Description of *Hypogeoppia belgicae*, a new species of cave mite (Acari, Oribatida), and comments on some characters

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ABSTRACT. The Oppiidae (Acari, Oribatida) are one of the largest families of Circumdehiscentiae. Within this family, the genus *Hypogeoppia* comprises few species, all soil organisms. Here we describe a new species, *H. belgicae*, from adult specimens collected in caves in South Belgium. Several characters showed a substantial variability in the two populations studied. In addition, *H. belgicae* displays some uncommon or unique apomorphic features such as a notogasteral posteromedian notch, prodorsal and podosomatic taenidia, elongated chelicerae, internal subcapitular septa, and tracheal vesicles III.

KEY WORDS : Oribatida, Oppiidae, Circumdehiscentiae, Hypogeoppia, taxonomy, description, cave, Belgium

INTRODUCTION

The present paper describes a new species of Oppiidae Grandjean, 1951 (see GRANDJEAN, 1953, for a definition of the family) which, according to SUBIAS (1981) and SUBIAS & BALOGH (1989), we assign to the genus *Hypogeoppia* Subias, 1981. Beside the new species, the genus *Hypogeoppia* consists of five species, one subspecies and two varieties. Most *Hypogeoppia* have a limited distribution, and have been collected only in Europe (but see SUBIAS, 1981, for an outstanding exception). They are soil dwelling organisms lato sensu. To date, no *Hypogeoppia* was found in Belgium. The new species, *H. belgicae*, has been collected in South Belgium (DUCARME et al., 2003).

New and uncommon characters were detected in this species. Additional information regarding some of these characters and in particular the possible role of some of them is provided in the discussion below.

MATERIAL AND METHODS

The terminology used follows that of F. Grandjean (see VAN DER HAMMEN, 1980, for definitions and references). Yet it should be noted that : (1) the terms 'adaxial' and 'abaxial' used for an element (a structure, a segment or a phanere) mean 'drawn up to' and 'moved away from' the plane of symmetry, respectively; (2) the prime (') and double prime ('') symbols are equivalent to the terms anterior and posterior, respectively; in the appendages, a ' phanere is anteriad of the plane of pseudosymmetry, and a '' phanere is posteriad; in addition, due to the destruction of the plesiomorphic, perpendicular parallelism of appendages (see GRANDJEAN, 1961a, for a discussion), the ' phaneres are

adaxial in the pedipalpi and legs I and II, and abaxial in the legs III and IV, and the "phaneres are abaxial in the legs I and II and adaxial in the legs III and IV; (3) the brackets are used to indicate the setae of a pair. The abbreviations not used in the text are defined in the keys of figures.

The length of the body, excluding the gnathosoma, was determined in dorsal projection. The length and height of chelicerae and rutella were measured in lateral projection (the largest sizes were taken into account for these measurements as well as for the data reported here). Some characters were studied by comparison with two closely related species, namely *H. perezinigoi*, some specimens of which were generously sent by Dr. L.S. Subias, and *Berniniella sigma conjuncta* (Strenzke, 1951), a soil dwelling oppid mite collected in some caves inhabited by *H. belgicae* (DUCARME et al., 2003). Observations were conducted in light microscopy (LM), in scanning electron microscopy (SEM) and, in collaboration with Prof. G. Alberti, in transmission electron microscopy (TEM).

DESCRIPTION OF *HYPOGEOPPIA BELGICAE* (FIGS 1-6)

Diagnosis

Hypogeoppia with the rostral setae *ro* inserted close to the plane of symmetry. A long and sinuous gutter *tp* developed on both sides in the prodorsum, and regarded as a taenidium. Notogaster : with anteromedian region occupied to a large extent by a pair of dorsosejugal apophyses Dp and their companion carinae ke and ki; with adaxial companion carinae ki substantially elongated; and with posterior border provided with a median, U-shaped notch. Epimeric furrows 4 transformed into gutters

regarded as taenidia. Tracheae III with two branches, the lower one in the form of a vesicle. Penis apparently with only two pairs of eugenital setae. Subcapitulum with a pair of strong internal septa separating on both sides the pharynx from the base of the pedipalpi. Mentum with a large, unpaired and U-shaped carina *cc*. Rutella with a pad-like free extremity. Chelicerae elongated.

Size, color, cerotegument, setae

Mean total length : 257 μ m in males (n = 10; range 248-271 μ m); 266 μ m in females (n = 10; range 256-282 μ m). Body colour yellowish brown, yet chelicerae and pedipalpi paler, dorsal region of the subcapitulum and rutella colourless and distal part of the leg tarsi apparently whitish when observed in reflected light.

Cuticle: (1) apparently smooth except in some places where a granular microsculpture exists (see below); (2) bright in reflected light, yet duller where a layer of cerotegument is developed. Parts of the body usually covered by the cerotegument according to observations in transparent light : (1) dorsally, the anterior and posterior, dorsosejugal apophyses Da and Dp, the prodorsum between the apophyses Da, the sejugal furrow ssj, and the parts of the notogaster abaxially with respect to apophyses Dp; (2) laterally, a large zone from the lateral gutter tp of the prodorsum to the border of the notogaster bng, except above the bothridia, and all the podosomatic region; (3) ventrally, the environs of the podocephalic fissures F, and a strip running abaxially on all the metapodosoma and widening out posteriorly. Note that observations by means of sections through freshly-collected individuals confirmed the existence of the cerotegument in the prodorsal gutters tp and in the epimeric gutters 4, and revealed that it spread out inside the bothridia (ALBERTI, pers. com.). Cerotegument composed of numerous, conical and pointed microprojections.

Setae : (1) usually in the form of thin phaneres tapering off substantially so that they end with a long point; (2) without a base tubercle discernible in LM, with a few exceptions (e.g. all the setae of the prodorsum).

Prodorsum

Rostral hood ending in a quite broad limbus (the breadth of the limbus near the plane of symmetry can be estimated in Fig. 1a insofar as its base corresponds to the extremity of the ducts originating from the alveoles of the rostral setae *ro*). The two rostral slits clearly V-shaped in apical view. Rostrum lanceolate between the slits.

Dorsovertex : (1) in the form of a robust bulge with well discernible, anterior and lateral borders, and depressed sagitally; (2) lateral borders forming steep carinae frequently obliterated anteriorly, and sometimes interrupted by a shallow groove not reaching the plane of symmetry, at the level with the interlamellar setae *in*. No true lamellae. Yet, anteriad of the dorsovertex, a pair of low and oblong convexities *kd*, parallel to the plane of symmetry, on which the lamellar setae *la* are inserted anteriorly. Prodorsal surface depressed between the convexities *kd*, and inclined up down to the sejugal furrow *ssj*, posteriad of the dorsovertex, between the dorsosejugal apophyses Da; ordinarily with an elongate, more or less oblique concavity in the middle of the sloping zone. Apophyses

Da prolonged adaxially, by a companion carina ordinarily bent towards the plane of symmetry, and abaxially, by the lateral border of the dorsovertex. Note that : (1) in some individuals, the apophyses Da were broader or narrower than in Fig. 1a; (2) in two individuals, the apophyses were divided into two on the left side.

