Comp. Parasitol.
73(1), 2006, pp. 24–34

Comparative Study of the Tegumental Surface of Several Species of *Gorgoderina* Looss, 1902 (Digenea: Gorgoderidae), as Revealed by Scanning Electron Microscopy

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ABSTRACT: Seven species representing Gorgoderidae Looss, 1899, previously have been examined by scanning electron microscopy. This study describes the papillary pattern on the body surface of 6 additional species—*Gorgoderina attenuata*, *Gorgoderina bilobata*, *Gorgoderina diaster*, *Gorgoderina megalorchis*, *Gorgoderina parvicava*, and *Gorgoderina megacetabularis*—from localities in the United States, Mexico, and Costa Rica. Four types of papillae (button, ciliated, rosette, and domed) were distinguished on the body surfaces of these trematodes and both the type and position of papillae varied among species. A consistent papillary pattern on the ventral forebody region and oral and ventral suckers is described. Three constant pairs of button papillae are around the stylet cavity. The pattern on the oral sucker consists of 10 papillae around the oral aperture. One of these pairs was doubled in *G. bilobata* and *G. diaster*; in addition, a variable number of papillae arranged in groups were usually present. Five pairs of button papillae were always present in a lateral position on the ventral surface of the forebody between both suckers. Six rosette papillae were observed on the ring of the ventral sucker, except in *G. megacetabularis*; 4 additional pairs of rosette papillae and 2 pairs of domed papillae were observed on the internal surface of this sucker. These papillae were not observed in *G. bilobata* and *G. parvicava*. Differences in the papillary pattern among species lie in the position of the different types of papillae.

KEY WORDS: Digenea, Gorgoderidae, *Gorgoderina attenuata*, *Gorgoderina bilobata*, *Gorgoderina diaster*, *Gorgoderina megalorchis*, *Gorgoderina parvicava*, *Gorgoderina megacetabularis*, Mexico, Costa Rica, United States, scanning electron microscopy.

Scanning electron microscopy (SEM) has become increasingly useful in describing the surface topography of helminth parasites, and many species of digenetic trematodes have been examined by this method. Recent ultrastructural studies of the body surface of adults, miracidia, and cercariae of digenetic trematodes have revealed a variety of sensory receptors (Thulin, 1980; Fried and Fujino, 1984; Sobhon et al., 1986; Tandon and Maitra, 1987; Busta and Nasincova, 1988; Cifrian and García-Corrales, 1988; Zdarska et al., 1988; Ferrer et al., 1996). More detailed studies on the presence, microtopography, and distribution of the tegumental papillae also have been performed (Nadakavukaren and Nollen, 1975; Edwards et al., 1977; Bakke and Lien, 1978; Fujino et al., 1979; Hoole and Mitchell, 1981; Cribb, 1987; Bakke and Hoole, 1988; Abdul-Salam et al., 2000; Moravec, 2002). However, within the Family Gorgoderidae Looss, 1899, only *Gorgoderina* sp.; *Gorgoderina attenuata* (Stafford, 1902) Stafford, 1905; *Gorgoderina vitelliloba* (Olsson, 1876) Ssinitzin, 1905; *Phyllodistomum conostomum* Olsson, 1876; *Phyllodistomum folium* (Olfers, 1816) Braun, 1899; and *Phyllodistomum umblae* Fabricius, 1780 have been subjects of SEM studies of tegumental surface microtopography (Nadakavukaren and Nollen, 1975; Bakke and Lien, 1978; Hoole and Mitchell, 1981; Hoole et al., 1983; Bakke and Zdarska, 1985; Bakke and Bailey, 1987; Bakke and Hoole, 1988). The papillary pattern seems to remain constant during development (Goodchild, 1943; Thomas, 1958), but it has been described in detail for only 4 gorgoderid species: *Phyllodistomum simile* Nybelin, 1926, and *Gorgodera amplicava* Looss, 1899, by light microscopy and *G. vitelliloba* and *Gorgoderina megacetabularis* Mata-López, León-Règagnon and Brooks, 2005, by SEM (Goodchild, 1943; Thomas, 1958; Bakke and Hoole, 1988; Mata-López et al., 2005). This study describes the types of papillae and the distinct papillary pattern observed on the ventral forebody region and oral and ventral suckers in 6 species of *Gorgoderina*.

MATERIALS AND METHODS

Adult gorgoderids were collected from the urinary bladder of naturally infected amphibians as follows (number of specimens examined by light microscopy/number of specimens examined by SEM presented parenthetically by species): *G. attenuata* (6/6), Pawnee Lake, Lancaster County, Nebraska, U.S.A., ex. *Rana catesbeiana* Shaw, 1802, and

