Diversity and arrangement of the cuticular structures of *Hyalella* (Crustacea: Amphipoda: Dogielinotidae) and their use in taxonomy

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ABSTRACT. This study describes the morphology and arrangement of the cuticular structures of *Hyalella castroi* González, Bond-Buckup & Araujo, 2006 and *Hyalella pleoacuta* González, Bond-Buckup & Araujo, 2006, to identify specific characters that can be used in taxonomstudies of this genus. The entire cuticular surface of both species was examined by optical and scanning electron microscopy. The data obtained were compared with available information for other members of Peracarida, mainly Amphipoda and Isopoda. Five different types of cuticular structures, including 30 types of setae, four types of microtrichs, three types of pores, and some structures formed by setules and denticles were identified. The results were compared with other groups of gammarids, and peracarideans, such as Thermosbaenacea and Isopoda. The use of cuticular structures as a tool for taxonomic studies showed important results, not only at species level, but also at genus, and family levels.

KEY WORDS. cuticular surface; Hyalellinae; microtrichs, pores, setae.

Amphipods of genus *Hyalella* Smith, 1874 occur in the continental waters of the Americas, where they constitute important links in the food chains, serving as a food resource for aquatic birds, fish, and other crustaceans (Grosso & Peralta 1999). This genus is morphologically quite diverse, mainly in South America (González *et al.* 2006), although some species have a very similar morphology that makes their differentiation and identification difficult.

Some workers such as Watling (1989) and Calazans & Ingle (1998) have suggested that the use of cuticular structures, mainly the setae, constitute an important tool for the study of Crustacea taxonomy. Many classification schemes for setae have been developed with the aim of facilitating the application of this knowledge in comparative studies, as exemples are those done with decapods by Thomas (1970), Farmer (1974), Drach & Jacques (1977), Watling (1989), Calazans & Ingle (1998), and Garm (2004a). For Peracarida, some prominent studies include those of Fish (1972), who described the setae of the aquatic isopod *Eurydice pulchra* Leach, 1815; Oshel & Steele (1988), who examined the setae of some gammaridean amphipods; and Wagner (1994), who described the structures of several species of Thermosbaenacea Monod, 1924. In addition to these, a wide variety of cuticular structures have been described for Peracarida, such as: sensory spine (Brandt 1988), pores (Halcrow 1978, Halcrow & Bousfield 1987), microtrichs (Oshel *et al.* 1988, Steele 1991, Olyslager & Williams 1993), and tricorn setae (Holdich & Lincoln 1974, Schmalfuss 1978, Holdich 1984). In relation to cuticular structures of species of *Hyalella*, only setae of both maxillae of *Hyalella azteca* Saussure, 1858 and *Hyalella montezuma* Cole & Watkins, 1977 are described (Wagner & Blinn 1987). Up to the present, a single amphipod, *Gammarus pseudolimnaeus* Bousfield, 1958, has had its cuticular surface inventoried by scanning electron microscopy by Read & Williams (1991).

In view of the scarcity of information of cuticular structures of Amphipoda and more precisely within species of the genus *Hyalella*, we analyzed the morphology and arrangement of the cuticular structures, of *Hyalella castroi* González, Bond-Buckup & Araujo, 2006 and *Hyalella pleoacuta* González, Bond-Buckup & Araujo, 2006.

MATERIAL AND METHODS

Specimens of *H. castroi* and *H. pleoacuta* were collected in fishponds near the source of the Rio das Antas, at the Vale das Trutas, Municipality of São José dos Ausentes, state of Rio Grande do Sul, Brazil (28°47'00"S, 49°50'53"W). Thirty adult specimens of both sexes of each species were kept in 500 ml beakers filled with distilled water, without food, for three days, in order to improve the cleanliness of the appendices. They were then fixed in 70% ethanol and dissected under a stereomicroscope. For the SEM analyses, the dissected appendages, together with four whole females and four whole males of each species were prepared according to the technique of Leistikow & Araujo (2001). The material was examined in a Jeol JSM 6060 scanning electron microscope (SEM) of the Microscopy Center of the Universidade Federal do Rio Grande do Sul, operated at 10 Kv. Part of the dissected appendages were mounted on slides in liquid glycerin under coverslips, and observed in an Olympus CX 31 microscope fitted with a drawing tube for observation of the internal morphology of the setae. The general description of each appendage follows González *et al.* (2006).

Up to the present, none of the classification schemes proposed for the cuticular structures of crustaceans has been able of embracing the full diversity of these structures among the group. The majority of these studies were conceived with an emphasis on only one type of structure, such as setae (Thomas 1970, Fish 1972, Farmer 1974, Oshell & Steele 1988) or microtrichs (Oshel *et al.* 1988). For this reason, in the present study a more inclusive classification was developed, including all of the diversity found in the two species of *Hyalella* worked here unified to the nomenclature of these structures found in the literature, facilitating their use in future comparative studies. To this end we opted to combine preexisting schemes, preferentially those that were developed based on data from electron microscopy. For the definitions of seta, setule, and denticle we employed the proposal of Garm (2004a). However, for didactic reasons, only the setules and denticles that issue directly from the surface of the cuticle were considered as cuticular structures. These same structures, when present on the setal shaft were considered as a character of the setae and were described as such.

The terminology used to describe the setae followed Watling (1989). To this terminology we added the term lamella, *sensu* Calazans & Ingle (1998), to describe structures of the setal shaft. The term "sensory spine" *sensu* Brandt (1988) was replaced by the term "cuspidate seta with accessory seta" as advocated in the definition of a seta by Garm (2004a). Microtrich was identified according to the proposal of Oshel *et al.* (1988).

All the setae were identified with a letter that indicates their category (A-G), and a number that indicates the number of variations found (Factor 1978, Coelho & Rodrigues 2001a, b). The pores were named according to their specific morphology. Setules (S) and the polygonal patterns described for pores (P) and denticles (T) were identified by a letter that indicates the nature of the structure that composes it, and a number corresponding to the number of variations found for these structures. Each description was illustrated with a SEM micrography.

As the terms microtrichs, setules, and denticles are not used in a uniform way in the crustacean literature, table I presents the comparisons between the terms used here and those used in other crustacean studies.

RESULTS

On the cuticular surface of *H. castroi* and *H. pleoacuta*, five categories of cuticular structures were found: setae, microtrichs, setules, pores, and denticles (Figs 1-4).

The setae were the most abundant and diverse structures found on the cuticular surface. Altogether, 30 variations of setae were observed (Figs 5-34), that were allocated to seven groups: simple, cuspidate, plumose, pappose, serrulate, serrate, and pappo-serrate (Tab. II). The table III shows the comparisons between the setae described in this study and those of other members of Peracarida.

Table I. Cuticular structures found in the present study for *H. castroi* and *H. pleoacuta* compared with other crustaceans with data from literature. Source: [1] Needham (1942), [2] Fish (1972), [3] Cuadras (1982), [4] Wagner & Blinn (1987), [5] Read & Williams (1991), [6] Bradbury *et al.* (1998), [7] Jaume & Christenson (2001), [8] Drumm (2005), [9] Garm & Hoeg (2000), [10] Calazans & Ingle (1998).

