SYSTEMATIC POSITION AND TAXONOMY OF THE GENUS HIRTUDISCUS FROM COLOMBIA (GASTROPODA: SCOLODONTIDAE)

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ABSTRACT

Hirtudiscus Hylton Scott, 1973 can be classified in the Scolodontidae because of the reduced jaw, the dagger-like lateral teeth with basal plates, which point away from the centre, the aulacopod foot and the elongate kidney. The minute central teeth, ovoviviparity and the course of the right ommatophoral retractor (which passes between penis and vagina) indicate that *Hirtudiscus* belongs to the subfamily Scolodontinae. The peculiar suture of the shell and the incision at the parietal angle of the aperture might be synapomorphies of *Hirtudiscus* and *Drepanostomella*. In addition to the type species, three species are described as new from the Cordillera Oriental in Colombia.

INTRODUCTION

Hylton Scott (1973) described the genus *Hirtudiscus* and classified it in the Endodontidae Pilsbry, 1895 (Punctoidea), on the basis of a single shell from the Cordillera Oriental in Colombia. Since the original description no new findings have been reported. During a land snail survey by the author and staff of the Facultad de Ciencias of the Universidad Militar Nueva Granada in Colombia, three species of the genus *Hirtudiscus* Hylton Scott, 1973 were found in the Departamentos Cundinamarca and Boyacá and the Distrito Especial. In the following account, the systematic position of the genus will be discussed on the basis of the anatomy and the shell, and three new species will be described.

MATERIAL AND METHODS

The counting of the shell whorls (exactness 0.25) follows Kerney & Cameron (1979: 13). The terms proximal and distal refer to position in relation to the gonad. The material on which this study is based is kept in the following collections: Museo de La Plata, La Plata (MLP); Senckenberg-Museum, Frankfurt a. M. (SMF); Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Santafé de Bogotá (UNAL); Zoologisches Museum der Universität Hamburg (ZMH).

Additional abbreviations: D, shell diameter; D3, shell diameter at three whorls; H, shell height; leg., collected by.

SYSTEMATIC DESCRIPTIONS

Scolodontidae H. B. Baker, 1925 Scolodontinae H. B. Baker, 1925 *Hirtudiscus* Hylton Scott, 1973

Hirtudiscus Hylton Scott, 1973: 128. Type species (by original designation): *Hirtudiscus hirtus* Hylton Scott, 1973.

Hirtudiscus hirtus Hylton Scott, 1973 (Figures 4A, 5A, B, 6)

Hirtudiscus hirtus Hylton Scott, 1973: 129, fig. 2 (Monte Redondo, Colombia oriental, entre Bogotá y Villavicencio, 3800 m alt.; holotype MLP 3965, seen).

Diagnosis: Hirtudiscus hirtus is characterized by a slightly sunken spire, distinct spiral striae on the protoconch and short hairs (up to 0.1 mm long, but it is possible that the maximal hair length is greater than 0.1 mm, because most hairs on the holotype are worn; see Table 1).

Shell (Figs 4A, 5A, B): Disc-like; spire slightly sunken; with 3.5 convex whorls; protoconch with distinct spiral striae; teleoconch with very dense, fine growth-striae carrying hairs up to 0.1 mm

Table 1.	Diagnostic characteristics and	l measurements of Hirtudiscus species.
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	H. hirtus	H. comatus	H. boyacensis	H. curei
Spire	Slightly sunken	Slightly sunken	Slightly elevated	Slightly or distinctly
		or slightly elevated		elevated
Protoconch sculpture	Distinct spiral striae	Without distinct	More or less	With or without
		spiral striae	distinct spiral striae	distinct spiral striae
Growth-striae and hairs	Very dense	Moderately dense	Dense	Very dense
Hair length	Up to 0.1 mm	Up to 0.3 mm	Up to 0.2 mm	Up to 0.05 mm
Number of whorls	3.5	3.5–4	3.25-4.5	3.5-3.75
Percentage of shell diameter occupied by umbilicus	38	39–48	37–48	42–45
D (mm)	3.9	5.1–6.3	3.1-5.2	3.8-4.0
D3 (mm)	3.1	3.1–3.8	2.3–2.8	2.5-3.4
H (mm)	1.8	2.1–2.5	1.5-2.0	1.6–1.8
D/H	2.17	2.32-2.64	2.07-2.60	2.11-2.50