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Santiago Tamazola, Oaxaca, Mexico, ex. *Rana zweifeli* Hillis, Frost and Webb, 1984; *Gorgoderina bilobata* Rankin, 1937 (5/2), Glacier National Park, Montana, U.S.A., ex. *Bufo boreas* Baird and Girard, 1852; *Gorgoderina diaster* Lutz, 1926 (2/1), Río Pizote, Área de Conservación Guanacaste, Costa Rica, ex. *Rana vaillanti* Brocchi, 1877; *Gorgoderina megalorchis* Bravo, 1948 (3/1), Paso Canoa, Oaxaca, Mexico, ex. *Bufo marinus* Linnaeus, 1758; *Gorgoderina parvicava* Travassos, 1922 (8/5), Laguna Escondida, Veracruz, Mexico, ex. *Rana vaillanti* Brocchi, 1877, and Río Pizote, Área de Conservación Guanacaste, Costa Rica, ex. *Rana vaillanti* Brocchi, 1877; *G. megacetabularis* (48/4), Río Pizote, Área de Conservación Guanacaste, Costa Rica, ex. *Rana vaillanti* Brocchi, 1877. Several specimens of each species were examined under a compound light microscope for identification and corroboration of papillary pattern. Gravid specimens were rinsed in 0.65% NaCl solution, killed, and fixed in hot 4% buffered formalin. Flukes were dehydrated gradually with ethanol and dried at critical point with the use of carbon dioxide. Dried specimens were mounted on aluminum specimen stubs, coated with a gold–palladium mixture with aid of a sputter-coater (Emitech K550), and examined with a scanning electron microscope (Hitachi S2460N operated at 15 kV).

RESULTS

Morphologic overview

Body oval and elongate, blunt anteriorly, tapering slightly posteriorly (Figs. 1–6). Forebody cylindrical and narrow; hindbody conical and tapered at posterior end. Tegumental surface aspinose, constricted, forming numerous ridges of variable width around body; surface between indentations filled with knob-like protuberances of variable size and distinct tegumental papillae (Figs. 7–14), producing a beaded appearance. Stylet cavity dorsal to the oral sucker on the anterior end of the body in all species, except for *G. diaster* and *G. parvicava*, in which the oral sucker opening is ventral and subterminal (Figs. 15–20). Oral sucker (Figs. 21–32) markedly smaller than the ventral sucker (Figs. 33–38), except in *G. parvicava*. In the 5 species in which the acetabulum is larger than the oral sucker, the ventral sucker is protruded ventrally, giving the body a typical dorsally flexed posture. Both the oral and ventral suckers show surface corrugations arranged radially, being more evident when the suckers are contracted. Genital pore located between both suckers on the midline of the body. No differential tegumental ornamentation around the genital pore. Excretory pore at the posterior end of body. Papillae covered the entire body surface and were more numerous on the forebody, particularly around the oral sucker. Papillae more abundant ventrally, with a tendency to bilateral symmetry (Figs. 39–44).

Tegumental papillary morphology

Four types of tegumental papillae were observed among the 6 species of *Gorgoderina* examined: button, ciliated, rosette, and domed (Figs. 7–14). Terminology and classification follows existing classifications of digenean papillae proposed by Hoole and Mitchell (1981) and Bakke and Hoole (1988).

Button papillae: These papillae lack a cilium, are constructed from a series of tegumental protuberances, and can function as contact receptors (Hoole and Mitchell, 1981). In this study, this was the predominant type on the body surface. Button papillae were arranged in 2 rings around the mouth, laterally to the frontal pit, and they were present on the lateral margins of the body and the dorsal and ventral surfaces of the preacetabular region of the flukes (Figs. 7, 8).

Ciliated papillae: These papillae are characteristically smooth-sided outgrowths with flat tops and a central knob-like structure (Figs. 9, 10); they could be sensitive to changes on the concentration of amphibian urine (Hoole and Mitchell, 1981). In this study, they were observed only on the oral sucker of *G. parvicava* and on the ventral surface between both suckers in *G. megacetabularis*.

Rosette papillae: These papillae are leaf-like tegumental outgrowths and are the largest of the papillary types; they could be stretch or contact receptors (Hoole and Mitchell, 1981). They were present on the external border and on the internal surface of the ventral sucker (Figs. 11–13).