Gutters tp. Higher extremity located just underneath the convexity kd (Figs 1a and 2); prolonged in front by an elongated hollow also situated below the convexity kd. Lower ending formed by an oblique carina kt in front of the legs I (Figs 1b and 2; note that, in Fig. 1b, the carina is merged into the lateral apparent outline of the podosoma). Between these two extremities, gutter tp made up of an upper part, directed upwards and backwardly curved, and a lower part, forwardly curved and encompassing dorsally and anteriorly the circumtrochanteral opening of the legs I, with an elbow-shaped junction (Fig. 2). Borders obvious everywhere except frequently above the carina kt for the anterior border, and less frequently above the elbow and in the elbow itself for the posterior border. Note that : (1) a broadening of the gutters was sometimes detected at the level with the elbow, whereas the lower part habitually widens out in front of the legs I; (2) in some cases, there was a narrowing before the gutter widens out. Dorsally, upper part of the gutters with a microsculpture made of roughly widthwise orientated ridges which usually block the gutter incompletely, and tend to demarcate small curved-walled chambers of variable number and outline. Moreover, often an oblique ridge, sometimes thick, at the level with the elbow (Fig. 2). Note that : (1) in consideration of their microsculpture, the prodorsal gutters comply unambiguously with the definition of taenidia sensu GRAND-JEAN (1944); (2) analogous lateral teanidia exist in Bernin*iella sigma conjuncta*, yet they are missing in *H. perezinigoi*.

Bothridia wide-open; borders : (1) provided with striae (not represented in Fig. 1a; as shown in Fig. 2, they are less numerous anteriorly); (2) higher, wider and longitudinally grooved posteriorly (the grooves are well marked and their walls are steep; they get narrower in their mid part so that the borders of bothridia seem to possess two small tubercles backwards). Sensilli bo with a relatively short stem, and with a fusiform club bearing small thorns at wide intervals. Region close to the trichobothria embossed and variable between individuals, yet with three elements usually found : (1) in front of the trichobothria, a short, transversal ridge sometimes changed into a small tubercle; (2) above the trichobothria, a longitudinal, curved convexity (note that the interlamellar seta in is inserted between the convexity and the lateral border of the dorsovertex); (3) posteriorly, an ordinarily rounded protuberance between the convexity and the apophysis *Ba*.

Setae. Lamellar setae *le* very short and slender. Other prodorsal setae long and thin. Setae *le* and apparently exobothridic setae *ex* smooth. Setae *in* and rostral setae *ro* bearing small barbs. Setae *in* longer than the others, similar to notogasteral setae; making their way upwards. Setae *ex* and *ro* orientated forwards. Base tubercle of the setae *ex* changed into a robust nodosity. Setae *ro* clearly bent to the plane of symmetry; their insertion slightly but invariably asymmetric.

Granular microsculpture constantly detected : (1) on a small surface before the upper part of the gutters tp as well as in the gutters tp; (2) behind this surface; (3) above the legs I; (4) on the apophyses Da.



Fig. 1. - Hypogeoppia belgicae n. sp., male, with the legs partially seen in the left side. - a, dorsal. On the left side, the hatching indicates the dorsosejugal enantiophysis Da-Dp and its companion carinae. On the right side, the hatching points out the thickness of the tegument beneath the upper ending of the lateral, prodorsal gutter tp and the hollow in front of it. The granular microsculpture is only shown before the gutters tp, on the free border of the pleural carinae kl, and on the supradiscidial carinae kp. The muscular impressions on the lateral sides of the prodorsum and those of the circumdorsal alignment in the notogaster are delimited by a dotted line. The punctuated areas in the trochanters III and IV and in the femora I, II and III are also marked by a dotted line (the punctuation is not shown). - b, ventral. The hatching marks : in the podosoma, an optical section through the cotyloid wall II on the left side (vertical hatching), and the base of the apodemes ap.2 and ap.sj on both sides and of the sternal apodeme (oblique hatching); in the opisthosoma, the internal anterior nervure of the right genital valve, and an optical section through the postanal fossa. The broken lines seen through the cuticle of the rutella and directed backwards mark the abaxial apparent outline of the lateral lips. The points Js indicate the upper oral commissures. On both sides, the curved line near the base of the pedipalpus represents a carina (the anterior, longitudinal part of the carinae is not shown); behind, the curved broken line marks the apparent outline of a protuberance borne by the subcapitular septum. The two broken lines behind the border bm of the mentotectum are the posterior apparent outline of the mentum, and the posterior limit of the epimeric band borders 1. The small ridges that interrupt the taenidial gutter tv are partially seen on the left side. The dots on the right genital valve indicate the base of the genital setae. The lines on the fold that the articular cuticle tgs of dorsoventral connection forms posteriorly at the level with the notogasteral notch, are lines of apparent outline. The granular microsculpture is only shown in places. The muscular impressions on the mentum, epimera (only on the right side) and opisthosoma, and those of the marginoventral alignment mu.mv in the ventral shield are delimited by a dotted line. For the punctuated areas in the femora I, II and III, see above. μ , insertion of a tendon. bt, base of the rostral tectum. bv", ev', proximoventral seta of the leg femora I and II, and III and IV, respectively. ca, line of apparent outline. d, l, v, dorsal, lateral and ventral setae of the appendages, respectively. ph, pharynx.



Fig. 2. – *Hypogeoppia belgicae* n. sp. – Scanning electron micrograph of the anterior part of the body laterally orientated; left side of an animal a bit inclined to the left. The prodorsum (*PD*), the notogaster (*NG*) and the legs are partially seen. The propodolateral prominence *P* is almost completely hidden. *FI*, *FII*, femur of the legs I and II. *RIII*, *RIV*, trochanter of the legs III and IV. Scale bar, $20 \mu m$.

Notogaster

Anterior border clearly convex in its middle (Fig. 1a). Dorsosejugal apophyses Dp and companion carinae ki and ke robust (Figs 1a and 2). Free border of the apophyses Dp: (1) forming an oblique and convex forwards line in dorsal projection (Fig. 1a) (note that, in some individuals, the free border was more rectilinear than in Fig. 1a, on one side or on both sides); (2) making a contrasted angle with the adaxial carina ki, yet prolonged linearly by the abaxial carina ke; (3) in contact with the prodorsal dorsosejugal apophysis Da when the animal is contracted. Carinae ki usually a bit undulating horizontally (even sometimes distinctly sinuous), and

extending longitudinally and a bit obliquely so that they meet posteriorly. Notogasteral surface depressed between the two carinae *ki*; ordinarily with one, rarely two short and weakly curved ridges in the depression. Oblique and more or less robust convexity developed on both sides between the carina *ke* and lyrifissure *ia*.

Articular cuticle present everywhere at the limit between the notogaster and the rest of the body : (1) anteriorly, narrow and tearing cleanly in the dissections; (2) posteriorly, making up a sagittal fold due to the notch of the notogaster (the cuticle of dorsoventral connection is labelled *tgs* in Fig. 3a); when the animal is contracted, the fold is directed towards a fossa located on the ventral shield behind the anal opening (postanal fossa), in the bottom of which it ends (Fig. 3b); beyond, directed upwards and backwards before attaching to the ventral shield (the line of attachment is labelled *at* in Fig. 3) so that, in lateral projection (Fig. 3b), conspicuously bent in the plane of symmetry. Note that according to observations in SEM, the borders of the notogasteral notch can draw even nearer to each another than represented in Fig. 3a.

Dorsophragma and pleurophragma absent. Circumdorsal groove apparently deficient according to a careful examination in transparent light, even after heating in lactic acid (this contrasts with many other Circumdehiscentiae, yet see similar examples in the Autognetidae, a family closely related to the Oppiidae; GRANDJEAN, 1963). Lyrifissures *ia*, *im* and *ip* (slit sense organs) well distinguishable; lyrifissures *ih* and *ips* apparently missing.

With 20 setae. Note that : (1) the chaetotaxy corresponds to the *Dometorina* type (GRANDJEAN, 1950, 1956a) shown by many Circumdehiscentiae in which the centrodorsal setae and two setae of the row c are lost; (2) for labelling the notogasteral setae, we used the *Dometorina* notations modified by LIONS (1970). All the setae long and slightly barbed, except the setae ps2 and ps3, which seem smooth. Setae c2 inserted on the lower wall of the carinae ki (Fig. 2), and with a base tubercle distinguishable in LM. On both sides, seta cp inserted at the junction of two short ridges, which diverge posteriorly.