Structures	Present study	*Asellus* [1]	*E. pulcra* [2]	Amphipoda [3]	*Hyalella* [4]	*G. pseudolimnaeus* [5]
Microtrichs	Ia		–	Pegs type A	–	Pegs type A
	Ib		Single microtrich		–	
	Ic		–	Pegs type A	–	
	Id			–	–	
Setules	S1		–		–	
	S2		–		Barbed seta	
Denticles	T1	Microtrich crescents	Microtrich crescent		–	
	T2					

Structures	Present study	Amphipoda [6]	*Metacrangonyx* [7]	Tanaidacea [8]	*Munida sarsi* [9]	*P. mullieri* [10]
Microtrichs	Ia	–		–		–
	Ib	–		–		–
	Ic	–		–		–
	Id	–		–		–
Setules	S1	–		–	Microseta	–
	S2	–		–		Setule with setulettes
Denticles	T1	Rugosities	scutellated scales	Microtrichs		Short spine spine like setules
	T2		caespitose patch			

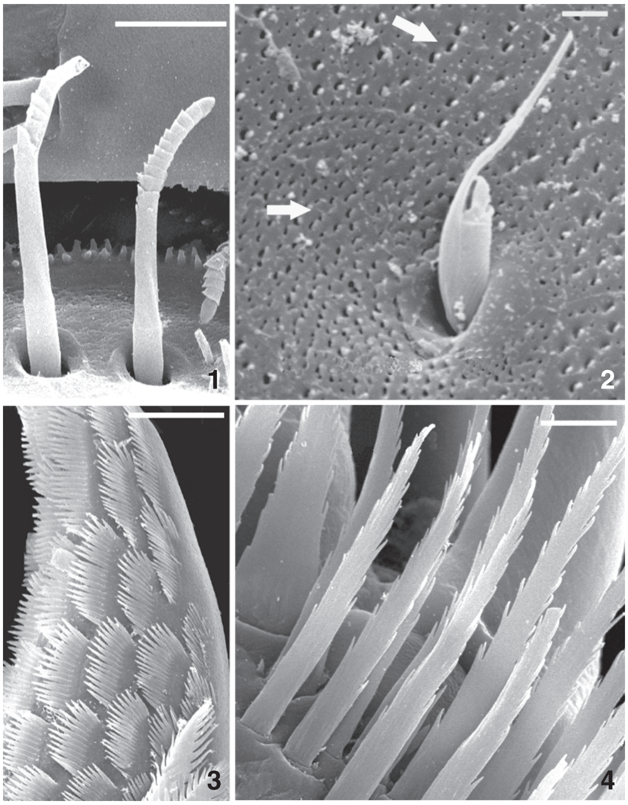
Table II. Description and distribution of setal types on the cuticular surface of *H. castroi* and *H. pleoacuta*.

Setal category	Label	Description	Distribution
Simple (A) Figs 5-14)	A1	Lamellate seta: shaft smooth, of varying length, lamellate tip varying in length, occupying between 1/2 and 1/5 of the terminal portion of the shaft, with a terminal pore (Fig. 5).	Antennae, maxillipeds, gnathopods and pereopods
	A2	Shaft long and smooth, of similar diameter along its entire length, with annulation and terminal pore (Fig. 6).	Maxilla 2 and maxillipeds
	A3	Shaft robust, with wide base, tapering toward apex (Fig. 7).	Propodus of pereopods
	A4	Shaft long and delicate, tapering gradually toward apex, terminal pore, articulation protected by a "skirt" of thin cuticle (Fig. 8).	Propodus of pereopods
	A5	Shaft short and robust, tapering abruptly near apex (Fig. 9).	Palp of maxilla 1
	A6	Curved seta: shaft long and smooth, annulation marked and subterminal pore with lamellate tip. Distal end of shaft curved and decorated with little. Articulation at an angle of approximately 45° (Fig. 10).	Uropod 1 of male
	A7	Shaft short and smooth, tapering slightly toward tip, and terminal pore (Fig. 11).	Antenna 1
	A8	Aesthetasc: shaft smooth, annulation present, distal half of shaft inflated (Fig. 12).	Antenna 1
	A9	Curl tipped seta: shaft long, slender, and smooth, with terminal portion expanded and hook-shaped; annulation present (Fig. 13).	Oostegites
	A10	Shaft short, terminal pore, apex lamellate (Fig. 14).	Coxal plates
Cuspidate (B) (Figs 15-17)	B1	Shaft robust, short and smooth. Annulation present (Fig. 15).	Apex of inner plate of maxillipeds
	B2	Shaft robust, long (± 130 µm), and smooth. Annulation strongly marked (Fig. 16).	Uropod 1
	B3	Shaft short, annulation little apparent (± 40 µm) (Fig. 17).	Uropods
Cuspidate with accessory seta (Figs 18-20)	B4	Shaft variable in size, with wide base gradually tapering to apex, terminal pore on accessory seta inserted on final third of shaft. Articulation comma-shaped (Fig. 18).	Palm of gnathopod 2 of males
	B5	Shaft short with wide base, slightly concave, tapering gradually to end, terminal pore on accessory seta inserted in final third of shaft on opposite side to concavity. Articulation wide (Fig. 19).	Anterior lobe of gnathopods
	B6	Very similar to type B4, but with variable length, and simple, round articulation (Fig. 20).	Pereopods, telson and uropods
Plumose (C) (Figs 21-22)	C1	Shaft very long, with setules densely arranged in two rows along entire lenght. (Fig. 21).	Pleopods
	C2	Shaft long, with setules beginning after the annulation. These setules usually roll around their own axis, forming loops on the sides of the shaft (Fig. 22).	Telson, propodus of pereopods, and moveable finger of gnathopods
Pappose (D) (Figs 23-26)	D1	Shaft short, annulation marked, distal half of shaft branched in long setules with smooth edges, forming a tuft. (Fig. 23).	Antennae
	D2	Shaft long and robust with proximal half smooth; distal half of shaft with three rows of long setae (Fig. 24).	Inner plate of maxilla 2
	D3	Shaft short, with setules on distal half of shaft, arranged in several rows grouped on one side of the shaft. On distal third, the setules are arranged around shaft (Fig. 25).	Ventral inner border of inner plate of maxilliped
	D4	Shaft long, with setules arranged randomly from basal. Annulation weak (Fig. 26).	Ventral inner border of inner plate of maxilliped
Serrulate (E) (Figs 27-28)	E1	Shaft long, with wide setules arranged in two opposite rows on distal two thirds. Annulation present (Fig. 27).	Inner plate of maxilla 2
	E2	Shaft long and slender, with short slender setules arranged in two opposite rows from distal half of shaft. Annulation weak (Fig. 28).	Inner plate of maxilla 2

Continue

Table II. Continued.

Setal category	Label	Description	Distribution
Serrate (F) (Figs 29-32)	F1	Seta comb: shaft very long and robust, slightly flattened on distal end; distal half of shaft with one row of long delicate denticles arrangend in a spiral pattern around shaft. (Fig. 29).	Outer plate of maxilla 2
	F2	Similar to type F1, but on distal one third, of the side opposite to the denticles, there is a row of short setules; subterminal pore (Fig. 30).	Outer plate of maxilla 2
	F3	Shaft variable in length, robust, with terminal pore on lamellate and curved tip. Denticles in two nearly opposite rows on distal half of shaft. Annulation present (Fig. 31).	Peduncle of antennae, palp of maxilliped and gnathopods
	F4	Very robust with long shaft, slightly curved, proximal half of shaft smooth. Distal half of shaft with one row of strong and acute denticles. Articulation with cuticle and annulation weak (Fig. 32).	Outer plate of maxilla 1
Papposerrate (G) (Figs 33-34)	G1	Shaft long and robust (± 120 µm), with few long delicate setae, arranged aroud basal half of shaft. Distal half of shaft with robust setules with smooth edges, arranged densely around the shaft (Fig. 33).	Inner plate of maxilla 2
	G2	Similar to type D5, but less robust. Setules on basal half of shaft arranged only one side of shaft. Final third with setules arranged randomly. (Fig. 34).	Palp of maxilla 1



Figures 1-4. Types of cuticular structures found on *Hyalella*: (1) seta; (2) microtrich, arrows indicate pores; (3) denticles; (4) setules. Scale bar: a,c = 10 µm, d = 5 µm, b = 1 µm.

Only type I microtrichs (*sensu* Oshel *et al.* 1988) were found in the two species of *Hyalella*, with four subtypes identified (Tab. IV, Figs 35-39). Subtype Id is described here for the first time. Type II microtrichs are absent in both species. The microtrichs are observed on antennae, mouthparts, gnathopods, pereopods and on dorsal surface.

The setules showed two variations (Tab. IV), one that occurs on the inner surface of the oostegites (Fig. 40) and another on the mouthparts (Fig. 41).

We also observed three types of pores: simple, knobbed and projected (Tab. IV, Figs 42 and 43). The first two occur on the entire cuticular surface, whereas the last occurs only on the surface of the mouthparts. In some areas of the cuticle, the simple and knobbed pores were arranged in small polygons bounded by a narrow bar of non-porous cuticle. In general, several of these polygons were grouped together, forming what was termed by Bradbury *et al.* (1998) as "polygonal patterns" Two distinct patterns of distribution of the pores were observed within these polygons (Tab. IV, Figs 43 and 44).

Denticles were found mainly on the gnathopods and pereopods. These structures did not show significant variations in their morphology and generaly were grouped in two ways, forming either polygonal patterns (Fig. 45) or a comb scale (Fig. 46, Tab. IV).