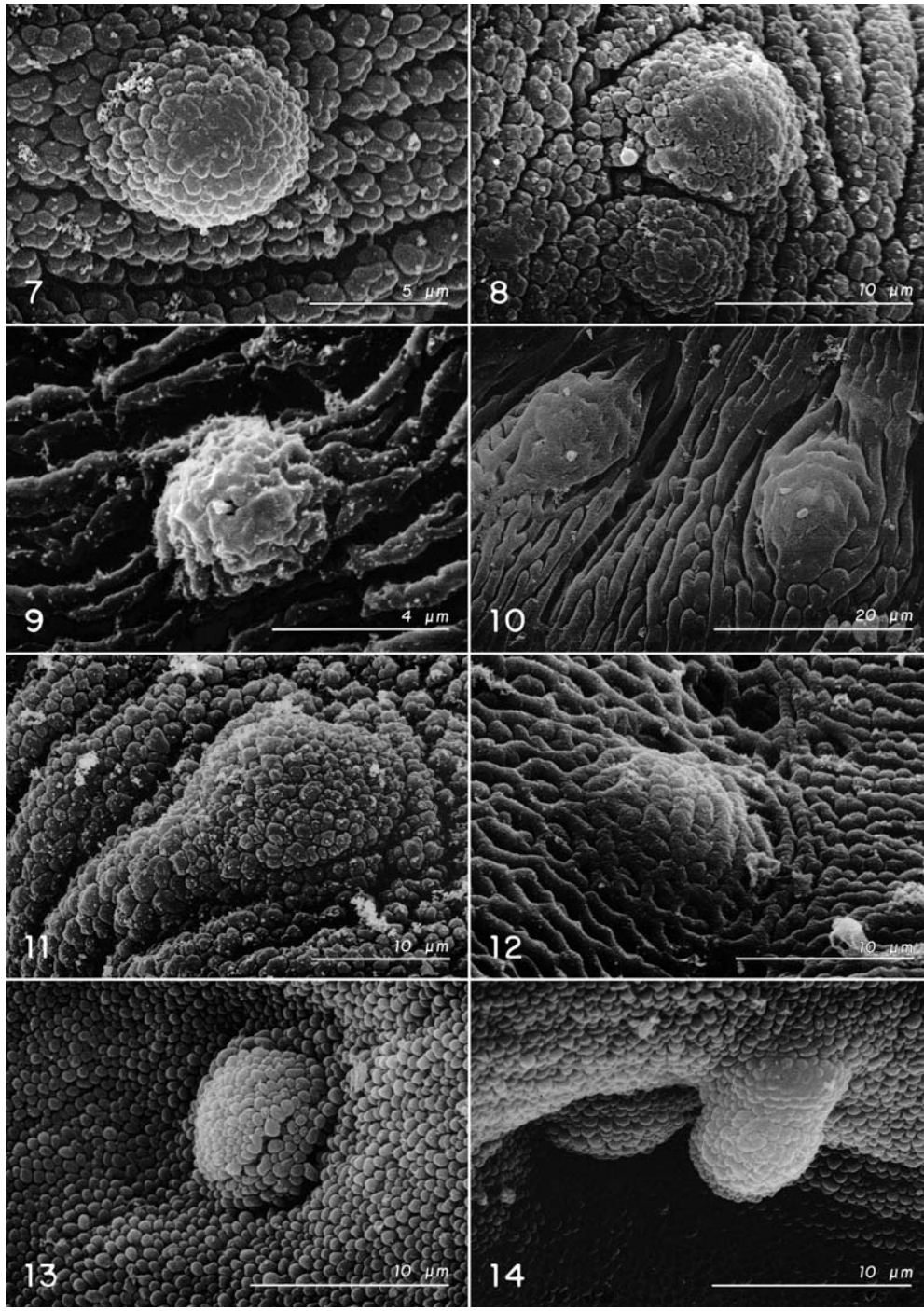
Domed papillae: Bakke and Lien (1978) described the domed papillae as a single papilla occurring on the internal surface of the ventral sucker covered by tightly packed tegumental protuberances. Bakke and Hoole (1988) noted these papillae in tight pairs, but on the basis of our observations, each of the domed papillae comprised 2 papillary components: a single, characteristically domed papilla overshadowing a smaller, flattened rosette papilla. Apparently, the flattened rosette papilla was protected by the domed papilla (Fig. 14). According to Hoole and Mitchell (1981), domed papillae function as tangoreceptors.

Tegumental papillary patterns among body regions

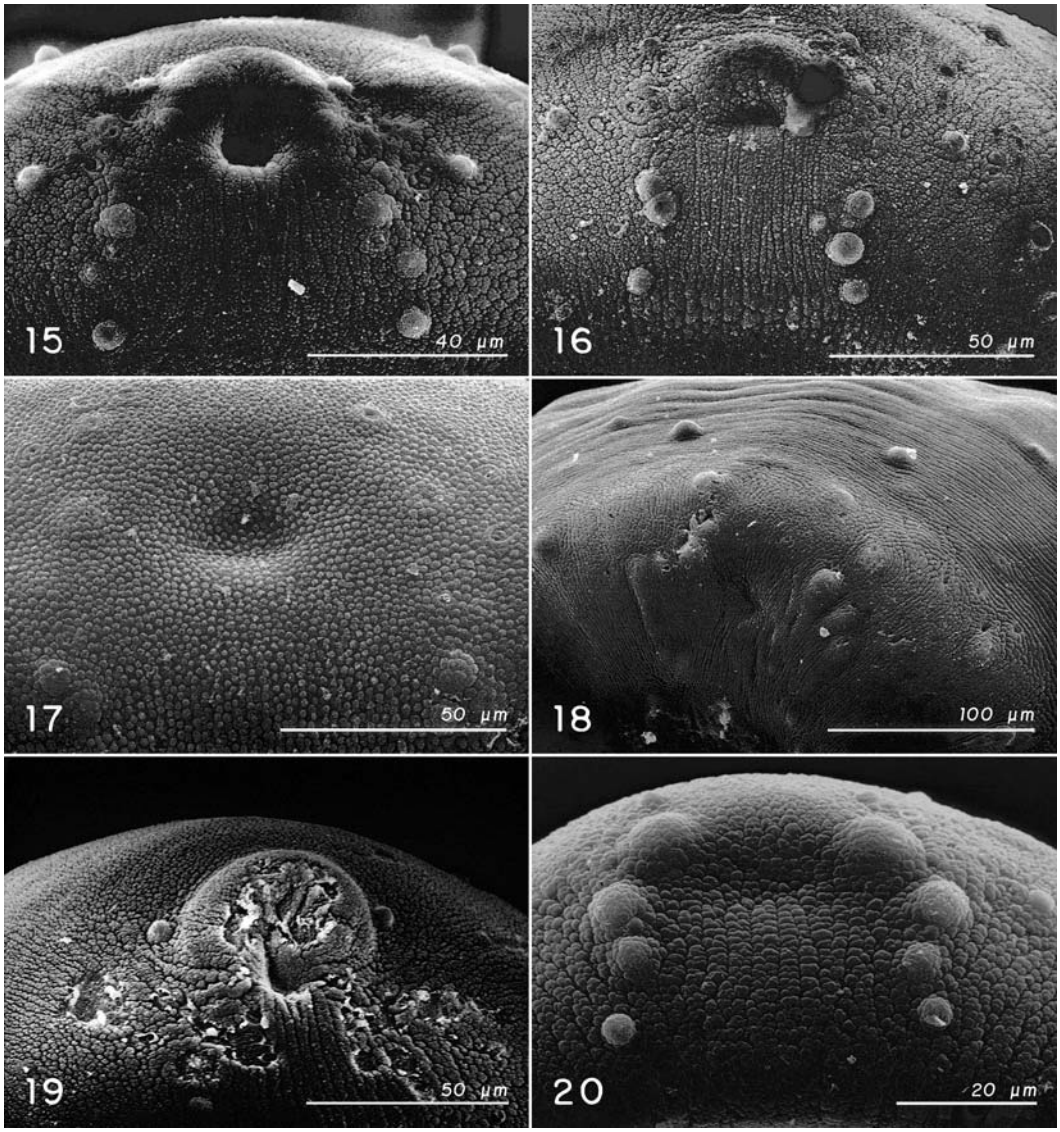
Apical region (Figs. 15–20, 39–44)*:* Stylet cavity present varying in shape and size among species. Large stylet cavity dorsal to the oral sucker in *G. attenuata*, *G. bilobata*, *G. megalorchis*, and *G.*