Lateroabdominal glands gla similar to small, oblong bags; usually opened near the setae h3.



Fig. 3. – *Hypogeoppia belgicae* n. sp., female. – Posterior parts of the notogaster and ventral shield in a contracted animal, partial, with the anal valves removed. – a, seen from the back. Lines (broken) of apparent outline in the median, posterior fold of the articular cuticle *tgs* of dorsoventral connection are shown through the cuticle of the notogaster. The part of *tgs* which turns beyond the fold towards the line *at* of attachment to the ventral shield and emerges from the postanal fossa (its border is indicated by the dotted line *fp*), is not distinguishable in this orientation. *mu.mv*, marginoventral alignment of insertions of dorsoventral, opisthosomatic muscles – b, right lateral. The horizontal hatching represents an optical section of the tegument passing through the plane of symmetry. *bs*, border of the ventral shield.

Ventral region of the podosoma

Epimeric furrow 3 absent. Epimeric furrow 2 and epimeric sejugal furrow obstructed by several short ridges arranged crosswise (some ridges robust, with widened extremities). Epimeric gutters 4 (labelled tv in Figs 1b and 2) : (1) ornated with granules and ridges of variable size, and roughly widthwise orientated; note that this microsculpture, though more compact and more variegated than that of the prodorsal gutters tp, led us to class the epimeric gutters tv as taenidia (GRANDJEAN, 1944); (2) adaxially, narrowing and ending close to the circumgenital opening; (3) with an anterior border obvious everywhere, and with a posterior border less pronounced abaxially; (4) showing a V-shaped deviation at the level with the seta 4a, in some individuals, in one side or in both sides; (5) passing round the acetabular region IV abaxially, and making their way longitudinally and a bit obliquely on the pleural region towards the large carina kl (Fig. 2). Note that epimeric taenidia with an analogous course were found in *H. perezinigoi* and *B. sigma conjuncta*.

Sagittal region of the podosoma, in the epimeron I, with a chitinous thickening anteriorly, joining the base of the mentotectum in front, and usually with a roughly triangular outline in ventral projection (note that, in some individuals, its surface was substantially reduced), and a sternal apodeme posteriorly (hatched in Fig. 1b). Sternal furrow absent.

Three conspicuous apodemes present, namely ap.1, ap.2 and ap.sj, each consisting of two half apodemes large and apparently not perforated. Half apodemes ap.1: (1) in their longitudinal part, connected with the lateral edges of the

sagittal thickening and with the free border of the sternal apodeme (note that the half apodemes *I* are not represented Fig. 1b except their posterior limit indicated by a transversal, forwardly curved broken line behind the seta *la*; note also that, in apical projection, the longitudinal parts of the the half apodemes 1 appear to be directed obliquely upwards; ALBERTI, in litt.); ordinarily, as shown in Fig. 1b, connexion not extending to the posterior end of the sternal apodeme; (2) in their transversal part, united as usual with the base of the mentotectum and with the cotyloid wall cot of the acetabulum I (GRANDJEAN, 1952, 1968). Half apodemes 2 apparently a bit higher than half apodemes *ap.sj*, yet with a base approximately of a size (Fig. 1b). Epimeric band borders bo3 indistinct. Band borders bo1, bo2 and bo.sj relatively narrow. Band borders bo2 and bo.sj apparently connected to each other in the sagittal region; connections usually broad (Fig. 1b), yet scarcely visible and even imperceptible in some individuals.

Setae. Formula of coxisternal setae : (3-1-3-3), i.e. the formula characterizing the Circumdehiscentiae without deficiency (GRANDJEAN, 1934). Setae 3b, 3c and 4c longer than the other setae. Setae 3c and 4c bearing some minute barbs; other setae apparently smooth. Setae 4c with a discernible base tubercle. Note that the labels 4a and 4b used for the posterior epimeric setae in Fig. 1b require a confirmation in so far as immatures are unknown.

Sculpture. On both sides : (1) anteriorly, a longitudinal carina kv extending from the mentotectum to the epimeric furrow I; (2) in the propodosoma, a lateral and longitudinal

carina km usually divided into two anteriorly, and to which three oblique carinae are joined posteriorly; (3) in the metapodosoma, a lateral and curved carina (not labelled) stretching between the sejugal furrow *ssj* and the discidium *di*. In addition, an unpaired, thin and apparently continuous ridge kz running parallel to the anterior border of the circumgenital opening and ending laterally close to the extremity of the gutters *tv*. Granular microsculpture only in the posteroabaxial areas of the ventral region of the podosoma.

Tracheal system

Tracheae I: (1) in contrast with many other Circumdehiscentiae (GRANDJEAN, 1968), common trunk orientated forwards, and posterior branch tr:1p usually not longer than the anterior one tr:1a; (2) posterior branch not entering into the opisthosoma.

Sejugal tracheae with the abaxial branch *tr.sj.* α going in the opisthosoma, and longer than the adaxial one *tr.sj.* π which ordinarily ends in the prosoma. Vestibulum short and narrow, located near the abaxial extremity of the half sejugal apodemes. Sejugal stigmata in the form of a small hole situated in the sejugal furrow *ssj.* at the level with the legs.

Tracheae III : (1) lower vesicle (labelled tr3i in Fig. 4a) a bit curved; (2) upper branch tr3s long, clearly twisted in the opisthosoma. Note that the position of the stigmata III could not be precisely determined, yet they definitely have an anterior location on the cotyloid wall of the acetabula III.



Fig. 4. – *Hypogeoppia belgicae* n. sp. – a, male, right trachea III, partial, and acetabulum III seen through the cuticle in a dissected fragment of the podosoma. The hind leg is on the left. The horizontal hatching marks the circumtrochanteral opening of the leg III. The oblique hatching represents an optical section of the cotyloid wall III *cot* and the posterior tooth Δ "of the trochanter III-podosoma articulation. – b, female, genital region, partial, in ventral projection, with the right genital valve removed so as to have a direct sight at the genital papillae. A part of the median papilla Vm is not represented in order to completely show the small papilla Va. The papillae are invaginated in their sheath. The sheath of papilla Va is pointed out by two lines of apparent outline whereas the sheath of papillae Vm and Vp are not discernible. The dots indicate the base of the two posterior genital setae. The granulation laterad and behind the circumgenital opening is partially shown. np, posterior, internal nervure of the genital valve. – c, male, preanal organ (hatched) in ventral projection after the removal of anal valves. The organ is almost horizontal. It has remained near the border of the circumanal opening. – d, same organ (vertically hatched) in lateral view. The gnathosoma is on the right. The oblique hatching represents an optical section of the cuticle passing through the plane of symmetry.

Lateral characters

Genal incisions, tutoria and pedotecta absent. Prominences *P*, thick, similar to low laminae (Figs 1 and 2), variable in form and size; not homologous with usual pedotecta, in consideration of their distance from the circumtrochanteral openings of the legs I (see discussion in GRANDJEAN, 1960a). Surface behind the circumtrochanteral opening of the legs I transformed into a crescentiform depression with a steep border (mean depth, measured just behind the trochanter, of around 4 μ m; n = 4). Note that the border of the depressions coincides anteriorly with the free border of the acetabular tectum I, and posteriorly with the prominence *P* on a short distance. Discidia *di* robust (Figs 1, 2 and 4a).