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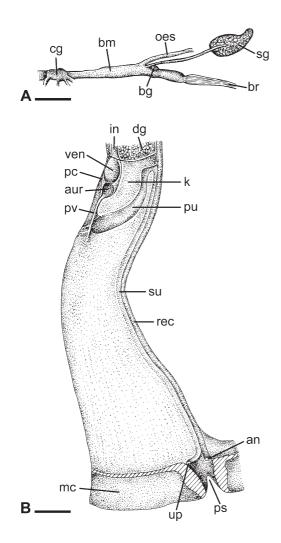


Figure 1. *Hirtudiscus comatus* new species, Colombia, Departamento Cundinamarca: La Calera 0.5 km towards Bogotá (ZMH 4019). **A.** Buccal mass. **B.** Pallial complex. Abbreviations: an, anus; aur, auricle, bg, buccal ganglion; bm, buccal mass; br, buccal retractor; cg, cerebral ganglion; dg, digestive gland; in, intestine; k, kidney; mc, mantle collar; oes, oesophagus; pc, pericardium; ps, pneumostome; pu, primary ureter; pv, pulmonary vein; rec,rectum; sg, salivary gland; su, secondary ureter; up, ureteric pore; ven, ventricle. Scale bar = 1 mm.

long in spiral rows; brownish-corneous; body whorl rounded; aperture oblique oval; upper insertion of the peristome not descending towards the aperture, strongly bent backwards and, close to the suture, abruptly bent downwards; thus, suture deeply impressed; peristome sharp, neither expanded nor thickened; umbilicus very wide, occupying about 38% of shell breadth.

Measurements: Monte Redondo (holotype) D = 3.9 mm, D3 = 3.1 mm, H = 1.8 mm, D/H = 2.17.

Distribution: Hirtudiscus hirtus is known only from the type locality, Monte Redondo, at 3800 m altitude. According to Hylton Scott (1973) that locality is between Bogotá and Villavicencio. There are several Monte, Cerro or Alto Redondo in Colombia. However, none could be localized between Bogotá and Villavicencio. The geographically closest locality with such a name and altitude is probably Alto Redondo south of Bogotá and west of Villavicencio, 04°01′07″ N 74°16′02″ W.

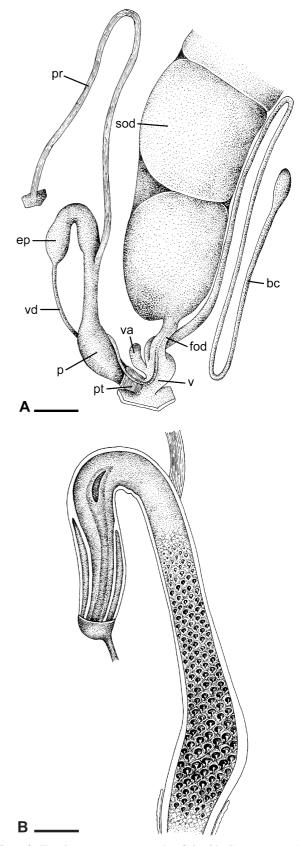


Figure 2. *Hirtudiscus comatus* new species. Colombia, Departamento Cundinamarca: La Calera 0.5 km towards Bogotá (ZMH 4019). **A.** Genitalia. **B.** Inner structure of male copulatory organs. Abbreviations: bc, bursa copulatrix; ep, epiphallus; fod, free oviduct; p, penis; pr, penial retractor; pt, penial tunica; sod, spermoviduct with eggs; v, vagina; va, vaginal appendage; vd, vas deferens. Scale bars: $\mathbf{A} = 0.5 \text{ mm}$; $\mathbf{B} = 0.25 \text{ mm}$.