Figures 1–6. Scanning electron micrographs of ventral body surface of 6 species of *Gorgoderina*. **1.** *Gorgoderina attenuata*. **2.** *Gorgoderina bilobata*. **3.** *Gorgoderina diaster*. **4.** *Gorgoderina parvicava*. **5.** *Gorgoderina megalorchis*. **6.** *Gorgoderina megacetabularis*.

megacetabularis. *Gorgoderina diaster* and *G. parvicava* have only a vestigial stylet cavity situated more ventrally in *G. parvicava*, near the oral opening (Figs. 18, 24). Three button papillae (I, II, III) flanking the stylet pit are present in all species (Figs. 39–44). However, the first pair (I) in *G. megacetabularis* is situated on the border of the stylet pit and is larger than other pairs (Fig. 20). In the remaining species, pair I is located outside and lateral to the stylet cavity. First pair of button papillae (I) present or absent in *G. attenuata*. When present, these papillae are smaller than those of *G. megacetabularis* (cf. Figs. 15, 20). Smaller ciliated papillae are present between 3 pairs of button papillae in *G. diaster* and *G. megacetabularis* (Figs. 17, 20). Ciliated papillae absent on the apical region of the other species. Two additional pairs of button papillae (IV) are present on each side of the stylet cavity of *G. diaster* (Fig. 41). One



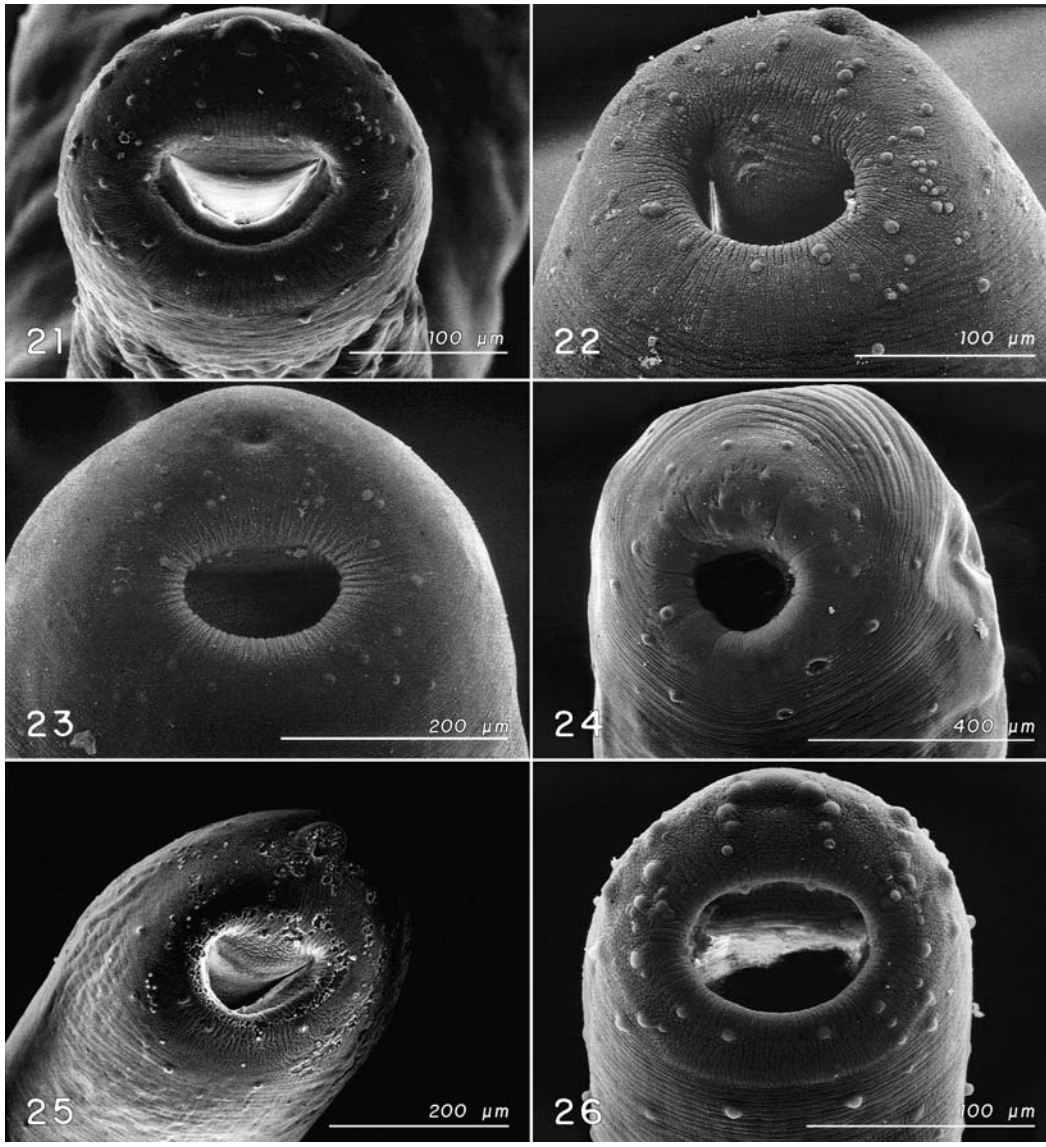
Figures 7–14. Scanning electron micrographs of papilla types from *Gorgoderina* spp. **7.** Button papilla on oral sucker of *Gorgoderina attenuata*. **8.** Button papilla on oral sucker of *Gorgoderina bilobata*. **9.** Ciliated papilla on body surface of *Gorgoderina megacetabularis*. **10.** Ciliated papillae on oral sucker of *Gorgoderina parvicava*. **11.** Rosette papilla on ventral sucker of *G. attenuata*. **12.** Rosette papilla on oral sucker of *G. parvicava*. **13.** Rosette papilla on internal surface of ventral sucker of *G. attenuata*. **14.** Rosette and domed papillae on internal surface of ventral sucker of *G. attenuata*.