Sculpture : (1) discidial carinae *cdi* prolonging in front the discidium and becoming a tectum as it crosses the sejugal furrow ssj; crossing tecta bearing the epimeric setae 3c on their upper side, often on a short ridge, and usually joining in front the lateral carina km of the propodosoma; (2) two anterior carinae getting to the podocephalic fissure F on both sides; upper one elongated and originating from the prodorsum; lower one thin, short and parallel to the lateral border of the camerostome bl.cam; (3) longitudinal carinae kl, long, robust, rugose and embossed (Figs 1a and 2); crossing the sejugal furrow ssj; habitually interrupted in one place at the level with the acetabular region II (more rarely with two cuts as exemplified in Fig. 2); upper side depressed at the level with the sejugal furrow ssj; reaching anteriorly the posterior border of the gutter tp of the prodorsum; made up posteriorly of two elements, namely a longitudinal, sometimes shortened carina, and a transversal, bulge-like element extending towards the circumtrochanteral opening of the legs III; (4) parietal, wavy carinae ks stretched out dorsally and anteriorly close to the circumtrochanteral opening of the legs II (2 in Fig. 1a); attaining posteriorly the circumtrochanteral opening after a bend; (5) several more or less elongated ridges associated with the carinae kl and ks; substantially variable in their aspect and characters (e.g., behind the prominences P, ridges tend to unite and form a reticulate microsculpture, including one to five depressed cells, different in size and shape); (6) posterior, oblique carinae kp extending above the discidium, between the carina kl and the circumtrochanteral opening of the legs IV; sometimes divided into two. Note that the carinae kl, kp, cdi and km, together with the posterior border of the gutter tp, form a sort of roughly trapezoidal structure enclosing completely the legs I, II and III.

Borders of the sejugal furrows *ssj* ordinarily ridgeshaped in places above the carinae kl (Fig. 2), yet sometimes slightly or incompletely discernible; usually well visible below the carinae kl. On both sides, two apophyses in opposition across the sejugal furrow *ssj*, referred to as postbothridic enantiophysis *Ba-Bp* in GRANDJEAN's (1960a) nomenclature (see also BEHAN-PELLETIER & NORTON, 1985); posterior apophysis *Bp* in contact with an elongated and oblique convexity. Bright spots : (1) upper one located near the exobothridic seta *ex*; sometimes indiscernible; probably a small, alveolar vestige of the second exobothridic seta; (2) lower one (labelled *z* in Fig. 2) situated near the posterior curvature of the carina *ks*; without doubt, the opening of a supracoxal gland, which is frequently found in oribatids at this place. Granular microsculpture developed here and there on the pleural regions : frequently in the surroundings of the legs IV, and constantly on the carinae kl, the discidial apophyses di, the carinae kp and the adjacent surface, and the apophyses Ba.

Ventral region of the opisthosoma

Except regarding the postanal fossa (Figs 1b and 3) and the anterior minitectum *mi.a* in the genital valves (Fig. 1b), the ventral superficial characters of the opisthosoma have nothing unusual. Yet note that : (1) the adanal setae *ad3* are in front of the anal valves and far apart from the plane of symmetry; (2) the adanal lyrifissures *iad* are large, close to the border of the circumanal opening *bta*, and parallel to this border (i.e. in 'paraanal' position according to SUBIAS & BALOGH, 1989).

Valves. Genital minitecta *mi.a* in the form of a narrow, abaxial shouldering at the anterior extremity of the hinge of the valves; note that similar shoulderings are observed in oribatid mites possessing teanidial epimeric furrows 4 (GRANDJEAN, 1968). As often in the Circumdehiscentiae, genital and anal valves with anterior and posterior internal nervures, and with a lock coaptation system on their adaxial border, consisting here of tooth-like or lamina-like elements and cavities which fit together; elements of the lock coaptation system, as follows : (1) small teeth in the anal valves in both sexes; (2) in the genital valves, a tooth-like piece in both sexes, anteriorly, and two teeth in the males and one lamina in the females, posteriorly.

Anterior genital papillae Va cone-shaped and pointed; much smaller and more distant from the surface of the genital valves than the other papillae (Fig. 4 b), as in several other Oppiidae (BEHAN-PELLETIER, 1991). Genital organs not studied in detail. Yet we report here the following observations regarding the ovopositor : (1) long and enlarged, with elongated lobes; (2) as in some other Circumdehiscentiae (LIONS, 1982), coronal setae at the circular stricture absent; (3) as usual, six pairs of eugenital setae detected on the lobes; (4) in each lobe, two setae clearly more proximal than the two others. Penis: (1) with two large and unpaired internal processes, i.e. an anterior rod-like piece and a posterior lamina, egg-shaped in ventral projection, and fringed except in its proximal part; (2) the four eugenital setae long, and in an anterolateral position.

Preanal organ : simple, similar to a chitinous lamina with a roughly trapezoidal outline in ventral view (Fig. 4c); convex in lateral projection (Fig. 4d); fastening to the border of the circumanal opening by means of two small articular sockets; note that in some individuals one articular socket was minute or even scarcely visible.

Cuticle, frequently in males and rarely in females, cut behind the genital opening by a pair of internal and longitudinal furrows of variable breadth. Note that the anoprogenital muscles are likely to be situated in the furrows. Anal lyrifissures absent.

Setae : (1) 11 pairs of setae present, namely five pairs of genital setae, one pair of aggenital setae ag, three pairs of adanal setae ad1-3, and two pairs of anal setae an1-2; (2) only adanal setae barbed, the others smooth; (3) setae ad2 longer than the other setae of the region, and the three

posterior genital setae the shortest; (4) the two anterior genital setae with a base tubercle.

Granular microsculpture found only in the genital region : (1) constantly in a zone situated behind the adaxial part of the gutter tv and laterad of the circumgenital opening; note that the granulation close to the circumgenital opening is usually thick and gives sometimes the impression that the cuticle is reticulated; (2) more rarely, behind the circumgenital opening.

Gnathosoma, chelicerae and pedipalpi

Subcapitulum diarthric, with atelebasic rutella (cf. GRANDJEAN, 1957a), and elongated so that its anterior elements, i.e. the rutella and lips, appear to be imperfectly protected by the rostral tectum at rest.

Mentum: (1) with a pair of deep, lateral notches in which the propodosomatic condyles K are placed; note that the notches are likely to be hollowed in the procuticle and covered by the epicuticle; (2) large carina cc everywhere parallel to the border (Fig. 1b); its posterior, rounded part robust, yet its anterior, longitudinal parts lessening in front; carina kx escaping forwards on both sides from the carina *cc*, and curved towards the plane of symmetry. Labiogenal suture *lg* broader in the sagittal region than laterally where it becomes thin and poorly discernible as coming near the base of the pedipalpi. As in some other oribatid mites (GRANDJEAN, 1964b; ALBERTI & COONS, 1999; ALBERTI et al., 2003), ventral cuticular ridge (or sclerite) vR associated with the pharynx floor, and connected with the tegument of the mentum over a short distance just behind the labiogenal suture lg (in Fig. 1b, the posterior limit of the attached part is marked by a transversal broken line). Note that : (1) the ridge appears to be developed a bit in front of the suture lg; (2) an analogous ridge exists in *H. perezinigoi* and *B. sigma* coniuncta.

Genae : (1) without lateral tectum for coaptation with the border of the camerostome; as a result, the pedipalpi are not completely hidden at rest as they keep discernible ventrally; (2) ventral side with a few scarcely discernible lines which appear to be external thin ridges attaining the adaxial border rather than grooves, yet a confirmation is required. Labrum and lateral lips not studied. Regarding the dorsal region of the subcapitulum, we report here only the following observations : (1) as in several other oribatid mites (GRANDJEAN, 1957b), a pair of dorsal and elongated apodemes *ne* (note that, in Fig. 1b, they are seen though the cuticle of the mentum); (2) opening of subcapitular glands (GRANDJEAN, 1957b) quite broad. Setae : (1) as usual, three pairs of subcapitular setae present, namely a, m and h (GRANDJEAN, 1957a); (2) two pairs of adoral setae; undiscernible in LM; actually, laid on the ventral, concave side of lateral lips according to observations in TM; (3) supracoxal spines of pedipalpi similar to baculiform and straight phaneres with a rounded tip.