SYSTEMATICS OF HIRTUDISCUS

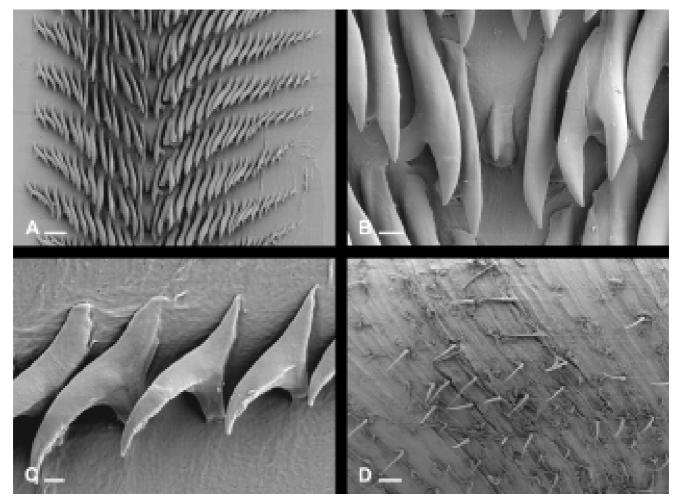


Figure 3. *Hirtudiscus comatus* new species, Colombia, Departamento Cundinamarca: La Calera 0.5 km towards Bogotá (ZMH 4019). **A.** Radula. **B.** Central part of the radula with central tooth and first lateral teeth. **C.** Outer lateral teeth. **D.** Microsculpture of the body whorl of the shell. Scale bars: $\mathbf{A} = 20 \,\mu\text{m}$; $\mathbf{B} = 5 \,\mu\text{m}$; $\mathbf{C} = 2 \,\mu\text{m}$; $\mathbf{D} = 100 \,\mu\text{m}$.

Hirtudiscus comatus new species (Figures 1–3, 4B, 5C, D, 6)

Types: Holotype: Colombia, Departamento Cundinamarca: La Calera 0.5 km towards Bogotá, farm Las Cabreras, Vereda San Rafael, Andean forest, N slope, 2840 m altitude, 04°42'30" N 73°58'20" W, leg. B. Hausdorf 11.03.2000, ZMH 4359, measurements: D = 5.6 mm, H = 2.2 mm. Paratypes: Colombia, Distrito Especial: Bogotá, brook above Calle 70-72, 2700-2800 m altitude, 04°39' N 74°03' W (SMF 323673); Bogotá, above Diagonal 72, 2700 m altitude (SMF 323674); Bogotá, above Parque Nacional, 2700-2800 m altitude, 04°36' N 74°05' W (SMF 323675). Departamento Cundinamarca: Santandercito, Finca El Eremitaño, primary Andean forest with sandstone boulders, E slope, 2310 m altitude, 04°34′16″ N 74°20′10″ W (ZMH 4276); La Calera 0.5 km towards Bogotá, farm Las Cabreras, Vereda San Rafael, 2820-2840 m altitude, 04°42′30″ N 73°58′20″ W (UNAL; ZMH 4019, 4035, 4067); La Calera, S of Entrada Fabrica de Cemento Samper, degraded Andean forest, NW slope, 2750 m altitude, 04°43'15" N 73°56'46" W (ZMH 4082); Cachipay 5.5 km towards Zipacón, small brook in forest with sandstone boulders, 2200 m altitude, 04°44′53″ N 74°24′06″ W (ZMH 4296); Tibatibá 5 km towards Guasca, 04°46' N 73°59' W (SMF 323676); Bosques de Torca, Andean forest, W slope, 2800 m altitude, 04°49'18" N 74°01'07" W (ZMH 4333). Departamento Boyacá: Villa de Leiva, oak forest near Manantiales de Iguaque in Vereda Capilla I, W slope, 2600 m altitude, 05°41′15″ N 73°28′53″ W (ZMH 4201);

Villa de Leiva, Cañon de Mamaramo near Carrizal in Vereda La Capilla II, entrance to Santuario de Flora y Fauna Iguaque, Andean forest, 2920 m altitude, 05°42'24" N 73°27'27" W (ZMH 4227).

Etymology: The specific epithet refers to the long hairs (latin *comatus*, long-haired).

Diagnosis: Hirtudiscus comatus differs from other *Hirtudiscus* species in the large shell with less dense growth-striae and hairs up to 0.3 mm long (see Table 1).

Shell (Figs 3D, 4B, 5C, D): disc-like; spire slightly sunken or slightly elevated; with 3.5–4 convex whorls; protoconch without distinct spiral striae; teleoconch with moderately dense, fine growth-striae carrying hairs up to 0.3 mm long in spiral rows; brownish-corneous; body whorl rounded; aperture oblique oval; upper insertion of the peristome not descending towards the aperture, strongly bent backwards and, close to the suture, abruptly bent downwards; thus, suture deeply impressed; peristome sharp, neither expanded nor thickened; umbilicus very wide, occupying about 39–48% of the shell breadth.