Figures 15–20. Scanning electron micrographs of apical region of 6 species of *Gorgoderina*. **15.** *Gorgoderina attenuata*. **16.** *Gorgoderina bilobata*. **17.** *Gorgoderina diaster*. **18.** *Gorgoderina parvicava*. **19.** *Gorgoderina megalorchis*. **20.** *Gorgoderina megacetabularis*.

additional papilla is present on each side of the stylet cavity in other species (Figs. 39, 40, 42–44), more ventrally situated in *G. parvicava* and *G. megalorchis*. Additionally, a group of 3 papillae is situated more externally in *G. megacetabularis*.

Oral sucker (Figs. 21–26)*:* Papillae consistent among 6 species. Ten papillae constant around the oral aperture, but in *G. bilobata* and *G. diaster*, 2 of these are double papillae, although located in a different position (Figs. 22, 23). Additionally, 1 pair of papillae occur on the border of the dorsal lip, and 1 papilla occurs on each side of the oral opening. These papillae are button papillae in all species except *G. parvicava*, in which they are rosette papillae. In contrast with the other 5 species, *G. megacetabularis* has 2 groups of 3 papillae on the tegumental surface of the oral sucker. Presence and position of small button papillae on the surface of the oral sucker variable in *G. attenuata*. It was difficult to establish the papillary pattern on the oral

