

Persistence of larval characteristics on the antennae of the neotenic female of *Drilus mauritanicus* Lucas, 1849 (Coleoptera, Elateridae, Agrypninae, Drilini)

Persistance de caractères larvaires sur les antennes de la femelle néoténique de Drilus mauritanicus Lucas, 1849 (Coleoptera: Elateridae: Agrypninae: Drilini)

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Abstract. The Drilini (Coleoptera, Elateridae) show a considerable sexual dimorphism : the males are small and winged, while the females are larger, larviform and wingless. The antennae of female *Drilus mauritanicus* are studied in order to compare them with those of the male and the larva previously described. Whereas the number of antennomeres equal to 11 is constant in the male, this number in the female is variable according to individuals and equal to 10 or 11 to which must be added a rudimentary distal antennomere. The most apparent 10 or 11 antennomeres are of the adult type and bear Böhm sensilla, aporous sensilla chaetica, uniporous sensilla chaetica and 4 types of sensilla basiconica, of which the most numerous types (B1 and B2) are multiporous sensilla. The rudimentary antennomere (11th or 12th) is of the larval type and possesses several common sensilla with larval sensilla, in particular the large multiporous sensillum basiconicum. This persistence of larval characteristics on the female antenna is related to the phenomenon on neoteny observed in the female. This makes it possible for the latter to preserve sensory capacities which enable it to exercise a predatory behaviour sometimes observed in certain females of Drilini but inexistent in the males.

Keywords: Drilini, female, neoteny, antenna, sensilla, larval characteristics.

Résumé. Les Drilini (Coleoptera Elateridae) montrent un dimorphisme sexuel considérable: les mâles sont petits et ailés tandis que les femelles sont plus grandes, larviformes et aptères. Les antennes de la femelle de *Drilus mauritanicus* ont été étudiées afin de les comparer à celles du mâle et de la larve décrites précédemment. Tandis que le nombre d'antennomères égal à 11 est constant chez le mâle, ce nombre chez la femelle est variable selon les individus et égal à 10 ou 11 antennomères auxquels s'ajoute toujours un antennomère distal rudimentaire. Les 10 ou 11 antennomères les plus apparents sont du type adulte et portent les sensilles de Böhm, les sensilles chétiformes sans pore, des sensilles chétiformes unipores, 4 types de sensilles basiconiques dont les deux types les plus nombreux (B1 et B2) sont des sensilles multipores. L'antennomère rudimentaire (11^{ème} ou 12^{ème}) est du type larvaire et possède plusieurs sensilles communes avec les sensilles larvaires, en particulier la grande sensille basiconique multipores. La persistance de caractères larvaires sur l'antenne femelle est en rapport avec le phénomène de néoténie présenté par la femelle. Elle permet à cette dernière de conserver les capacités sensorielles lui permettant d'avoir un comportement prédateur parfois observé chez les femelles de Drilini mais toujours inexistant chez les mâles.

Mots-clés: Drilini, femelle, néoténie, antenne, sensilles, caractéristiques larvaires.

INTRODUCTION

The genus *Drilus* Olivier, 1790 shows such a considerable sexual dimorphism that early authors interested in the question were unaware that they were dealing with two sexes of the same species; they consequently classified the male, which is small and winged, in one group and the female, which on the contrary is very large, apterous and larviform, in a quite different group. It was Desmarest (1824) who, after developing the larvae, obtained the two sexes of *Drilus flavescens* Olivier, 1790, observed their copulation and realised that the male and the female belonged to the same genus and species. *Drilus mauritanicus* Lucas, 1849 discovered in Algeria by Lucas (1849) is also present in Morocco because it was made in synonymy with *Drilus tangerianus* Escalera, 1914 by Bahillo de la Puebla *et al.* (2004) and in the Iberian Peninsula (Bahillo de la Puebla 2004). The sexual dimorphism in *D. mauritanicus* also concerns the antennae. The male possesses serrate antennae made up of 11 antennomeres (Fauchaux & Agnas submitted). According to Cros (1926), the female possesses 11 visible antennomeres, all well developed and a 12th rudimentary antennomere, surmounting 11th, of which it occupies barely

the internal half of the terminal surface. Furthermore, the 11th antennomere possesses dimensions comparable to those of 10th antennomere. We have found the same characteristics in certain females (if not all) obtained by breeding of larvae from Oualidia (Fauchaux & Agnas 2011, Fauchaux & Kundrata 2014). Certain structures of the supplementary rudimentary antennomere recalled certain sensilla observed on the antenna of the primary larva (Fauchaux 2014); this may be due to the persistence of larval characteristics on the antennae of neotenic females of *D. mauritanicus* (Fauchaux & Kundrata 2014). It is this hypothesis that we intend to justify by the study of sensilla on the female antenna of *D. mauritanicus*.