Subcapitular septa : (1) originating dorsally from the bottom of the cheliceral groove, in front of the nervure *ne* (ALBERTI, in litt.); (2) attached ventrally to the lateral region of genae (note that, in Fig. 1b, the ventral insertions are indicated by a thick broken line, and not represented in front because they are concealed by the pedipalpal femora); (3) merging anteriorly into the lateral wall of genae. Note that : (1) further work examining the rela-

tionships between the subcapitular septa and genae is currently under way; (2) analogous septa seem to exist in *H. perezinigoi* and *B. sigma conjuncta* in so far as elements likewise shaped and similarly located are present.

Rutella : (1) plump shape demonstrated distally in dorsal or ventral projection (Fig. 1b) due to a lateral (abaxial) deviation of their free extremity; (2) showing a roughly trapezoidal outline in lateral projection (Fig. 5a); (3) actually, in the form of elongated laminae a bit widthwise curved, thicker dorsally than ventrally, and forming an imperfect gutter in so far as, despite the existence of small ventral lobes, their ventral borders are not joined axially (Fig. 1b); (4) devoid of distal teeth, yet with a dorsal denticle, and with a minute notch at the ventrodistal angle; (5) adaxial side with a comb made up of five or six barbs, and with two ridges: a longitudinal ridge ku which, according to observations in TEM, forms the boundary line between the dorsal and ventral parts of rutella (note that it was not possible to determine whether the ridge ku actually is longer than what is shown in Fig. 5a), and a transversal ridge developed at the base of the distal, inflected part (not shown in Fig. 5a). Manubrial zone large and punctuated (in Fig. 5a, the line αf represents the abaxial part of the manubrial articulation; cf. GRANDJEAN, 1957a).

Chelicerae (Fig. 5b) remarkable for : (1) their lengthening since they show a height/length ratio of around 0.28, i.e. according to GRANDJEAN (1964a), a value significantly below the mean value in the Circumdehiscentiae (see illustrative data in SCHUSTER, 1956); (2) the weakness of their dentition since the proximal teeth are blunt, some being even rounded in lateral projection (Fig. 5b). As usual, two setae on each chelicera, namely cha, proximal and barbed, and *chb*, distal and smooth. Ventral intumescence, denticulate crests and squama (GRANDJEAN, 1959) absent, yet with the following elements: (1) a Trägårdh's organ Trg, as in several other Circumdehiscentiae (GRANDJEAN, 1959); (2) a pair of minute spines ep close to cha; (3) as usual (NORTON, 1998), a striated fossa fc on the adaxial side (striations not shown in Fig. 5b); (4) two fossae, not striated, on the abaxial side; (5) a proximal, ventral extension e' beyond the thickened base border. Cuticular punctuation indistinguishable except proximally on the adaxial side, behind the fossa fc. Tendons hard to see except the abaxial tendons $t\alpha$ of cheliceral retractor muscles.

Pedipalpi five-segmented (Fig. 1b). Tarsi slightly (but indubitably) curved downwards (Fig. 5c). Ventral ridges : (1) proximal and longitudinal in femora; (2) oblique in patellae (apparently replaced by a furrow in some patellae); (3) in tarsi, U-shaped and intersecting the plane of pseudosymmetry just behind the seta vt' (the ridge climps up further on the adaxial side than on the abaxial side). Solenidion ω (probably an olfactory organ; cf. ALBERTI, 1998) : baculiform, with a rounded tip, and hard to see in LM because it is laid dorsolaterally on the tarsal cuticle; note that, according to observations in TEM, its base is likely to be more proximal than what is represented in Fig. 5c. Setae : (1) formula normal : (0-2-1-3-9); (2) all the setae apparently smooth except the tarsal, posteroventral setae vt" equipped with barbs; (3) lower femoral setae v' clearly ventral and inserted far from the

other seta (an uncommon position; cf. GRANDJEAN, 1935); (4) in patellae seta *d* in a dorsal position (a primitive condition; cf. GRANDJEAN, 1935); (5) anteroculminal eupathidium *acm* in tarsi (probably a gustatory receptor; cf. ALBERTI, 1998) not associated with the solenidion ω (i.e. no double horn); note that the internal canal in all the eupathidia of pedipalpal tarsi was undiscernible in LM even at high magnification and after heating in lactic

acid; actually, observations in TEM were required to attest the existence of an internal canal; (6) shiftings : no basculation in the paired ultimal eupathidia *(ul)* (a primitive condition; GRANDJEAN, 1958); paired ventral setae *(vt)* nearly lined up longitudinally, demonstrating a clear (double prime) disjunction. Apparently only the femoral setae v' and tarsal setae lt" with a base tubercle perceptible in LM.



Fig. 5. – Hypogeoppia belgicae n. sp., female. – a, right rutellum, seen laterally, with a part of the gena. The dots below the line ku depict the base of barbs of the comb on the adaxial side of the rutellum seen through the cuticle. The labrum and the lateral lips are not represented. c, collar of the rutellum – b, right chelicera, separated and seen laterally. Only the proximal part of Trägårdh's organ Trg is shown. The part of the chelicera behind the line of attachment *en* of the cheliceral sheath is inside the body. It is represented as if it is exposed. In this orientation, the dorsal adaxial spine is hidden by the abaxial spine ep which is the only spine to be shown through the dorsal cuticle. The weakly undulating line behind the movable digit marks a longitudinal carina on the abaxial side of the cheliceral body. The hatching directed to the left covers the posterior, more coloured part of the movable digit. The hatching directed to the right indicates partially the base border of the cheliceral body. – c, tarsus of the right pedipalp seen laterally. The solenidion ω is vertically hatched. The oblique hatching marks an optical section of the tegument through the plane of pseudosymmetry of the segment. *cm*, culminal seta. *su*, subultimal eupathidium.

Legs

Noticeable traits in the leg setae : (1) a lot of tibial and tarsal setae contrasting by their bulk with the setae of proximal segments which are thin and similar to most setae borne by the body (Figs 1 and 6); note that some setae of proximal segments appear slightly more robust than the others (e.g. the anterolateral seta l' in the patellae I and II); (2) in the tarsi II, a clearly proximal location of the antelateral seta a' (Fig. 6b); note that the double prime disjunction of the antelateral pair resulting from the displacement of the seta a' towards the body is consistent with the rule enacted for other lateral setae (GRANDJEAN, 1960a).

Legs moniliform in dorsal projection, with clearly bulbous segments beyond the trochanters; note that this aspect is less apparent in lateral projection for the tarsi I, II and III because the peduncle is poorly discernible dorsally in these segments (Fig. 6). Legs IV longer than the other legs, and legs II the shortest.

Formulae of the phaneres : for setae, from trochanters to ambulacra : I (1-5-2-4-20-1), II (1-5-2-4-13-1), III (2-3-1-3-13-1), IV (1-2-2-3-10-1); for solenidia, from patellae to tarsi : I (1-2-2), II (1-1-2), III (1-1-0), IV (0-1-0). Taking into consideration that (1) there is no dorsal companion seta *d* in patellae and tibiae, (2) the iteral pairs *(it)* are found only in I, II and III, (3) the fastigial seta *ft'* is lost in IV, (4) there are two accessory setae (i.e. v' and v'') in the tarsi I, and (5) the proral pairs *(p)* are suppressed in II, III and IV as in other Oppiidae (GRANDJEAN, 1953), the formulae for setae appear to be ordinary.