Measurements: La Calera 0.5 km towards Bogotá (n = 10): D: 5.1–5.8 mm, $\bar{x} = 5.6$ mm; D3: 3.1–3.8 mm, $\bar{x} = 3.5$ mm; H: 2.1–2.5 mm, $\bar{x} = 2.3$ mm; D/H: 2.32–2.64, $\bar{x} = 2.44$.

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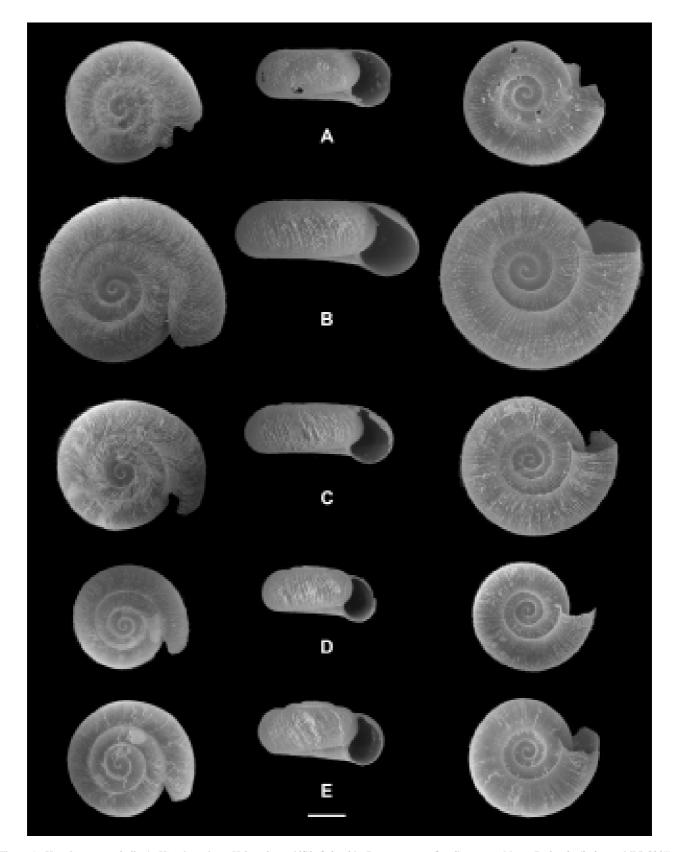


Figure 4. *Hirtudiscus* spp., shells. A. *Hirtudiscus hirtus* Hylton Scott, 1973, Colombia, Departamento Cundinamarca: Monte Redondo (holotype MLP 3965). B. *Hirtudiscus comatus* new species, Colombia, Departamento Cundinamarca: La Calera 0.5 km towards Bogotá (holotype ZMH 4359). C. *Hirtudiscus boyacensis* new species, Colombia, Departamento Boyacá: Villa de Leiva 5.8 km towards Gachantiva (holotype ZMH 4360). D. *Hirtudiscus boyacensis* new species, Colombia, Departamento Boyacá: Villa de Leiva 5.8 km towards Gachantiva (holotype ZMH 4360). D. *Hirtudiscus boyacensis* new species, Colombia, Departamento Boyacá: Villa de Leiva 5.8 km towards Gachantiva (holotype ZMH 4360). D. *Hirtudiscus boyacensis* new species, Colombia, Departamento Boyacá: Barbosa 5 km towards Arcabuco (paratype ZMH 4166). E. *Hirtudiscus curei* new species, Colombia, Departamento Cundinamarca: Cachipay, Finca El Porvenir (paratype ZMH 4305). Scale bar = 1 mm.