MATERIAL AND METHODS

The 4 females of *D. mauritanicus* studied were obtained by breeding of larvae having reached their last instar, captured at Oualidia (Atlantic coast of Morocco) in 2008-2009. For SEM study, the heads of the females were cleaned in acetone, dehydrated in pure alcohol and mounted both on the dorsal and the ventral face, on specimen holders. After coating with gold and palladium, preparations were

examined in a Jeol J.S.M. 6 400F SEM at 10 kV. Sensillum terminology follows Zacharuk (1980), Altner & Prillinger (1980), and Faucheux (1999).

RESULTS

Gross morphology of antennae

The moniliform antennae are inserted laterally and measure from 2.0 to 2.20 mm according to individuals (Fig. 1, 2).

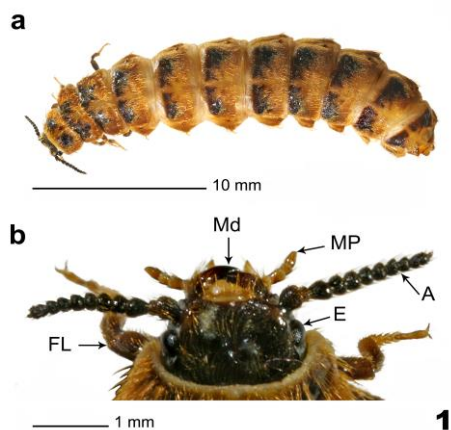


Figure 1. *Drilus mauritanicus*, female; **a.** habitus in dorsal view; **b.** ventral face of the head A. antenna; E. eye; FL. flagellum; Md. mandible; MP. maxillary palp (photographs Gérard Beaulieu).

The number of antennomeres of imaginal aspect must be calculated from the base of antenna up to the presence of structures of larval aspect, i.e. up to what Corbière (1969) called the « lobe membraneux » and which we have called « large multiporous sensillum basiconicum B1 » in the larva of *D. mauritanicus* (Faucheux 2014). In studied individuals, this number is 10 or 11. On the 4 females studied, two possessed 10 antennomeres and the two others 11 antennomeres (Fig. 2b, c).

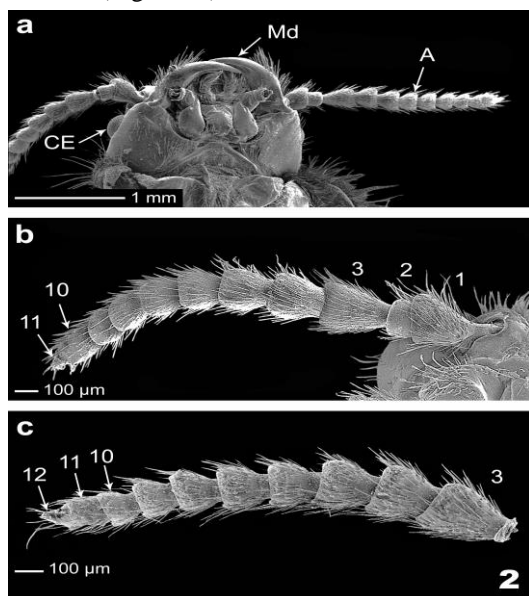


Figure 2. *Drilus mauritanicus*, female; **a.** ventral view of the head in SEM; **b.** antenna with 11 antennomeres (1-11); **c.** flagellum of an antenna with 12 antennomeres. A, antenna; CE, compound eye; Md, mandible; 1-12, antennomeres.

This number is identical for both antennae of the same individual. The numerical difference is due to the fact that the 10th antennomere is sometimes alone and sometimes divided into two antennomeres 10 and 11. A kind of joint membrane occurs between the 10th (or 11th) antennomere and the larviform sensory structures which extend this antennomere and which form a rudimentary 11th (or 12th) antennomere.

This terminal segment occupies the surface of the internal half of the joint membrane (Fig. 3i). On the outer part of the joint membrane, there occurs a typical sensory organ in the form of a small stick with a cone-shaped end corresponding to the "large multiporous sensillum basiconicum" (Fig. 3i).

The limit between the adult-type antennomeres and the larval-type antennomere is not very clear in dorsal view (Fig. 4a) or in ventral view (Fig. 4b) but appears more clearly in lateral view (Fig. 3i).