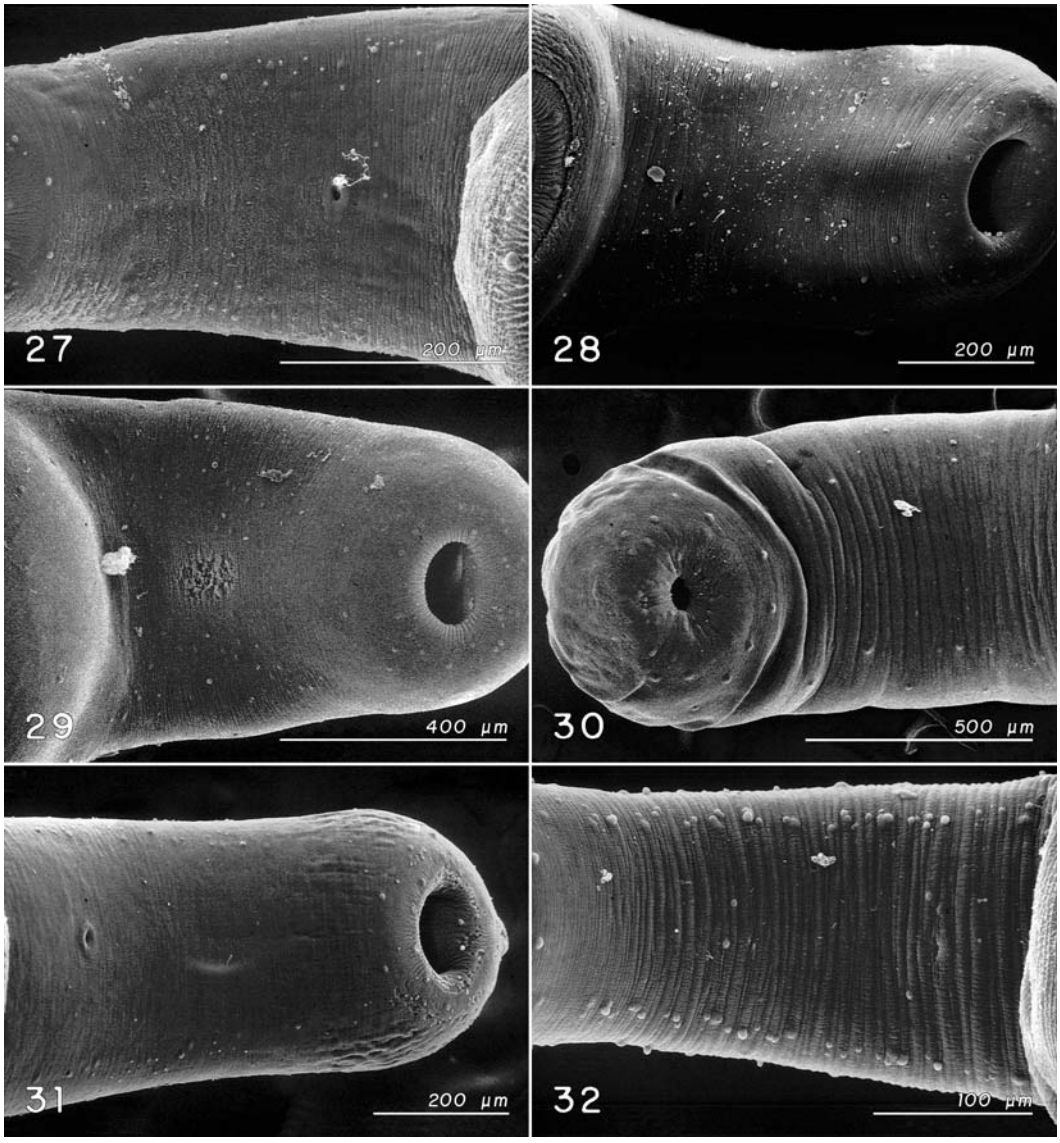


Figures 21–26. Scanning electron micrographs of the oral sucker of 6 species of *Gorgoderina*. **21.** *Gorgoderina attenuata*. **22.** *Gorgoderina bilobata*. **23.** *Gorgoderina diaster*. **24.** *Gorgoderina parvicava*. **25.** *Gorgoderina megalorchis*. **26.** *Gorgoderina megacetabularis*.

sucker of *G. megalorchis* because of the small size of the papillae.

Ventral forebody region (Figs. 27–32)*:* Ten large button papillae (5 on right lateral side and 5 on left lateral side) and a variable number of smaller button papillae arranged in 2 longitudinal rows on ventral surface between oral and ventral sucker. Additional ciliated papillae appear in the same area on *G. megacetabularis* and *G. parvicava*. This pattern could not be clearly observed in *G. megacetabularis* because of the large number of button papillae present in this area (Fig. 32). Presence and position of small button papillae were variable in *G. attenuata* (Fig. 27).

Ventral sucker (Figs. 33–38)*:* Eighteen papillae arranged in a bilaterally symmetrical pattern clearly visible in *G. attenuata*, *G. bilobata*, *G. megalorchis*, and *G. megacetabularis*. Six rosette papillae normally present on external ring of acetabulum but absent in