Fig. 6. – *Hypogeoppia belgicae* n. sp., females, legs seen laterally, partial. The femur in the legs I and II and trochanter in the leg IV are incompletely represented. No indication is shown for the dorsoproximal, tarsal lyrifissures ly except in II. A hatching marks the solenidia. The limit of punctuated areas developed on the segments is indicated by a dotted line (the punctuation is not depicted). – a, distal segments of the right leg I. – b, idem, right leg II. The seta without label in the patella is the posterolateral seta l''. In the tibia, only the root (partially hidden by the seta l'') and mid part of the seta v are drawn. In the tarsus, the broken line below the seta it'' marks the dorsal outline of the seta a seen through the cuticle. – c, left leg III, without the trochanter. As usual, no convexity is developed dorsoproximally on the femur. There are three thin ridges on the tarsus. – d, left leg IV. The proximal, adaxial ridge of the femoral bulb is partially seen through a punctuated area of the anterior (abaxial) side. The proximal convexity of the femur is poorly marked dorsally but discernible whereas in some other femora it was non-existent. Eight thin ridges are found on the tarsus.

Solenidia. Number usual for the Circumdehiscentiae, corresponding to the first hitch in the numerical regression which affects the solenidia in this group (GRAND-JEAN, 1964c). Tactile solenidia (sensu GRANDJEAN, 1935), namely σI , φII , σII and φIV : (1) quite elongated, yet σII and φIV less long than the others; (2) σI and φII taking a direction towards the body (Fig. 6a); σI frequently twisted (Fig. 6a), with a distal part usually orientated towards the ambulacrum; (4) course shown by σII variable, yet frequently twisted with the distal curvature directed towards the ambulacrum as shown in Fig. 6b; (5) φIV usually directed towards the ambulacrum (Fig. 6d). Baculiform solenidia, namely $\omega''I$, $\varphi 2I$ and σIII : (1) σIII thick and short, and $\omega''I$ and $\varphi 2I$ thin and longer; (2) $\omega''I$ curved upwards, and $\varphi 2I$ and σIII bent towards the ambulacrum, the former being also curved abaxially. Ceratiform solenidia, namely $\omega'I$, ωaII , ωpII , φII and φIII : (1) relatively thick, yet φIII more slender than the others; (2) φIII rectilinear, and the others bent towards the ambulacrum, an additional curvature being detected in $\omega'I$ (adaxial curvature) and frequently in *wall* (abaxial curvature).

Areae porosae apparently absent. Yet areas clearly punctuated but not really porous detected in all the segments except in the patellae and trochanters I and II, as follows : (1) in the trochanters III and IV where they are the largest, and extend over the dorsal and lateral sides (Figs 1 and 6); (2) in femora where they are the most numerous; (3) in tibiae where, in addition to a ventral area in I, III and IV, there are a dorsal area in III and IV, a quite large dorsoabaxial one in I and II, and a adaxial one in III; (4) in tarsi where they are located dorsally in I and II, and abaxially in all the legs.

Trochanters. Trochanters I and II similar ventrally to a protrusion on which their seta (labelled vR in Fig. 1b) is inserted. Trochanters III and IV apparently rounded in dorsal projection (see the left trochanter III in Figs 1a and b), and elongated and approximately oval in lateral view (see the left trochanter IV in Fig. 1b). Note that some trochanters III surveyed in this study appeared perceptibly more angular in dorsal projection as their dorsal side was depressed adaxially. Trochanters III with a distal rim indented adaxially so that the anterior condyle of the trochanterofemoral joint is substantially more proximal than the posterior condyle. Trochanters IV with two thin ridges on the adaxial side, the upper ridge being shorter than the lower one. Setae : (1) all the trochanteral setae bearing small barbs; (2) trochanteral setae in III and VI with a base tubercle.

Femora. Sculpture : (1) a pad-like convexity developed in the proximal part of the bulbs, as follows : on all the sides in the femora I in most females (note that as shown in Fig. 1 the convexity in the femora I is always more pronounced than in the other legs); on all the sides in some femora IV in both sexes (Fig. 6d); usually on the adaxial side, sometimes on the dorsal and ventral sides, and rarely on the abaxial side in the femora II and III; (2) a pair of short, transversal, roughly parallel but not adjoining ridges on the adaxial side of the femora IV (Fig. 6d). Setae : (1) all the femoral setae equipped with small barbs; (2) lateral pair (l) in I and II showing both a double prime basculation and a prime disjunction.

Patellae. Approximately all of a size. Bulb II ordinarily with a thin ridge on the dorsal, abaxial and ventral sides. Solenidia σ without a base tubercle. Chaetotaxy normal, i.e. abiding by the rules of numerical predominance (GRANDJEAN, 1942). Setae : (1) dorsal seta *d* in patellae IV apparently smooth; (2) usually no disjunction or a weak disjunction of the lateral pair (*l*) in I and II, yet some patellae I with a disjunction more marked than in Fig. 6a; note that, in agreement with the rule, the disjunction was double prime (cf. GRANDJEAN, 1960a).

Tibiae. Peduncle IV longer than in the others, and bulb I the most voluminous. Sculpture : (1) a low, strip-like convexity in I, II and III; in I and II, developed proximally on the bulb (in I, in the dorsal and lateral sides, and more rarely in the ventral side; in II, only in the dorsal and adaxial sides); in III, making dorsally and abaxially the distal limit of the peduncle; note that the convexity extended on the ventral side in some tibiae, and was replaced by a ridge in some others; (2) two furrows sp and sa on the dorsal side of the bulb I; note that the proximal furrow sp was occasionally prolonged on the abaxial side, and that the distal furrow sa was sometimes scarcely perceptible; (3) a poorly prominent carina on the dorsal and lateral sides of the bulb II; (4) thin ridges in the peduncle III and IV; in III, one or two ridges on the dorsal and lateral sides; note that, in some tibiae, the distal ridge was adaxially undiscernible; in IV, two ridges on both the dorsal and abaxial sides, which unite ventrally in the abaxial side; sometimes a third ridge found a bit more distally on the dorsal side. Solenidia : (1) φII not inserted at the anterodorsal extremity of the tibiae, yet in an unusual, dorsal and a bit abaxial position; borne on a large and not very salient prominence; note that sometimes the prominence was less perceptible in lateral projection than in Fig. 6a; (2) $\varphi 2I$ inserted anteriad of φII on the prominence; (3) ϕII dorsal and slightly abaxial; (4) ϕIII and φIV axiodorsal or nearly axiodorsal. Setae : (1) lateral seta l' in I and II with a base tubercle; (2) lateral pairs (l) with a double prime basculation in most of tibiae I and II; note that sometimes the basculation was weak or null, and a slight, usually double prime disjunction was observed in

I; (3) ventral setae v' and v'' in I and II, and seta v' in III and IV affected by a conspicuous downward displacement so that pairs (v) with a prime basculation in III and IV; (4) pairs (v) with a double prime disjunction in I, and a prime disjunction in III and IV; note that only the disjunctions in III and IV are consistent with the rule of prime disjunction applied to tibial ventral pairs (cf. GRANDJEAN, 1960a).