SYSTEMATICS OF HIRTUDISCUS

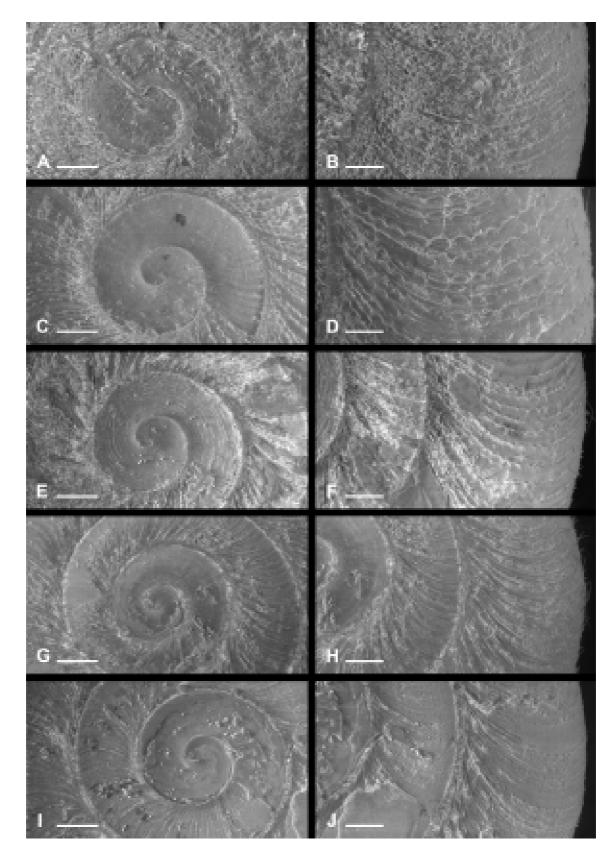


Figure 5. *Hirtudiscus* spp. A, B. *Hirtudiscus hirtus* Hylton Scott, 1973, Colombia, Departamento Cundinamarca: Monte Redondo (holotype MLP 3965). A. Protoconch. B. Shell sculpture. C, D. *Hirtudiscus comatus* new species, Colombia, Departamento Cundinamarca: La Calera 0.5 km towards Bogotá (holotype ZMH 4359). C. Protoconch. D. Shell sculpture. E, F. *Hirtudiscus boyacensis* new species, Colombia, Departamento Boyacá: Villa de Leiva 5.8 km towards Gachantiva (holotype ZMH 4360). E. Protoconch. F. Shell sculpture. G, H. *Hirtudiscus boyacensis* new species, Colombia, Departamento Boyacá: Valla de Leiva 5.8 km towards Gachantiva (holotype ZMH 4360). E. Protoconch. F. Shell sculpture. G, H. *Hirtudiscus boyacensis* new species, Colombia, Departamento Boyacá: Barbosa 5 km towards Arcabuco (paratype ZMH 4166). G. Protoconch. H. Shell sculpture. I, J. *Hirtudiscus curei* new species, Colombia, Departamento Cundinamarca: Cachipay, Finca El Porvenir (paratype ZMH 4305). I. Protoconch. J. Shell sculpture. Scale bars = 0.2 mm.

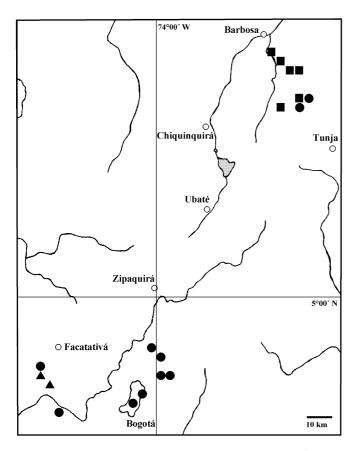


Figure 6. Distribution of *Hirtudiscus* species in Colombia (2' grid). *H. comatus* new species, ■ *H. boyacensis* new species; ▲ *H. curei* new species.

Anatomy (Figs 1–3): Four specimens (ZMH 4019) from La Calera 0.5 km towards Bogotá, Colombia, have been examined.

Animal grayish; foot aulacopod; tail without distinct caudal pit and caudal horn, not distinctly truncated; sole not distinctly divided.

Buccal mass (Fig. 1A) extraordinarily elongated; oesophagus inserts at about two-thirds of the length of the buccal mass; tongue-shaped salivary glands about one-third as long as buccal mass; no jaw found; odontophore restricted to the posterior third of buccal mass.

Radula (Fig. 3) long and narrow, with minute, narrow central tooth (Fig. 3B) with elongate base and 19 dagger-like lateral teeth (Fig. 3C) on each side in each V-shaped row. The slightly curved cusps of the lateral teeth point toward the centre and are connected by an extension to the basal plates that point away from the centre. First lateral tooth about as large as the adjacent laterals.