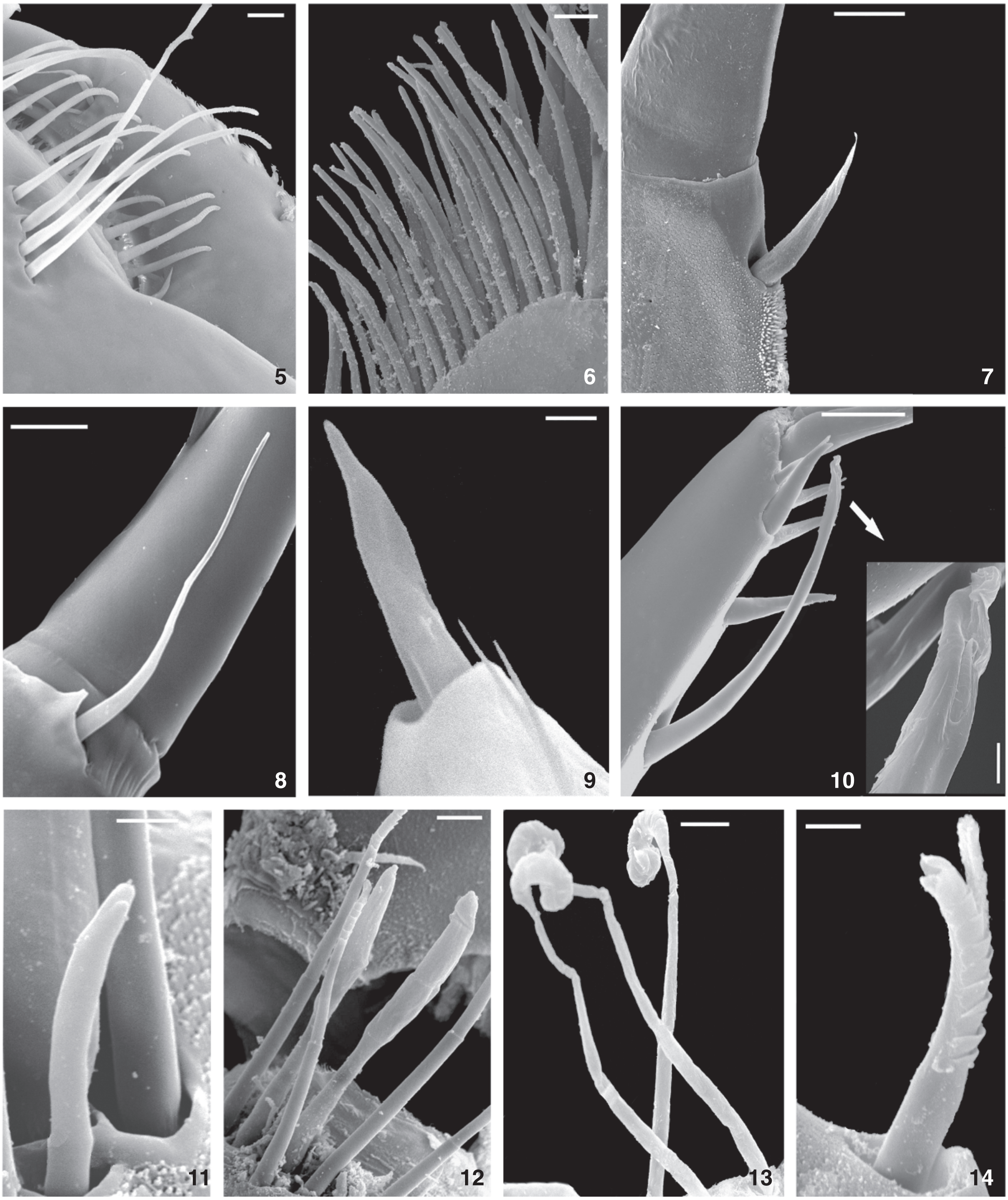
Hyalella castroi and *H. pleoacuta* are very similar in respect to type, morphology, and arrangement of the cuticular structures (Figs 47-75). However, differences were observed in the number of setae on the appendages and between the structures of the gnathopods of males and females in both species. Table V shows the arrangement of the structures on the appendages of the two species.

DISCUSSION

Diversity of cuticular structures

Setae

In both *H. castroi* and *H. pleoacuta*, three distinct types of cuspidate setae with an accessory seta were observed: B4, B5,



Figures 5-14. Simple setae found on cuticular surface of *Hyalella*: (5) seta A1 from gnathopod 1; (6) seta A2 from inner plate of maxilla 2; (7) seta A3 from dactylus of pereopods; (8) seta A4 from dactylus of pereopods; (9) seta A5 from maxilla 1; (10) seta A6 fom uropod 1 fom male, detail shows the distal end of the seta A6; (11) seta A7 from antenna 1; (12) seta A8 (Aesthetasc) from antenna 1; (13) seta A9 ("Curl tipped") from oostegites; (14) seta A10 from posterior margin of the coxa of pereopods. Scale bar: 5-9, 11 and 13 = 10 µm, 10, 12 = 5 µm, 14 = 2 µm.

Table III. Comparison of setal types found in *H. castroi*, *H. pleoacuta* with other Peracarids. Source: Fish (1972) [1], Brandt (1988) [2], Oshel & Steele (1988) [3], Wagner & Blinn (1987) [4], Read & Williams (1991) [5], Jaume & Christenson (2001) [6].

Setal category	Isopoda			Amphipoda			
	Present study	*E. pulchra* [1]	*S. hookeri* [2]	Gammarids and hyperiids [3]	*H. azteca*, *H. montezuma* [4]	*G. pseudolimnaeus* [5]	*Metacrangonyx* [6]
Simple	A1	Seta with nodules	–	3av	–	Simple seta	
	A2	Seta with blunt apex	–	3v	Club seta	–	
	A3	–	–		–	–	
	A4	–	–	3av	–	–	
	A5	–	–	3v	–	–	
	A6	–	–		–	–	
	A7	–	–		–	–	
	A8	Aesthetasc	–	Aesthetasc	–	Aesthetasc	
	A9	–	–		–	–	
	A10	–	–		–	–	
Cuspidate	B1	–	–	4f	–	–	
	B2	–	–	4f	–	–	
	B3	–		4f	–	–	
	B4	–	Sensory spine	3aiv	–	–	Bifid flagellate spines
	B5	–	Sensory spine	3aiv	–	Cone shaped	Bifid flagellate spines
	B6	Simple spine	Sensory spine	3aiv	–	–	Bifid flagellate spines
Plumose	C1	Plumose seta	–	4bi	–	Plumose seta	
	C2	Brush seta	–	4bi	–	–	Smooth setae with brush-like tip
Pappose	D1	–	–	4bii	–	–	
	D2	–	–	4bii	–	–	
	D3	–	–	4bii	–	–	
	D4	–	–	4bii	–	–	
Serrulate	E1	–	–	–	Rasp setae	–	
	E2	–	–	–		–	
Serrate	F1	–	–	–	Comb seta	Comb seta	
	F2	–	–	–	–	–	
	F3	Serrate bristle	–	3ai	–	–	Flagellate seta
	F4	Serrated spine	–	4d	Apical pectinate spine	–	
Papposerrate	G5	–	–	4bii	–	–	
	G6	–	–	4bii	Plumose seta	–	

Table IV. Description and distribution of microstructures on cuticular surface of *H. castroi* and *H. pleoacuta*.