Tarsi. Peduncles III and IV longer than the others, and bulb I the most voluminous. Sculpture : (1) in I, two furrows on the ventral side, proximally with regard to the antelateral pair (a), the distal furrow apparently forming the limit between the bulb and the slimmed part of the segment, and the proximal furrow ordinarily climbing up the adaxial side of the bulb; (2) in the other tarsi, thin ridges developed at least on the dorsal and lateral sides; only one ridge found in the slimmed part in II, yet two to four ridges in III and still more in IV; note that one or two ridges in III and the majority of the ridges in IV showed a circular course. Dorsoproximal lyrifissures lv: (1) lateral shifting in prime direction detected in I, III and IV, yet in double prime direction in II; consequently, the displacement of lyrifissures appears to be an evolution not consistent with the rule of 'parallel homology' (see a defini-tion in GRANDJEAN, 1939); (2) lyrifissure II longer than the others; as a result its shifting seems relatively less pronounced than it is in the other segments. Solenidia: (1) in I, solenidia ω' and ω'' in a dorsoabaxial position (Fig. 6a); (2) in II, proximal solenidion ωp axiodorsal or nearly axiodorsal, and distal solenidion ωa dorsoadaxial. Setae. Subunguinal setae s in I not eupathidic but ordinary setae just as exemplified by a few other oribatids in which the setae s are inserted in the vicinity of the antelateral pair (a) (see e.g. GRANDJEAN, 1948); note that: (1)accordingly, the proral setae (p) in I are the only eupathidia found in the legs; (2) just as indicated above for the distal setae of pedipalpi, the internal canal in the setae (p) was unperceivable in LM. As usually observed in eupathidia, setae p in I smooth. Distal setae, i.e. ultimal setae *u* and iteral setae *it*, bearing short barbs, and more robust barbs detected in the other setae, with a few exceptions (e.g. the tectal setae tc in I and IV). A small base tubercle detected in : (1) the seta u' in all the legs; (2) the pair (*it*) in the legs I, II and III; (3) the seta a" in the legs I, III and IV; (4) the seta u " in the legs II, III and IV; (5) the setae tc', a' and s in the legs I and III; (6) the setae tc' and pv" in the legs I; (7) the seta ft" in some tarsi IV. Disjunctions (see GRANDJEAN, 1960a, for the rules of disjunction) : (1) in I, the fastigial pair (ft) (prime disjunction, as in many other oribatid mites), the tectal pair (tc) (prime disjunction, contrary to the rule; in some tarsi, the disjunction was more marked than in Fig. 6a), the primilateral pair (pl) in several tarsi (prime disjunction, contrary to the rule), and the ventral pair (v) (double prime disjunction, contrary to the rule); (2) in II, besides the antelateral pair (a) (see above), the ultimal pair (u) (double prime disjunction, contrary to the rule applying to other ventral setae); (3) in III, the fastigial pair (ft) (double prime disjunction, according to the rule); (4) in IV, the antelateral pair (a) (prime disjunction, contrary to the rule applying to other lateral setae), and the primiventral pair (pv) (prime disjunction, according to the rule). Basculations : (1) in I, the primilateral pair (pl) (double

prime basculation; note that, in some tarsi, the basculation was less pronounced than in fig. 6a), and the ventral pair (v) (double prime basculation; note that sometimes a slight basculation was observed, always on account of a descent of the seta v' rather than an ascent of the seta v''); (2) in II, the primiventral pair (pv) (double prime basculation); (3) in III, the fastigial pair (ft) (prime basculation, as in many other oribatid mites; cf. GRANDJEAN, 1961b); (4) in IV, the antelateral pair (a) (prime basculation). Famuli e in the form of a thin, erected and relatively long phanere with a rounded tip. Lower tendons of the ambulacrum guided proximally owing to a canal bored through the ventral cuticle of the peduncle; as shown in Fig. 6, all the canals have a thick roof.

Apoteles. Ungues simple, without tooth and without either ridges or barbs; in the legs I and II more curved and shorter than in the legs III and IV.

Type material

The material examined for this description consisted of some thirty males and females from two caves : a cave in Freyr near the city of Dinant, and a cave in Tilff near the city of Liège (DUCARME et al., 2003). Samples were collected from earth deposit, on locations that were not flooded at any time of the year. The mites were extracted using BERLESE-TULLGREN method or dibromoethane flotation (DUCARME et al., 1998). Immatures are unknown.

The types, namely one male holotype and three female paratypes, are deposited in the collections of the Royal Belgian Institute of Natural Sciences, Brussels. In pursuance of TRAVÉ's (1965) recommendations, the type specimens were not dissected but used only for a rough study.

DISCUSSION

Key to the species and subspecies of Hypogeoppia

The position of the rostral setae ro and the existence of unpectinate sensilli allow H. belgicae to be unambiguously distinguished from the other Hypogeoppia. On the other hand, as in H. dungeri Schwalbe, 1995, and H. exempta (Mihelčič, 1958), the anterior border of the notogaster in *H. belgicae* is equipped with a pair of dorsal apophyses between the bothridia and the plane of symmetry. In fact, in H. belgicae, H. dungeri and maybe H. exempta, the notogasteral apophyses and the apohyses located in front on the prodorsum appear to be analogous with the dorsosejugal enantiophyses Da-Dp found in other Circumdehiscentiae as e.g. in the Damaeidae (GRANDJEAN, 1960a; BEHAN-PELLETIER & NORTON, 1985), a circumdehiscent family not closely related to the Oppiidae (note that enantiophyses are apophyses in opposition staking off a primitive furrow; GRANDJEAN, 1954; NORTON, 1978). By contrast, two pairs of notogasteral apophyses, a culminodorsal pair Cp and a laterodorsal pair Lp in GRANDJEAN'S (1960a) nomenclature, are detected in H. perezinigoi Subias & Arillo, 1996, H. terricola terricola Subias, 1981 (note that according to SCHWALBE, 1995, H. festoneata Moraza & Moreno, 1988, is a synonym of *H. terricola terricola*; see also SUBIAS & ARILLO, 1996, and SUBIAS, 2004), and H. terricola sal*manticensis* Morell Zandalinas, 1987. In addition, in *H. hypogeum* (Paoli, 1908) and in two closely related varieties recognized by LIONS (1972, p. 148), the notogaster either lacks apophysis or has two pairs of dorsal apophyses (MAHUNKA, 1966; LIONS, in litt.). Taking into account these works except the one by LIONS (1972) because the data about the two varieties of *H. hypogeum* are too fragmentary, we provide the provisional following key.

- Without dorsal apophyses in front of the notogaster; without rostral slits (i.e. 'rostral not really tridentate' according to SCHWALBE, 1995); length = 287-315 μm
- With dorsal notogasteral apophyses anteriorly; with rostral slits
- 2(1) With one pair of notogasteral apophyses anteriorly
- With two pairs of notogasteral apophyses anteriorly
- 3(2) Club of sensilli with thorn-like barbs; length = $256-282 \ \mu m$ *H. belgicae*
- Club of sensilli pectinate
- 4(3) Rostral setae inserted on a carina; length = 300-320 μm
- No rostral carina; length = $200-210\mu m$
- 5(2) Part of rostrum between the slits long; length = $212-226 \ \mu m$
- Part of rostrum between the slits short
- 6(5) With two rows of protuberances in front of the lamellar setae; length = $237-262 \ \mu m$
- *H. terricola salmanticensis* Without rows of protuberances dorsally on the prodorsum; length = 196-255 μm

.....Ĥ. terricola terricola

Annotations on some unusual characters

1. To our knowledge, all the observations performed to date in the Oribatida indicated that the penis bears six to eight pairs of eugenital setae (e.g. GRANDJEAN, 1955, 1956b; LIONS & NORTON, 1998). Yet two remarks must be made, as follows : (1) to demonstrate that the partial denudation of the penis in *H. belgicae* is an uncommon trait, the examination of the penis in a greater number of oribatid species is imperiously required; (2) in consequence of the small size of the organ making its study difficult, minute, poorly discernible setae could have escaped our investigation.

2. Rather than areae porosae, the punctuated zones detected in the legs (Figs 1 and 6) could be muscular insertions. Yet observations by SHULTZ (1989) on the leg musculature in mites (see also YASTREBTSOV, 1987) provide strong evidence that the ventral areas in the tibiae I, III and IV (Fig. 6) are not muscular insertions. This is probably also the case for the area on the abaxial side in

all the tarsi. As a result, further work is needed to determine the nature of punctuated zones shown by the legs.