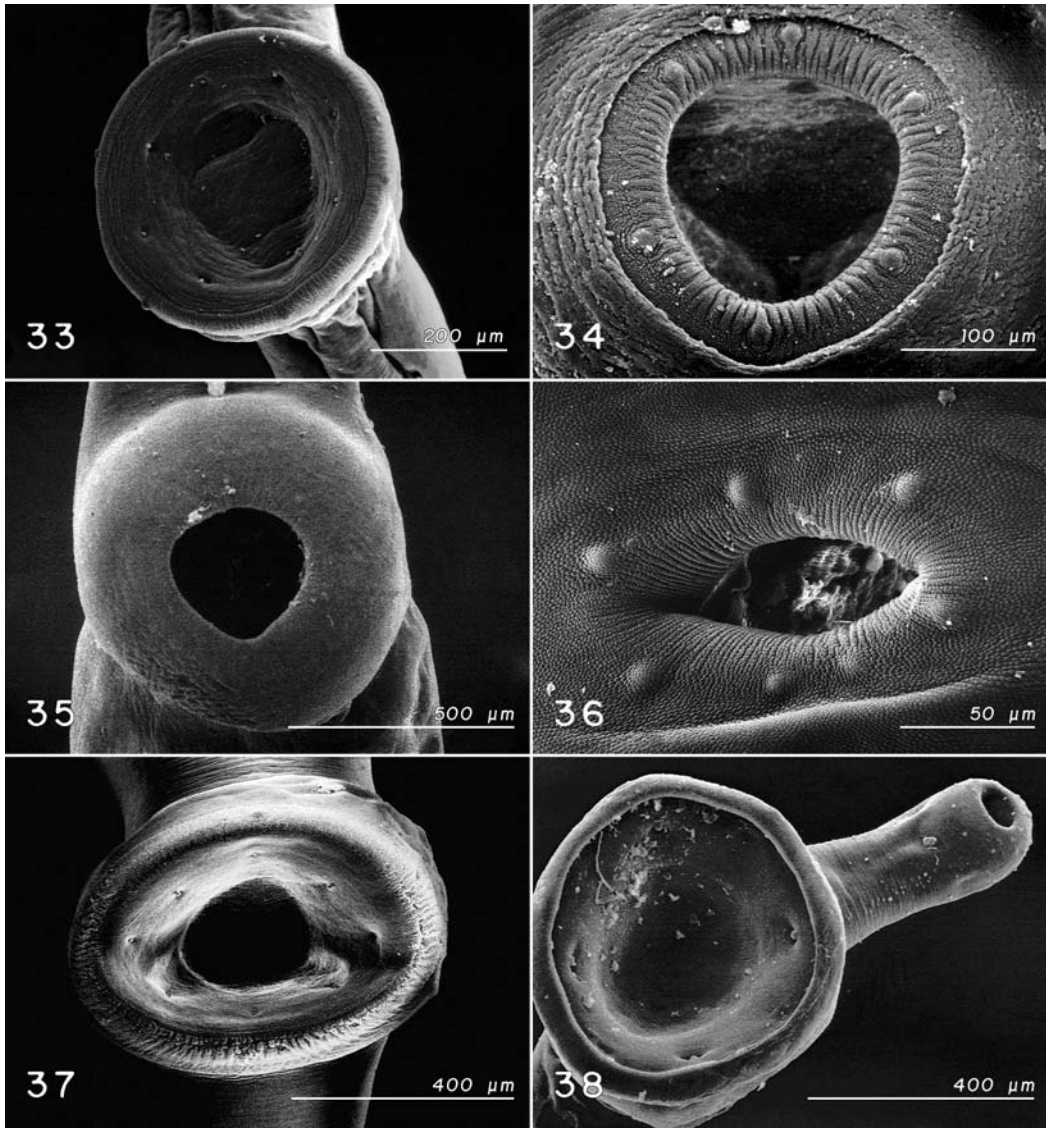


Figures 27–32. Scanning electron micrographs of ventral forebody region of 6 species of *Gorgoderina*. **27.** *Gorgoderina attenuata*. **28.** *Gorgoderina bilobata*. **29.** *Gorgoderina diaster*. **30.** *Gorgoderina parvicava*. **31.** *Gorgoderina megalorchis*. **32.** *Gorgoderina megacetabularis*.

G. megacetabularis (Fig. 38). Four domed papillae on internal surface of ventral sucker; 1 pair on each lateral side, and 8 flattened rosette papillae, 4 of them arranged in 2 pairs: 1 pair on the longitudinal line and 1 pair on the transverse line of the sucker. Remaining 4 flattened rosette papillae situated beneath a domed papilla. It was not possible to observe the papillary pattern on the internal surface of the ventral sucker of *G. diaster* (Fig. 35) and *G. parvicava* (Fig. 36) because of the classical contracted condition of this structure in these species. However, in *G. parvicava*, we could observe 1 papilla on its internal surface, which suggests that other papillae might be present.

DISCUSSION

Original descriptions of the species studied herein do not mention any tegumental structures, except for *G. megacetabularis* (Mata-López et al., 2005). The presence of papillae on the oral sucker surface of