The 1st antennomere is the scape, the 2nd the pedicel, the 3rd–10th or 11th apparent antennomeres form the flagellum thus composed of 8 or 9 flagellomeres. For a 10-segmented antenna of 2.15 mm (Fig. 2b), the lengths of the antennomeres A1-A10 are the following: the scape is the longest, with 440 µm, and is as long as the pedicel (100 µm) and the 1st flagellomere (320 µm) combined; the 1st flagellomere (A3) is the longest of all the flagellomeres and the length of the others diminishes from A4 to A9 (225, 200, 175, 160, 150, 125 µm), the last adult-type antennomere A10 being more longer than the preceding one (180 µm). The rudimentary larval type antennomere measures 75 µm. The diameter of A1 to A9 varies from 275 µm to 150 µm; A10 measures only 75 µm.

The normally smooth integument presents a scale-like structure at the base of scape and pedicel. The scale-like structure is more visible, presenting greater relief over the proximal third and the distal edge of antennomeres A3-A7. It tends to develop over the whole surface of the segments from A8 to A10. In fact, the scales are present over the surfaces which present no sensilla. The localization and number of sensilla on the ventral face of the flagellum of an antenna with 10 visible antennomeres are indicated on Fig. 3a-h.

Sensilla of antennomeres of adult type

The adult-type antennomeres A1-A10 or A11 bear 3 sensillum types: Böhm sensilla, three types of sensilla chaetica, and 4 types of sensilla basiconica. Sensilla campaniformia are not observed.

Böhm sensilla are located only on the two first antennomeres (Fig. 5). The base of scape possesses a latero-external area composed of 7 sensilla 12-15 µm long, a latero-internal area with 9 sensilla and a medio-dorsal with 25 sensilla (Fig. 5a, b, c). The latero-external and latero-internal areas of pedicel comprise 13 and 10 sensilla respectively, 8-9 µm long (Fig. 5c, e, f). The greater length of sensilla on the scape is related to the greater amplitude of movement for the scape than for the pedicel.