Pallial complex (Fig. 1B) about four times as long as kidney; kidney about twice as long as pericardium; kidney elongate with a narrow transverse extension towards the hindgut and a reflexed primary ureter; primary ureter continued by a secondary ureter along hindgut, which forms a tube initially (about up to the distal tip of the kidney), but seems to be an open groove distally; near the pneumostome the secondary ureter again forms a short tube, which is directed to the side of the pneumostome opposite the anus; lung long and narrow, without coarse venation; there are no distinct lappets at the mantle collar.

Genitalia (Fig. 2) ovoviviparous; penis with a broad distal section, which gradually passes into the longer, narrower proximal section; there is a short penial tunica around the base of the distal section; there are numerous papillae with recurved, corneous hooks in the penis; papillae become smaller towards proximal end of penis; in one specimen (without eggs) corneous hooks not (yet) developed; penis retractor inserts near proximal end of penis; in one examined specimen it inserted on diaphragm, in another it was connected with the left ommatophore retractor; short epiphallus broader than distal section of penis and partly double-walled; there is a roll in the epiphallus; vas deferens inserts asymmetrically on epiphallus; it does not run through penial tunica; vagina very short; there is an appendage at the vagina which is either club-shaped or ends with two tips; peduncle of the bursa copulatrix exceptionally long; small bursa of bursa copulatrix reaches digestive gland; free oviduct short; spermoviduct contains up to nine eggs, partly with embryos; albumen gland very small; right ommatophoral retractor runs between penis and vagina.

Distribution (Fig. 6): *Hirtudiscus comatus* is known from Andean forests at 2200–2920 m altitude in the Departamentos Cundinamarca and Boyacá, and the Distrito Especial in Colombia.

Remarks: The spire of most specimens is slightly sunken. However, the spire is slightly elevated in the specimens from the surroundings of Villa de Leiva and in a few other specimens.

Hirtudiscus boyacensis new species (Figures 4C, D, 5E, 6)

Types: Holotype: Colombia, Departamento Boyacá: Villa de Leiva 5.8 km towards Gachantiva, dry forest La Cabrera in Vereda La Sabana, 2170 m altitude, 05°40'31" N 73°32'15" W, leg. B. Hausdorf 15.03.2000, ZMH 4360, measurements: D = 4.4 mm, H = 1.8 mm. Paratypes: Colombia, Departamento Boyacá: Villa de Leiva 5.8 km towards Gachantiva, dry forest La Cabrera in Vereda La Sabana, 2170 m altitude, 05°40'31" N 73°32'15" W (ZMH 4213); Villa de Leiva 9 km towards Arcabuco, disturbed oak forest near farm, 2400 m altitude, 05°42'05" N 73°29'56" W (ZMH 4192); Moniquira 16.7 km towards Arcabuco, primary Andean forest, W slope, 2500 m altitude, 05°48'11" N 73°29'05" W (ZMH 4127); Moniquira 5.4 km towards Arcabuco, disturbed forest rest near quarry Cantera el Porvenir in La Roca, 2150 m altitude, 05°50'58" N 73°32'47" W (UNAL; ZMH 4166); Moniquira 13.2 km towards Arcabuco, waterfall above road, 2400 m altitude, 05°49'23" N 73°30'31" W (ZMH 4141); Barbosa 5 km towards Arcabuco, forest near quarry El Cairo in Vereda Pueblo Viejo, 1840 m altitude, 05°53'55" N 73°35'08" W (SMF 323677; UNÅL; ZMH 4184).

Etymology: The specific epithet refers to the occurrence of the species in the Colombian Departamento Boyacá (*boyacensis* used as an adjective).

Diagnosis: Hirtudiscus boyacensis differs from *H. hirtus* in the slightly elevated spire and hairs, which are on average longer, and from *H. comatus* in the smaller shell with more whorls, more or less distinct spiral striae on the protoconch, denser growth-striae and hairs that are on average shorter (see Table 1).

Shell (Figs 4C, D, 5E–H): Disc-like; spire slightly elevated; with 3.5–4.5 convex whorls; protoconch with more or less distinct spiral striae; teleoconch with dense, fine growth-striae carrying hairs up to 0.2 mm long in spiral rows; brownish-corneous; body whorl rounded; aperture oblique oval; upper insertion of the peristome not descending towards the aperture, strongly bent backwards and, close to the suture, abruptly bent downwards; thus, suture deeply impressed; peristome sharp, neither expanded nor thickened; umbilicus very wide, occupying about 40–48% of the shell breadth.