Microstructure	Label	Description	Distribution
Microtrichs (M) (Figs 35-39)	Ia	Shaft short, with terminal pore directed to one side, and lamellas decorating the shaft on the side opposite the opening of the pore. On this same side, a hood projects apically, covering the pore (variation of type Ia of OSHEL *et al.* 1988) (Fig. 35).	Coxae of pereopods
	Ib	Similar to type Ia, but has a long filament proceeding from the hood, which exceeds the length of the shaft (variation of type Ib of OSHEL *et al.* 1988) (Fig. 36).	Antennae, palp of maxillipeds, gnathopods, and telson
	Ic	Shaft short and plumose, with branches of long filaments originating on distal third (variation of type Ic of OSHEL *et al.* 1988) (Fig. 37).	Coxal plates of a female of *H. pleoacuta*
	Id	Shaft short, wide, and flattened, with lamellar decoration (Fig. 38).	Coxal plates
Setules (S) Figs 40-41)	S1	S1: setules long, fine, and delicate, with long serrate edges, well spaced (Fig. 40).	Inner surface of oostegites
	S2	S2: setules of variable size and width, with serrate edges short and close together (Fig. 41).	Mouthparts
Pores (Figs 42-44)	Simple	Simple and rouded pores on three sizes: small, medium, and large.	Covered the surface of body
	Knobbed	Medium-sized pores with a knob on one side.	Covered the surface of body
	Projected	They have a tube-shaped prolongation so that the pore opening is above the cuticular surface (Fig. 42).	Mouthparts
Pores "polygonal patterns" (P) (Figs 43-44)	P1	Each polygon has several "knobbed" pores randomly arranged, with small simple pores between them. One large simple pore is present at some points where the polygons converge (Fig. 43).	Surface of telson
	P2	Similar to P1, but only the simple middle pores are present (Fig. 44).	Dactylus of maxillipeds
Denticles (T) (Figs 45-46)	T1	Polygonal pattern: the denticles are arranged in increasing, crescentic rows, and the inner part is filled by smaller denticles, forming a geometric pattern similar to a polygon. Several of these fit side by side and cover large areas on some appendages (Fig. 45).	Uper lip and gnathopods
	T2	Comb scale: the denticles are arranged in increasing straight rows or in crescents with no inner filling. Each row of these denticles has a united base that may be raised above the cuticle, forming a scale-like structure (Fig. 46).	Dactylus of maxilliped and gnathopods

and B6 (Figs 18-20). In other peracaridans such as the amphipod *G. pseudolimnaeus* and the isopod *E. pulchra*, only two types were recorded (BRANDT 1988, READ & WILLIAMS 1991). The seta B4 (Fig. 18), which has a movable socket, until the present was observed only in *Hyalella* males. The other two setae, B5 and B6, have a similar morphology to those observed in *G. pseudolimnaeus* and *E. pulchra*, but differ from these mainly in their arrangement on the appendages and the ornamentation of the accessory seta (Tab. VI). The cuspidate seta with accessory seta is, up to the present, exclusive to the Peracarida, and its morphology, ornamentation, and arrangement can characterize families, genera, or even species (BRANDT 1988). Our data, together with the above information, show that the arrangement of the cuspidate setae with accessory seta and the ornamentation of the accessory seta constitute a genus character for *Hyalella*. It is also worthy of mention that the analysis of these structures must take into account both aspects, morphology and arrangement, as the combination of them constitutes a genus characteristic.

In Decapoda, the articulation of plumose setae is always supracuticular (GARM 2004a, b). However, in Peracarida these setae can show two types of articulation, infra or supracuticular, as observed in Thermosbaenacea by WAGNER (1994). In *Hyalella*, the plumose setae always have an infracuticular articulation (Fig. 21), a characteristic also observed in the lotic amphipod *G. pseudolimnaeus* (READ & WILLIAMS 1991), in the marine amphipod *Gammaropsis inaequistylis* (Shoemaker, 1930) and *Hyale nilsoni* Hatke, 1843 (OSHEL & STEELE 1988), and also in the intertidal isopod *E. pulchra* (FISH 1972). Comparison of our data with available information in the literature indicates that the type of infracuticular articulation of the plumose setae is a character shared between amphipods and isopods. A close relationship between these two taxa was proposed by POORE (2005), and is now corroborated by this character.

Microtrichs

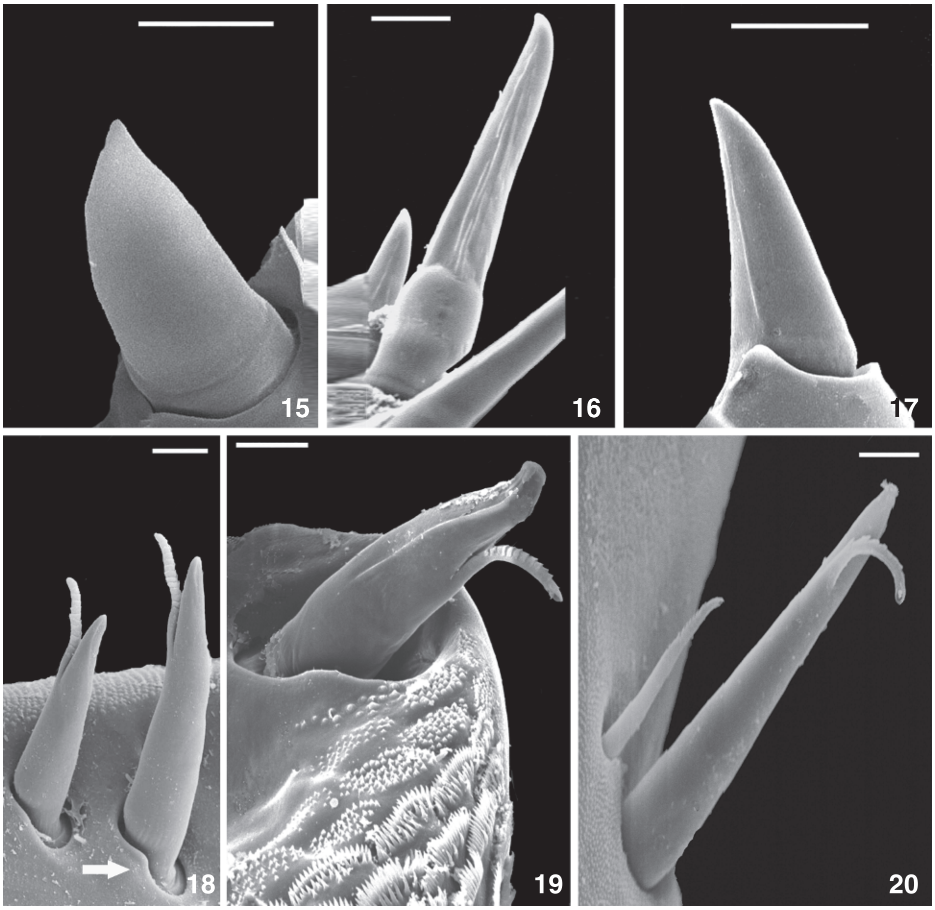
Differing from what were observed for the majority of amphipods by LAVERACK & BARRIENTOS (1985), OSHEL *et al.* (1988), and OLYSLAGER & WILLIAMS (1993), and also for some isopods

Table V. Distribution of cuticular structures of *H. castroi* e *H. pleoacuta*. setae: (A) simple, (B) cuspidate, (C) plumose, (D) pappose, (E) serrulate, (F) serrate, (G) papposerrate. Setal formula: article + (apex) x number of groups. (I) Microtrichs, (S) setules, (T) denticles. Segments: (ba) basal article, (c) carpus, (cl) carpal lobe, (da) distal article, (dab) disto anterior border of propodus, (fl) flagellum, (ir) inner ramus, (or) outer ramus, (pa) proximal article, (pb) posterior border of propodus, (pd) propodus dorsal view, (pv) propodus ventral view.

Appendages	Segment	*H. castroi*	*H. pleoacuta*
Antenna 1	ba	1-3 A1, 2C2 + 4A1,7F3,2B6	1-3 A1, 2C2 +4F3, 7A1, 2B6
	pa	3-4F3, 2-3 C2 +A1	2-4A1, 4-10F3, 2-3 C2 + A1
	da	liso + A1	0-2A1, 2C2 + A1
	fl	liso+ (2A7, 4A8, 4-6A1) x2	liso+ (2A7, 4A8, 4-6A1)x2
Antenna 2	ba	liso + 4-5F3, 9-10 A1	liso +9A1, 5F3
	pa	6-9F3, 2-3C2 0-2A1+ 4-6F3, 8-6A1	2-4A1, 2-3C2, 4-10F3 + A1, 2C2
	da	10-20A1, 2-3C2 + A1	6-18A1, 2C2 + A1
	fl	liso + (3-4A1)X4	liso + (3-4A1)X4
Gnatopod 1 male	dab	1-3F3	1-3F3
	pb	0-1 A1, 2-3 F3	0-1A1, 2-3F3
	pv	7-10 F3 + A1	6-9F3 + A1
	pd	A1	A1
	c	7F3, A1	5F3, A1
	cl	T1	T2
Gnatopod 2 male	dab	0-3F3	–
	pb	3-8A1	4-6A1
	pv	6-10A1 +17-20 B6, A1	3-5 A1 +18-20B6
	pd	3-4A1	3-4 A1
	c	T1	T2
	cl	F3	9F3
Gnatopod 1 female	dab	0-4 F3	1-4F3
	pb	1-6A1	1-6 A1
	pv	9-10,F3, A1	8F3, A1
	pd	4A1	3-5 A1
	c	5 F3, A1	5 F3, A1
	cl	T1	T2
Gnatopod 2 female	dab	1-2F3, 0-1A1	2-4, 0-1A1
	pb	2-5A1	1-6A1
	pv	5-8F3	4-5F3
	pd	4 A1	A1
	c	T1	T2
	cl	5-7F3	2F3
Uropod 1	ir	3 or 4 B6, 1 or 2 A6 male, 4 or 6 B6,1B2,1B3	3B6, 1 or 2 A6 male, 4B6,1B2,2B3
	or	5B6,1B2,2B3	4 or 5 B6,1B2,2B3
Telson		6C2, 2-4 B6	6C2, 6 B6