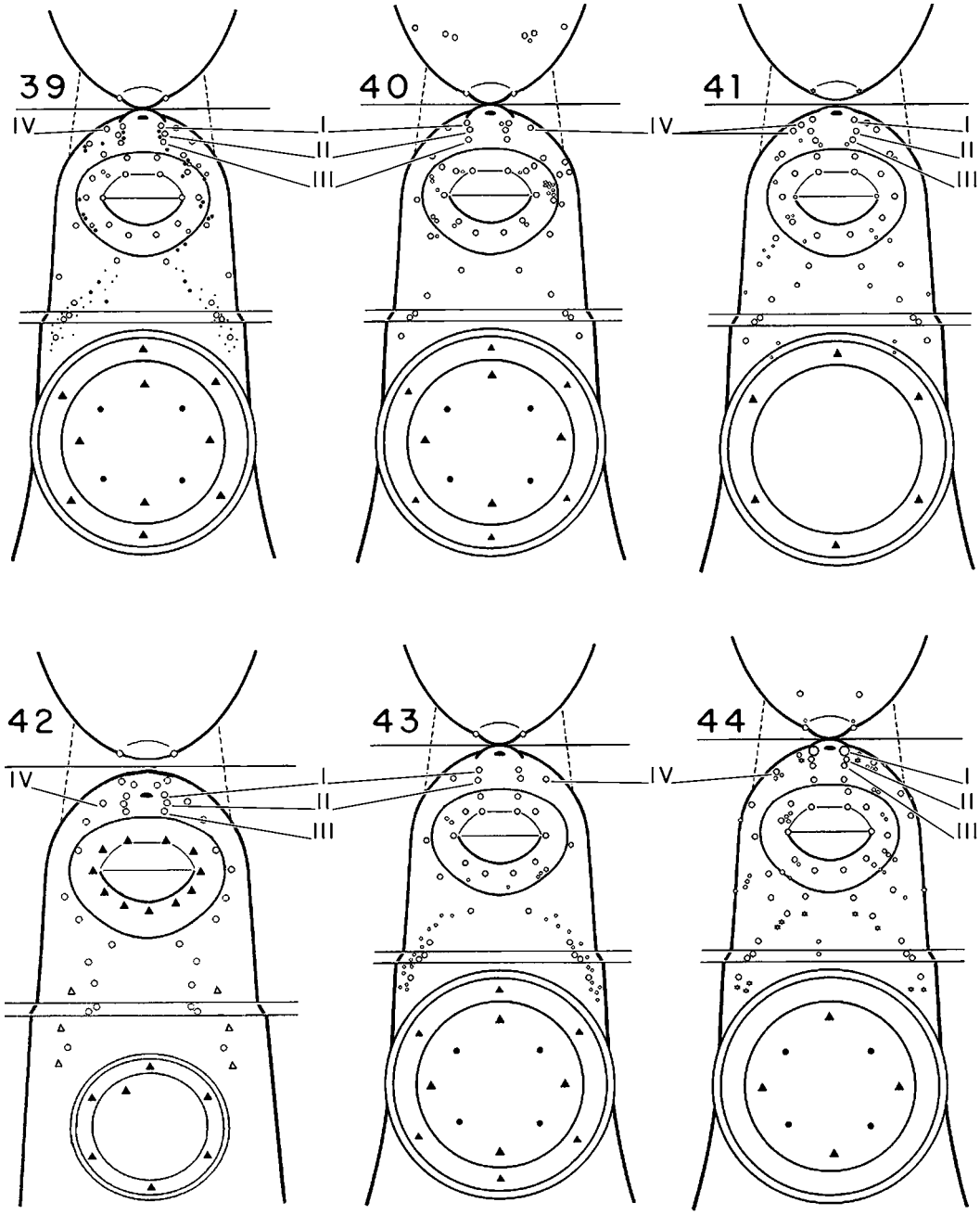


Figures 33–38. Scanning electron micrographs of the ventral sucker of 6 species of *Gorgoderina*. **33.** *Gorgoderina attenuata*. **34.** *Gorgoderina bilobata*. **35.** *Gorgoderina diaster*. **36.** *Gorgoderina parvicava*. **37.** *Gorgoderina megalorchis*. **38.** *Gorgoderina megacetabularis*.

G. attenuata was described by Nadakavukaren and Nollen (1975).

SEM studies have revealed a papillary system on the body surface of species of *Phyllodistomum* that could be of taxonomic interest (Bakke, 1984, 1985; Bakke and Zdarska, 1985; Bakke and Bailey, 1987). We think that this is also the case in species of *Gorgoderina*. The papillary pattern observed on the ventral forebody surface (2 longitudinal lines of 5 button papillae on each side of the body) appears to be homogeneous among all species examined. However, it could not be distinguished in *G. megacetabularis* because of the large number of papillae on this region.

Ultrastructural observations by Hoole and Mitchell (1981) and Hoole et al. (1983) revealed the presence of a frontal stylet cavity associated with penetration gland pores in *G. vitelliloba*. Hoole et al. (1983) suggested that the stylet cavity or frontal pit has no apparent function in juveniles or adults, and it might



Figures 39–44. Papillary pattern diagram of 6 species of *Gorgoderina* (modified from Bakke and Hoole, 1988). **39.** *Gorgoderina attenuata*. **40.** *Gorgoderina bilobata*. **41.** *Gorgoderina diaster*. **42.** *Gorgoderina parvicava*. **43.** *Gorgoderina megalorchis*. **44.** *Gorgoderina megacetabularis*. (Open circles indicate consistent papillae; full circles on ventral sucker, domed-rosette papillae; full triangles on ventral sucker, rosette papillae; full circles on oral sucker and between oral and ventral suckers, papillae occasionally missing.)

be a vestigial structure. Similar structures can be observed only in *G. diaster*, *G. parvicava*, and *G. megacetabularis*, whose penetration glands were confirmed with observations by light microscopy. However, the function of these structures on gravid specimens is still uncertain. Ontologic and physiologic studies are needed to clarify their activity.

In this study, we confirmed the observations of Nadakavukaren and Nollen (1975), Hoole and Mitchell (1981), and Bakke and Hoole (1988), who observed 4 types of sensory papillae. However, we found that the form of these papillae among the 6 studied species was different. The button and ciliated papillae in *G. attenuata*, *G. megalorchis*, *G. diaster*, *G. bilobata*, and *G. megacetabularis* were similar to those described in *G. attenuata*, *P. conostomum*, and *G. vitelliloba* by Nadakavukaren and Nollen (1975), Bakke and Lien (1978), and Bakke and Hoole (1988). However, the button and rosette papillae present in *G. parvicava* differ in size and form from the other species studied. The arrangement of the tubercles on the button papillae is more regular than in the other species, and they were flattened in contrast with the rounded button papillae observed in the remaining species. The presence of rosette papillae on the ring and internal surface of the ventral sucker has been mentioned by these authors, but they did not mention differences among them. The rosette papillae on the lip of the ventral sucker are rounded and well developed, whereas the rosette papillae within this structure are larger in diameter and more flattened. These authors described the domed papillae as a single papilla, but on the basis of our observations, each of these comprises 2 papillae: 1 papilla with the characteristics described by these authors for domed papillae and the other papilla beneath the first one, resembling the rosette flattened papillae on the internal surface of the ventral sucker. It seems that 1 papilla is protecting the other.

Detailed studies on the ultrastructural characteristics of digeneans can provide useful information in the taxonomic study of the groups. Particularly, the differentiation of species of gorgoderids, as well as the delimitation of genera in this family of digeneans, has been very difficult with the use of traditional morphologic characters. The information provided herein helps to clarify the complex taxonomic history of the group.

ACKNOWLEDGMENTS

We are grateful to Florencia Bertoni, Mathew Bolek, Elisa Cabrera, Agustín Jiménez, Elizabeth Martínez, Rogelio Rosas, Alejandro Oceguera, and Alejandro Zaldivar for their help in the field. Thanks also to Daniel R. Brooks and Anindo Choudhury for the donation of specimens. Special thanks to Sara Fuentes Soriano and Berenit Mendoza Garfias (Instituto de Biología, Universidad Nacional Autónoma de Mexico) for their help with the SEM and Gerardo Pérez-Ponce de León, Adrián Nieto Montes de Oca, and Victor Hugo Reynoso Rosales for revising a preliminary version of the manuscript. This study was funded in form of scholarship to R.M.L. by Dirección General de Estudios de Posgrado, Universidad Nacional Autónoma de Mexico and by a research grant from the National Science Foundation DEB-0102383 to J. A. Campbell and V.L.R.

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