Measurements: Barbosa 5 km towards Arcabuco (n = 5): D: 3.1–4.0 mm, $\bar{x} = 3.5$ mm; D3: 2.3–2.6 mm, $\bar{x} = 2.5$ mm; H: 1.5–1.8 mm,

 $\bar{x} = 1.6$ mm; D/H: 2.07–2.33, $\bar{x} = 2.23$. Villa de Leiva 5.8 km towards Gachantiva (n = 4): D: 4.4–5.2 mm, $\bar{x} = 4.7$ mm; D3: 2.5–2.8 mm, $\bar{x} = 2.6$ mm; H: 1.8–2.0 mm, $\bar{x} = 1.9$ mm; D/H: 2.44–2.60, $\bar{x} = 2.53$.

Distribution (Fig. 6): Hirtudiscus boyacensis is known from forests at 1840–2500 m altitude in the Departamento Boyacá in Colombia.

Remarks: The specimens from the surroundings of Barbosa and Moniquira (Figs 4D, 5G–H) differ from those from the surroundings of Villa de Leiva (Figs 4C, 5E–F) in the smaller shell with more strongly arched whorls, a weaker spiral sculpture on the protoconch and an umbilicus that is on average narrower. More material is necessary to establish whether these populations belong to a distinct taxon.

Hirtudiscus curei new species (Figures 4E, 5I, J, 6

Types: Holotype: Colombia, Departamento Cundinamarca: Cachipay, Finca El Porvenir, primary forest, 1600 m altitude, $04^{\circ}43'45''$ N $74^{\circ}25'45''$ W, leg. B. Hausdorf 20.03.2000, ZMH 4361, measurements: D = 5.0 mm, H = 2.2 mm. Paratypes: Colombia, Departamento Cundinamarca: La Mesa 12 km towards Bogotá, Los Alpes near El Rosario, W slope with forest, 1700 m altitude, $04^{\circ}40'14''$ N $74^{\circ}23'43''$ W (SMF 323678; UNAL; ZMH 4316); Cachipay, Finca El Porvenir, primary forest, 1600 m altitude, $04^{\circ}43'45''$ N $74^{\circ}25'45''$ W (ZMH 4305).

Etymology: This species in named in honour of Professor Dr José Ricardo Cure, Universidad Militar Nueva Granada in Bogotá, who took me to the sites where this species occurs.

Diagnosis: Hirtudiscus curei can be distinguished from the other *Hirtudiscus* species by the very short hairs. Moreover, the shell is usually brighter and has a more elevated spire (see Table 1).

Shell (Figs 4E, 5I, J): Disc-like; spire slightly or distinctly elevated; with 3.5–4.0 convex whorls; protoconch with or without distinct spiral striae; teleoconch with very dense, fine growth-striae carrying hairs up to 0.05 mm long in spiral rows; light corneous; body whorl rounded; aperture oblique oval; upper insertion of the peristome not descending towards the aperture, strongly bent backwards and, close to the suture, abruptly bent downwards; thus, suture deeply impressed; peristome sharp, neither expanded nor thickened; umbilicus very wide, occupying about 41–46% of shell breadth.

Measurements: all localities (n = 5): D: 3.8–5.0 mm, $\bar{x} = 4.2$ mm; D3: 2.5–3.4 mm, $\bar{x} = 3.0$ mm; H: 1.6–2.3 mm, $\bar{x} = 2.0$ mm; D/H: 1.96–2.50, $\bar{x} = 2.18$.

Distribution (Fig. 6): *Hirtudiscus curei* is known from forests at 1600–1700 m altitude in the Departamento Cundinamarca in Colombia.

SYSTEMATIC POSITION OF HIRTUDISCUS

Hylton Scott (1973) classified *Hirtudiscus* in the Endodontidae Pilsbry, 1895 (Punctoidea) based on shell characters alone. However, anatomical examination showed that *Hirtudiscus* does not belong to the Punctoidea.