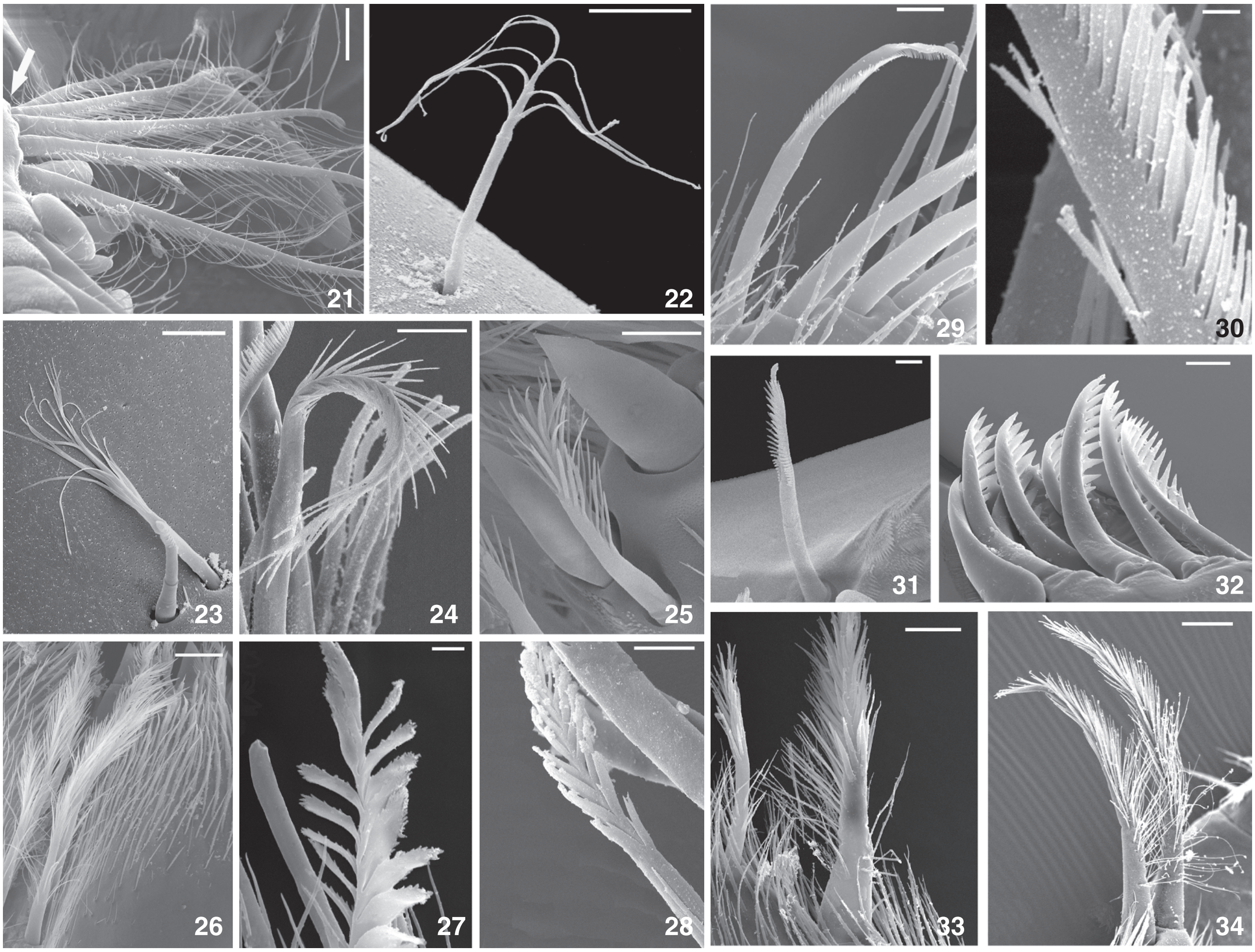
Table VI. Distribution and morphology of cuspidate seta with acessory seta in some Amphipoda and Isopoda. Source: Read & Williams (1991) [1], Brandt (1988) [2].

Type of setae	B4		B5		B6	
Species	Distribution	Decoration of acessory setae	Distribution	Decoration of acessory setae	Distribution	Decoration of acessory setae
Hyalella (present study)	Gnathopod 2 of males	Lamellate	Distal lobe of propodus of gnathopods	Lamellate	Pereopods, telson and uropods	Lamellate
G. pseudolimnaeus [1]	–	–	Gnathopods	Smooth	Pereopods, telson, uropods and antennae	Smooth
E. pulchra [2]	–	–	Gnathopods	Smooth	Pereopods	Smooth



Figures 15-20. Cuspidate setae found on cuticular surface of *Hyalella*: (15) seta B1 from inner plate of maxillipods; (16) seta B2 from distal margin of uropod 1 (17) seta B3 from distal margin of uropod 1; (18) seta B4 from gnathopod 2 males, arrow indicates the movable socket; (19) seta B5 from lobe of gnathopod 1; (20) seta B6 from uropod 1. Scale bar = 10 µm.

(Halcrow & Bousfield 1987), the two species of *Hyalella* have only type I microtrich (*sensu* Oshel *et al*. 1988). This type of microtrich generally shows a wide variation in the morphology of its socket (Oshel *et al*. 1988). In both species of *Hyalella* this ornamentation is quite simple, with only simple or knobbed pores. In *G. pseudolimnaeus* and *Gammarus oceanicus* Segerstråle, 1947, this socket has a lateral flap and short filaments (see Oshel *et al*. 1988b: 102, fig. 3a, Read & Williams 1991: 857, fig. 2c-1), and in *Gammaracanthus loricatus* (Sabine, 1821) the socket has only small filaments (see Oshel *et al*. 1988b: 102, figs 2b and 3a).



