranted for the Gnathorhynchidae until such time that homology of these characters, and characters of the proboscis, are evaluated in greater detail (e.g. ultrastructure).

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