Hirtudiscus can be classified in the Scolodontidae H. B. Baker, 1925 (= Systrophiidae Thiele, 1926) because of the reduced jaw, the dagger-like lateral teeth with basal plates, which point away from the centre, the aulacopod foot and the elongate kidney. The minute central teeth, ovoviviparity and the course of the right ommatophoral retractor, which passes between penis and vagina, indicate that *Hirtudiscus* belongs to the subfamily Scolodontinae (= Systrophiini, see Tillier, 1980). *Hirtudiscus* differs from that subfamily as diagnosed by Tillier (1980) in having a non-truncated caudal foot end, a first lateral tooth, which is not distinctly smaller than the following laterals, and a short kidney that is only about one-quarter the length as the pallial cavity. The importance of these differences should not be overstated because only a few species of the Scolodontidae are anatomically well known.

Hirtudiscus is further characterized by a vaginal appendage, corneous hooks in the penis, an extraordinarily elongated buccal mass and a shell with long hairs, a peculiar suture and an incision at the parietal angle of the aperture.

The peculiar suture and the incision at the parietal angle of the aperture might be synapomorphies of *Hirtudiscus* and *Drepanostomella* Bourguignat, 1889. Furthermore, there are periostracal structures on the shell of *Drepanostomella* (papillae, etc.; see Baker, 1925), which might be homologous with the hairs of *Hirtudiscus* and the number of lateral teeth (19) corresponds in both genera. Thus, *Hirtudiscus* is probably more closely related to *Drepanostomella* than to any other Scolodontidae. *Hirtudiscus* differs from *Drepanostomella* in the hairs and the smaller central teeth. Unfortunately, the anatomy of *Drepanostomella* is hardly known.

Tillier (1980) and Schileyko (2000) classified Drepanostomella with the Tamayoinae because its central teeth are rather large and the first lateral teeth are not distinctly smaller than the adjacent laterals. However, both character states are probably symplesiomorphies. Tillier (1980) and Schileyko (2000) missed the fact that Baker (1925) had noted that Drepanostomella ammonoceras (L. Pfeiffer, 1855) is ovoviviparous. Ovoviviparity is an autapomorphy of the Scolodontinae. Thus, Drepanostomella should be transferred to the Scolodontinae. Hirtudiscus + Drepanostomella might be the sister group of the other Scolodontinae (Happia, Wayampia, Systrophia and probably the anatomically unknown Zilchistrophia), which are characterized by the reduction of the first lateral teeth and, perhaps, some of the other characters listed by Tillier (1980) as characteristic for the Scolodontinae, but which are not found in Hirtudiscus (see above). More material for anatomical examinations is necessary for a cladistic analysis of the relationships within the Scolodontidae.

The vaginal appendage of *Hirtudiscus* might be homologous with a swelling at the vagina of *Wayampia lutea* (Tillier, 1980) described by Tillier (1980: 98, fig. 77). Vaginal appendages are known from several stylommatophoran lineages. Some of these appendages share a common pattern and are homologous (Hausdorf, 1998). However, the homology of simple appendages like that in *Hirtudiscus* is difficult to prove.

The peculiar corneous hooks in the penis of *Hirtudiscus* are not known from any Scolodontidae, but are thought to characterize the Streptaxidae Gray, 1860 and the Streptaxoidea (e.g. Schileyko, 2000). Hirtudiscus differs from the Streptaxidae in its aulacopod foot, the course of the right ommatophoral retractor, which passes between penis and vagina, and the kidney, which extends distally beyond the pericardium. Corneous hooks inside the penis evolved several times in unrelated groups of the Stylommatophora, for example Balcanodiscus (Zonitidae) and Vitrinoxychilus (Oxychilidae; Riedel, 1980). Nevertheless, the occurrence of such hooks in a scolodontid raises the question how closely the Scolodontidae and the Streptaxidae are related, and whether it is justified to classify them in different superfamilies (see, for example, Schileyko, 2000). These questions can be resolved only in a cladistic analysis, which is beyond the scope of the present paper.

The *Hirtudiscus* species are usually found under stones in moderately moist forests. The different species show an altitudinal zonation. *Hirtudiscus curei* occurs at 1600–1700 m altitude, *Hirtudiscus boyacensis* at 1840–2500 m, *Hirtudiscus comatus* at 2200– 2920 m and *Hirtudiscus hirtus* at 3800 m. This might indicate that ecotones played a role in speciation in *Hirtudiscus*.

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