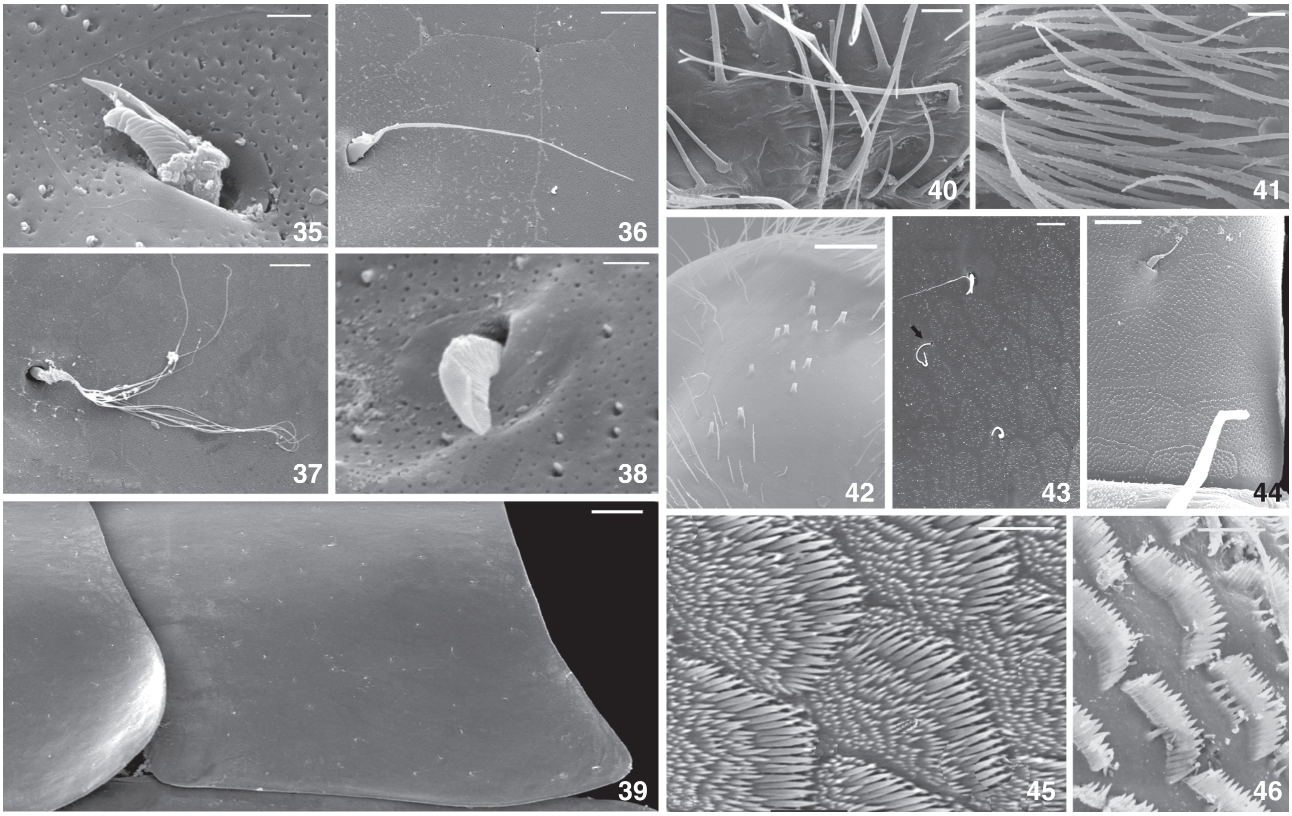
Figures 21-34. Plumose, pappose and serrulate setae found on cuticular surface of *Hyalella*: (21) plumose seta C1 from pleopods, arrow indicates the infracuticular articulation; (22) plumose seta C2 from telson; (23) pappose seta D1 from antenna 2; (24) pappose seta D2 from inner plate of maxilla 2; (25) pappose seta D3 from inner plate of maxillipeds; (26) pappose seta D4 from inner plate of maxillipeds; (27) serrulate seta E1 from inner plate of maxilla 2; (28) serrulate seta E2 from inner plate of maxilla 2; 29) serrate seta F1 from outer plate of maxilla 2; (30) serrate seta F2 from inner plate of maxilla 2; (31) serrate seta F3 from gnathopod 2; (32) serrated seta F4 from maxilla 1; (33) papposerrate setae G1 from inner plate of maxilla 2; (34) papposerrate setae G2 from inner plate of maxilla 1. Scale bar: 21, 26, 29, 30 and 34 = 20 µm; 22-25, 31 and 33 = 10 µm; 27-28 = 2 µm; 32 = 1 µm.

Setules

The record of setules S1 occurring on the inner surface of the oostegites of both species of *Hyalella* is new for Peracarida. However, their morphology corresponds to that of the "barbed seta" found by Wagner & Blinn (1987) on the maxilla of *H. azteca* and *H. montezuma*.

Pores

Little is known about the arrangement of pores on the cuticular surface of Amphipoda, but it's known that these are abundant and show quite varied arrangements (Halcrow & Bousfield 1987). In *H. castroi* and *H. pleoacuta* we observed two different patterns of pore arrangement, always within polygons. Each pattern is found in a specific area of the cuticle, with an identical arrangement in both species. Comparing these patterns with those described for other gammarideans by Halcrow & Bousfield (1987), we percive that pattern P1 (Fig. 42) is identical in form as well as arrangement on the cuticle, to that observed for another dogielinotid, *Proboscinotus loquax* (Barnard, 1967). Pattern P2 (Fig. 43), although identical in form to that observed for *Eohaustorius washingtonianus* (Thorsteinson, 1941), differs from this in its arrangement on the cuticle. None of the patterns found here is comparable to that observed by Read & Williams (1991) for the freshwater gammarid *G. pseudo-*



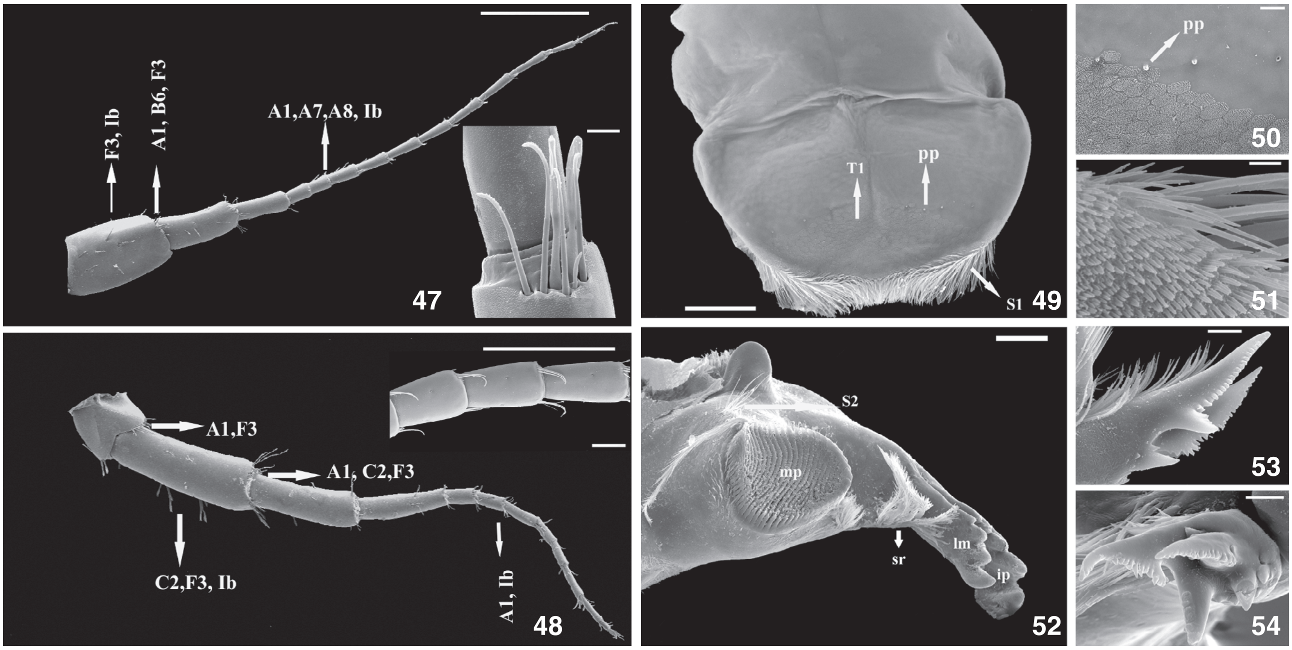
Figures 35-46. Cuticular surface of *Hyalella*. (35-39) Microtrichs: (35) type Ia from coxa; (36) type Ib from dorsal surface of the body; (37) type Ic from coxal plate; (38) type Id from coxal plate; (39) arrangement of microtrichs Ib on dorsal body surface; (40-46) pores and denticles: (40) setule S1 from oostegites; (41) setule S2 from maxilla 2; (42) projeted pore from lower lip; (43) pores polygonal pattern P1 from telson, arrow shows some being extruded from pore; (44) pores polygonal pattern P2 from antenna 2; (46) denticles polygonal pattern T1 from gnathopod 2; (46) "comb scales" denticles T2 from posterior lobe of gnathopod 2. Scale bar: 35, 36 and 38 = 1 µm; 39 = 100 µm; 40 = 2 µm; 37, 43, 44 and 46 = 10 µm; 41 and 42 = 20 µm; 45 = 5 µm.

limnaeus, which suggests that this characteristic is not associated with the environment. According to HALCROW & BOUSFIELD (1987) and HALCROW & POWELL (1992), the arrangement of pores on the cuticular surface of Amphipoda is a family-level character. This hypothesis is corroborated by our data, and at the same time reinforces the proposal of SEREJO (2004), who recently transferred the genus *Hyalella* to the family Dogielinotidae.