3. The setae labelled vx in the femora I and II (Fig. 1a) are probably metahomologous (i.e. had primitively the same position on the femora I and II). The phaneres vx could then be regarded as abaxial setae v" having shifted in lateral (adaxial) direction. Another possibility is that the seta vx in the femora I is actually an adaxial seta v', yet this seta is less frequent in the Circumdehiscentiae (see e.g. GRANDJEAN, 1960b, 1965).

Considerations on the role of some uncommon characters

1. It appears that taenidia running laterally on the prodorsum in H. belgicae (Figs 1a and 2) and B. sigma conjuncta have no equivalent among Oribatida (TRAVÉ, 1986). By contrast, the ventral taenidia tv in H. belgicae, *H. perzinigoi* and *B. sigma conjuncta* are analogous with epimeric taenidial furrows 4 found in some Circumdehiscentiae (GRANDJEAN, 1968). Yet there is one main difference : the taenidial gutters are open in the oppiid species whereas they are covered with a minitectum in the other species. According to GRANDJEAN (1964a, 1968) and TRAVÉ (1986), the main role of taenidia would be both to hold out against moistening and to keep some air in reserve against the body during a period of immersion. Yet no air pellicle was detected in taenidia of living H. belgicae plunged in water, in glycerine or in liquid paraffin. Therefore, a question remains to be answered concerning the function of taenidia in this species.

2. The action of dorsoventral opisthosomatic muscles generates not only a lowering of the notogaster towards the ventral region of the body but also a forward movement of the notogaster caused by the elements contained in the opisthosoma, which oppose the compression. In fact, this latter movement is prevented by the anterior part of articular cuticle of the notogaster, which acts as a fixed (immobilizing) point. Since the extremity of notogasteral dorsosejugal apophyses Dp rests on the prodorsal dorsosejugal apophyses Da in contracted individuals (Fig. 2), it is possible that the apophyses Dp are also fixed points of the notogaster.

The lowering of the notogaster is the usual method of haemolymph pressure generation in the body. In oribatid mites, several motions and functions have been reported to rely on internal haemolymph pressure (see e.g. WOODRING & COOK, 1962; GRANDJEAN, 1969; AKIMOV & YASTREBTSOV, 1991; ALBERTI & COONS, 1999): (1) limb extension; (2) protraction and retraction of the mouthparts; (3) opening of genital and anal valves; (4) extrusion and turgidity of the penis and ovipositor; (5) circulation of haemolymph; (6) mix of the contents of tubular organs (e.g. digestive tract); (7) expulsion of genital products and fecal pellets; (8) discharge of products secreted by exocrine glands. In addition to the lowering of the notogaster, contraction of dorsoventral opisthosomatic muscles might also induce a lateral compression of the notogaster in *H. belgicae*. This view is supported by observations with SEM, which show that borders of the notogasteral notch (Fig. 3) are appreciably brought together in contracted individuals. If the two movements were independent, lateral compression would allow a

more acute control of haemolymph pressure to be achieved (e.g. to fill a specific leg). If the two movements were concomitant, lateral compression would counterbalance the drop in internal pressure due to haemolymph flow from the dorsal region of the notogaster towards its ventral, larger region, when the notogaster comes down. The latter hypothesis suggests that internal hydraulic pressure might be high under certain circumstances. In this case, it could be that the capability to reach high internal pressure and the enlarging of apophyses *Dp* combined with the adjunction of robust companion carinae became linked in *H. belgicae*.

It should be noted that the existence of a postanal fossa (Figs 1b and 3) should also contribute to the generation of high hemolymph pressures at least if the postanal fossa is designed to allow an important lowering of the notogaster with regard to the ventral shield to occur.

3. The existence of two branches in tracheae III has been reported to date only in some Liacaridae (GRAND-JEAN, 1968), a circumdehiscent family not closely related to the Oppiidae. In contrast with H. belgicae, the lower branch in Liacaridae is shaped either like a more or less elongated simple duct or like a bud. Even though most of the surveyed populations inhabited parts of caves irregularly flooded or apparently never immersed (DUCARME et al., 2003), we cannot neglect the possibility that the vesicles III could improve the resistance to immersion in water. Indeed, the vesicles III appear to be air holders just as the external taenidia usually are (see references above). Further information on the ability to survive a long period of dipping in water is necessary to assess this hypothesis (note that preliminary observations revealed no mortality in individuals immersed in water for more than 16 hours).

The acquisition of a respiratory vesicle, a very peculiar apomorphic character, agrees with the fact that evolution has given rise to a significant novelty occurring in the most lately derivative oribatid mites, i.e. the Circumdehiscentiae (GRANDJEAN, 1966; DUCARME et al., 2004).

4. The large carina *cc* of the mentum is probably used for the coaptation with both the camerostome and the mentotectum. Indeed, in contracted individuals studied with SEM, the carina is drawn close to the border *bl.cam* of the camerostome anteriorly, and to the border *bm* of the mentotectum laterally and posteriorly. Thus, the carina *cc* appears to be analogous with the hysterostomatic carina found in the Plasmobatidae (GRANDJEAN, 1961b), a circumdehiscent family not closely related to the Oppiidae.

5. The modifications undergone by both the chelicerae (i.e. lengthening of the cheliceral body and weakening of the teeth) and rutella (e.g. lengthening, loss of distal teeth, and deviation of the free extremity) abides by the rule of concomitant evolution of these two organs in the Oribatida (e.g. GRANDJEAN, 1957a, c). The lengthening of chelicerae and rutella in *H. belgicae* is similar to that detected in the Suctobelbidae, a circumdehiscent family closely related to the Oppiidae. For instance, the height/length ratio for the chelicerae is a bit lower than 0.3 in *H. belgicae* and in the suctobelbid *Allosuctobelba grandis* studied by GRANDJEAN (1951) (see WOAS, 1986, for other examples in the Suctobelbidae). In the same way, the ratio for the rutella is lower than 0.5 in the two species, i.e. clearly below the values yielded by rutella regarded as typical in the Circumdehiscentiae (between 0.75 and 1.10).

The gnathosoma of the Suctobelbidae has been affected by a suctorial evolution characterized by both a lengthening of chelicerae and a transformation of rutella into elongated and edentate laminae. Yet, in contrast with many suctorial oribatids (GRANDJEAN, 1957a), the rutella in H. belgicae are not typically foliaceous since, for instance, they are partially thinned down and incompletely edentate. In addition, H. belgicae possesses two characters that a lot of non suctorial oribatids exhibit : (1) a labiogenal zone (labelled lg in Fig. 1b) (GRANDJEAN, 1957a); (2) long cheliceral setae *cha* and *chb*, whereas a shortening or a complete loss of these setae is usually associated with suctorial evolution (GRANDJEAN, 1964a). In fact, regardless of their evolutionary origin, cheliceral and rutellar modifications would denote a peculiar diet in *H. belgicae*. Attempts to determine the diet using food choice experiments in the laboratory were unfortunately unsuccessful (DUCARME, 2003).

In other respects, it should be noted that elongated chelicerae have already been reported in the genus *Cheloppia* Hammer, 1971, classified by SUBIAS & BALOGH (1989) in the Oppiidae, yet a careful study of the chelicerae and rutella has not been done.

6. The function of subcapitular septa is unclear except that they induce an increased stiffness in the surrounding exoskeletton. Now, if this reinforcement affects the movements of genae and rutella (see GRANDJEAN, 1957a, for a discussion), an increased expenditure of energy for feeding might be required, at least if the rutella still ensure their scraping function in *H. belgicae*.

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