Further, with respect to the pores, we observed that some material is expelled through the larger pores (Fig. 43), as previously suggested by HALCROW (1978, 1985), BOROWSKI (1985), MOORE & FRANCIS (1985), and HALCROW & BOUSFIELD (1987).

Denticles

The polygonal patterns (Fig. 45) and the comb scales (Fig. 46) formed by the denticles have been reported for gammaridean amphipods by many workers as "polygonal pattern" WILLIAMS & BARNARD (1988); "echinate fields" *sensu* HOLMQUIST (1989); "rugosities" sensu BRADBURY *et al*. (1998); "scutellated scales" and "caespitose patch" *sensu* JAUME & CHRISTENSON (2001). In adition, comb scale-like structures were also reported for some isopods "microtrich crescentic" *sensu* NEEDHAM (1942) and FISH (1972). Both types of comb scale-like structures were used by WILLIAMS & BARNARD (1988) in characterizing the freshwater families Neoniphargidae and Crangonyctidae. However, comparisons between literature data and our results are difficult because the avaiable descriptions and photographs are not detailed and there is no consensus in the use of terminology. BRADBURY *et al*. (1998), working with different families of marine gammarideans, stated that their "rugosities", located basically on both gnathopods, are produced by microsetae, that is, structures that show a point of articulation with the cuticle; however, in some of his figures, it is clear that these rugosities are denticles. The "echinate fields" of *Talitroides alluaudi* (Chevreux, 1896) and *Talitroides topitotum* (Burt, 1934) (HOLMQUIST 1989) are actually produced by small setae, and because of this cannot be compared to the formations observed here. Similarly, the cuticular polygons cited by



Figures 47-54. Distribution of cuticular structures of *Hyalella*. (47-48) From antenna 1 e 2: (47) antenna 1, detail of arrangement of setae on flagelum of antenna 1; (48) antenna 2, detail of arrangement of setae on flagelum of antenna 2; (49-54) on mouthparts: (49) upper lip, dorsal view; (50) detail of arrangement of cuticular structures on dorsal surface of upper lip; (51) detail of transition of denticles to setules on distal bord of upper lip; (52) Rigth mandible, arrow indicates the penicilium; (53) typical left lacinia mobilis of *Hyalella*; (54) The left lacinia mobilis of *H. pleoacuta* could be trifurcate. Scale bar: 47-48 = 500 µm; 49, 52 = 50 µm; 50, 53 and 54 = 10 µm; 51 = 2 µm. (A-G) Setae, (S) setules, (I) microtrichs, (lm) Lacinia mobilis, (ip) incisor process, (mp) molar process, (pp) projected pores, (sr) setal row, (T) denticles.

Williams & Barnard (1988) were observed only with a light microscope, which makes it difficult to define the kind of cuticule structure that compose them.

For the genus *Hyalella*, this cuticular structures and its arrangement on the appendages were shown to be important characters (see discussion below) for separation of the species.

Location of cuticular structures

Mouthparts

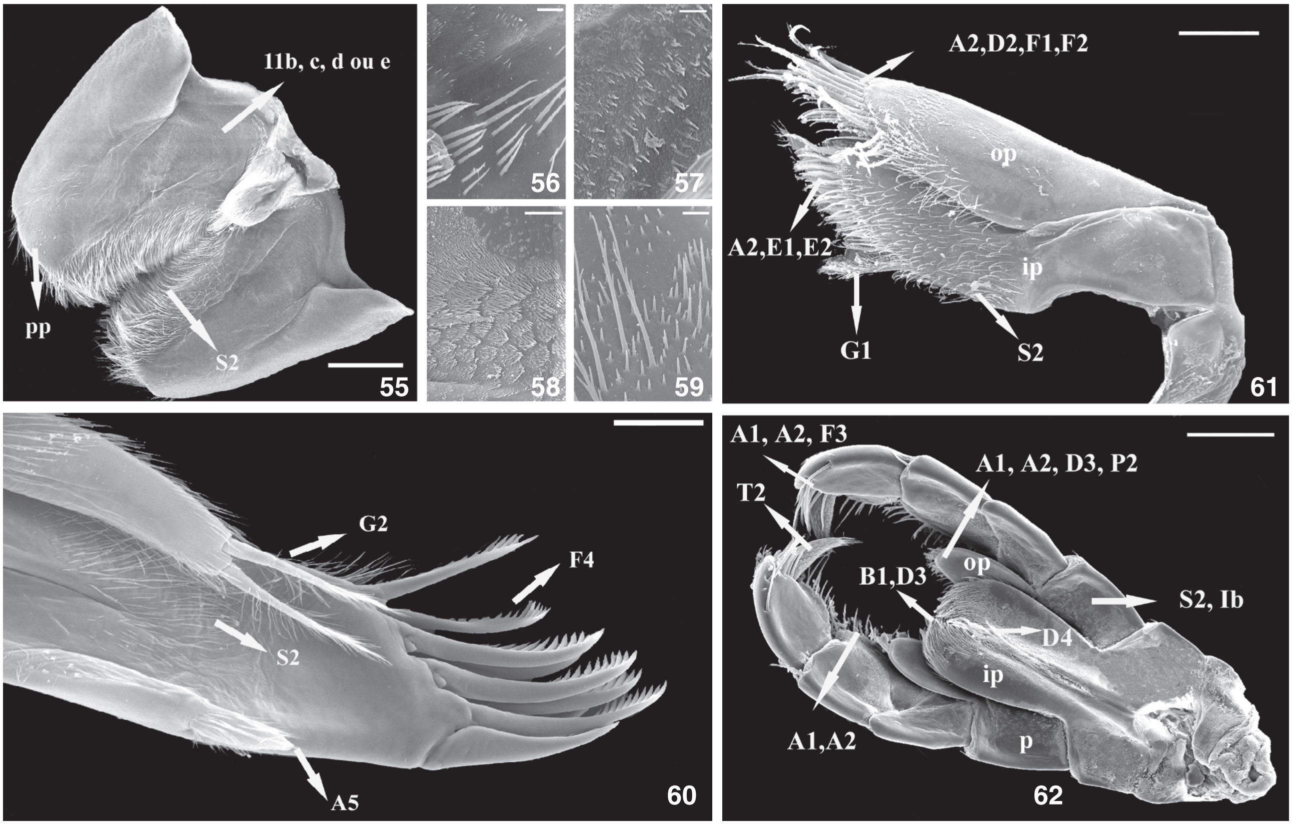
Examination of the mouthparts of *Hyalella* species (Figs 49-62) revealed great similarity in form as well as in structure. The setae found on maxillas 1 and 2 of the two species did not differ, at least in general morphology and diversity, from those observed by Wagner & Blinn (1987) for *H. azteca* and *H. montezuma*. This similarity was expected, because the morphology of the mouthparts differs little among related species of Amphipoda (Arndt *et al.* 2005). However, some intra- and interspecific variability in the type of structure (setules and/or denticles) as well as in their distributional pattern (Figs 56-59) was observed in the ornamentation of the ventro-proximal surface of the lower lip.

Similar to observed in Thalassinidea by Coelho & Rodrigues (2001a, b) and Pinn *et al.* (1999) a wide diversity of setal types was found in the mouthparts of the two species, indicating that they are capable of manipulating a wide variety of food items and can use more than one feeding mode (Macneil *et al.* 1997, Arndt *et al.* 2005). When more than one feeding modes are possible, the principal mode that the animal uses to obtain food can vary with the microhabitat and its available resources. From the ecological perspective, this character constitutes a great adaptive advantage for this genus.

A peculiar character of the mouthparts of both species is the presence of elongated pores. Similar pores, called excretory pores, were also found in *Lophogaster typicus* M. Sars, 1857 by de Jong *et al.* (2002), and in Isopoda (Gorvett 1946). These pores probably function to lubricate food particles, as suggested for the shrimp *Penaeus merguiensis* De Man, 1888 (McKenzie & Alexander 1989). The arrangement of pores on the mouthparts is different in all the species and groups previously mentioned; however, the sparse information on the subject does not allow us to evaluate its taxonomic value.

Other appendages

On the other appendages, the most significant differences between the two species were observed in the ornamentation of gnathopods 1 and 2. The distal end of the both gnathopods



Figures 55-62. Distribution of cuticular structures on mouthparts of *Hyalella*: (55) lower lip, ventral view; (56-59) details of diferent types of decoration found on ventral surface of lower lip; (60) maxilla 1, ventral view; (61) maxilla 2 of *H. castroi*, dorsal view; (62) maxillipeds, ventral view. Scale bar: 55, 61 and 62 = 100 µm, 56-59 = 5 µm; 60 = 50 µm. (A-F) Setae, (S) setules, (pp) projected pores, (ip) Inner plate, (op) outer plate, (p) palp, (T) denticles, (P) pores, (I) microtrichs.

carpal lobe is ornamented with many denticles, which in *H. castroi* form a continuous bar in a polygonal pattern (Fig. 66), and in *H. pleoacuta* form two consecutive rows of comb scales (Fig. 67). The denticle ornamentation has been analyzed on the carpus of gnathopods of several other species of *Hyalella* (Bond-Buckup and Araujo pers. comm.), and has shown important differences for species separation. The same occurs with the ornamentation of the distal portion of the posterior border of both female gnathopods of, which in *H. pleoacuta* bears comb scales, and in *H. castroi* is smooth (Figs 68-71). The sexual dimorphism observed in gnathopod 2 is accentuated by the absence of the B4 cuspidate setae in females, a character of *Hyalella*.

The distribution of B6 on uropod 1 and the number of cuspidate setae on the telson were also considered a species character for *Hyalella*.

The morphology, arrangement, and diversity of cuticular structures of *Hyalella* constitute important tools for taxonomic analyses, principally at the genus and species levels. Moreover, the comparisons made here provide strong indications that cuticular structures can contribute very significantly to elucidate the systematics of Peracarida.

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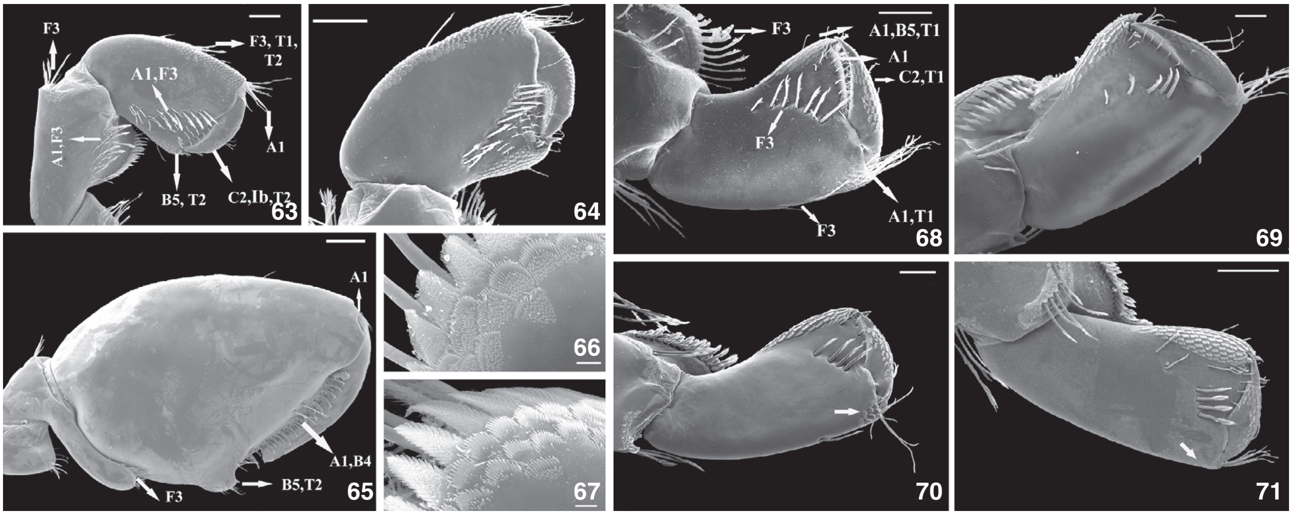

Figures 63-71. Distribution of cuticular structures on gnathopods of *Hyalella*. (63-67) Male: (63) gnathopod 1 of *H. castroi*, ventral view; (64) gnathopod 1 of *H. pleoacuta*, ventral view; (65) gnathopod 2 of *H.castroi*; (66) detail of ornamentation of carpus of gnathopod 2 of *H. castroi*, ventral view; (67) detail of ornamentation of carpus of gnathopod 2 of *H. pleoacuta*, dorsal view; (68-71) females: (68) gnatopd 1 of *H. pleoacuta*, ventral view; (69) gnathopod 1 of *H. castroi*, ventral view; (70) gnathopod 2 of *H. pleoacuta*, ventral view, arrow shows "comb scales" on bordo antero distal margin; (71) gnathopod 2 of *H. castroi*, arrow shows the absence of "comb scales" on antero distal margin. Scale bar: 63, 64, 68 and 70 = 100 µm; 65 = 200 µm; 66 and 67 = 5 µm; 69 and 71 = 50 µm. (A-F) Setae, (S) setules, (T) denticles, (I) microtrichs, (P) pores.

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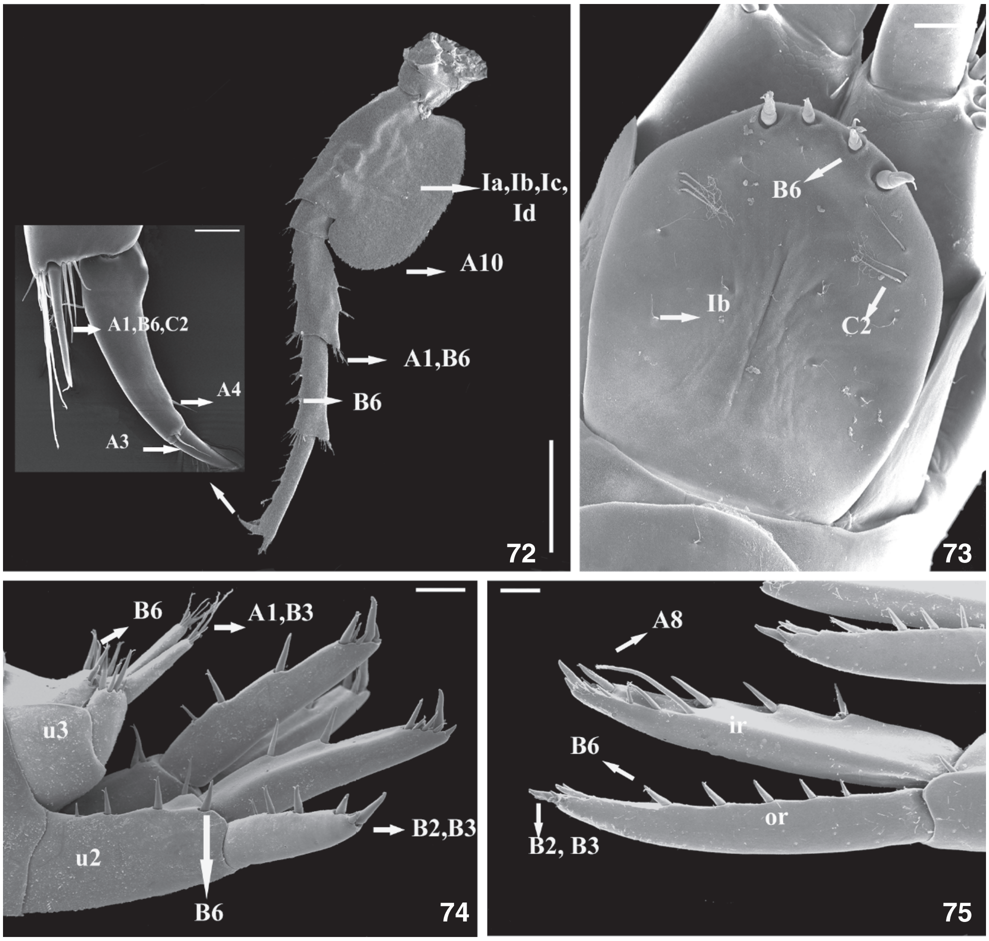

Figures 72-75. Distribution of cuticular structures on pereopods, telson and uropods of *Hyalella*: (72) pereopod 7, detail shows dactylus; (73) telson, dorsal view; (74) uropods 2 and 3; (75) uropod 1, male. Scale bar: 72 = 1mm; 73 = 50 µm; 74, 75 = 100 µm. (A-F) Setae, (S) setules, (T) denticles, (I) microtrichs, (ir) inner ramus, (or) outer ramus, (u1) uropod 1, (u2) uropod 2.

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