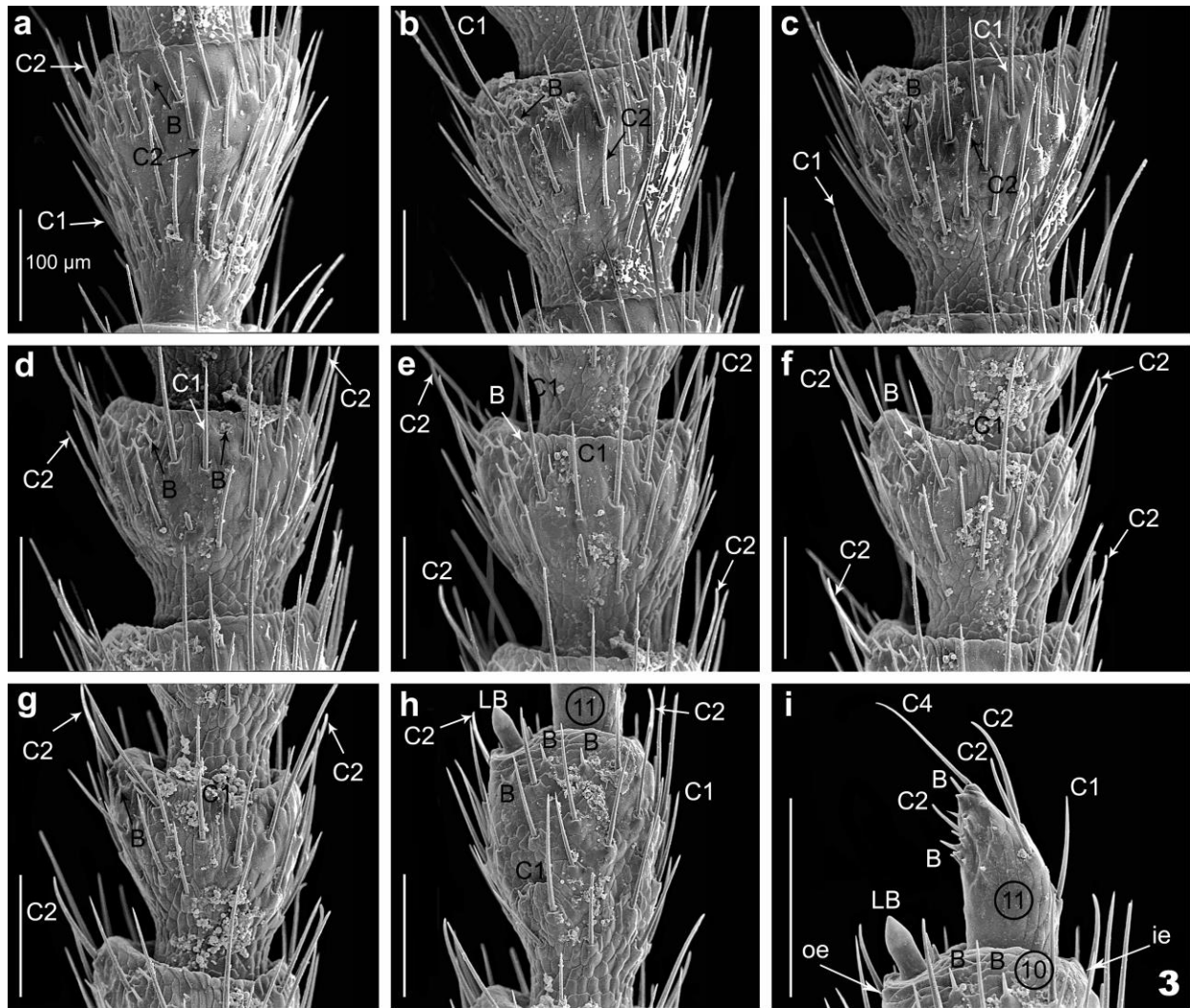


Figure 3. *Drilus mauritanicus*, female; ventral face of a left antenna with 11 antennomeres; **a.** 3rd antennomere; **b.** 4th antennomere; **c.** 5th antennomere; **d.** 6th antennomere; **e.** 7th antennomere; **f.** 8th antennomere; **g.** 9th antennomere; **h.** 10th antennomere; **i.** 11th antennomere in lateral view. B. sensilla basiconica; C1. aporous sensilla chaetica; C2. uniporous sensilla chaetica; C4. terminal aporous sensillum chaeticum; LB. large multiporous sensillum basiconicum; ie. inner edge; oe. outer edge. Scale bars a-i: 100 µm.

Aporous sensilla chaetica C1 are the longest sensilla and are both the most noteworthy and the most numerous on the antenna; they are spread out over both faces of the antenna (Fig. 2, 3). They are pointed and marked by 10-12 longitudinal striae, articulated at the base inside a narrow socket which limits the movement of the hairs (Fig. 6a-b). They form an angle of 30-45° with the integument of the antenna. On the scape, they are located on the distal part. Their average length is of 93 µm (range 66-175 µm) and the basal diameter is 2.6-4.0 µm.

On the following antennomeres, the sensilla C1 occupy 2/3 of the distal part of the segments but the proximal part is free of them. They display a great variation in length: 82-125 µm on A3, 60-113 µm on A9. Their number on the ventral face of the antennomeres has been calculated on one antenna.

It diminishes from scape (A1) to the 10th antennomere (A10): 40, 25, 33, 18, 15, 14, 13, 12, 14, 8. The dorsal face of the antennomeres reveals an identical localization but a different number of sensilla: 12, 6, 40, 29, 22, 15, 17, 13, 16, 6.

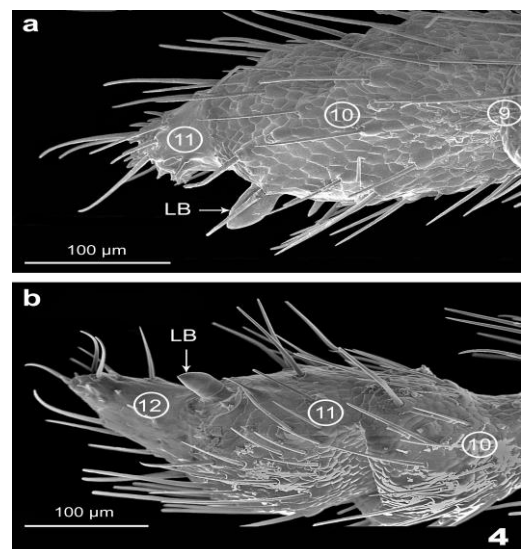


Figure 4. *Drilus mauritanicus*, female; **a.** dorsal view of tip of antenna with 11 antennomeres; **b.** ventral view of tip of antenna with 12 antennomeres; 9, 10, 11, 12, antennomeres 9-12; LB. large multiporous sensillum basiconicum.

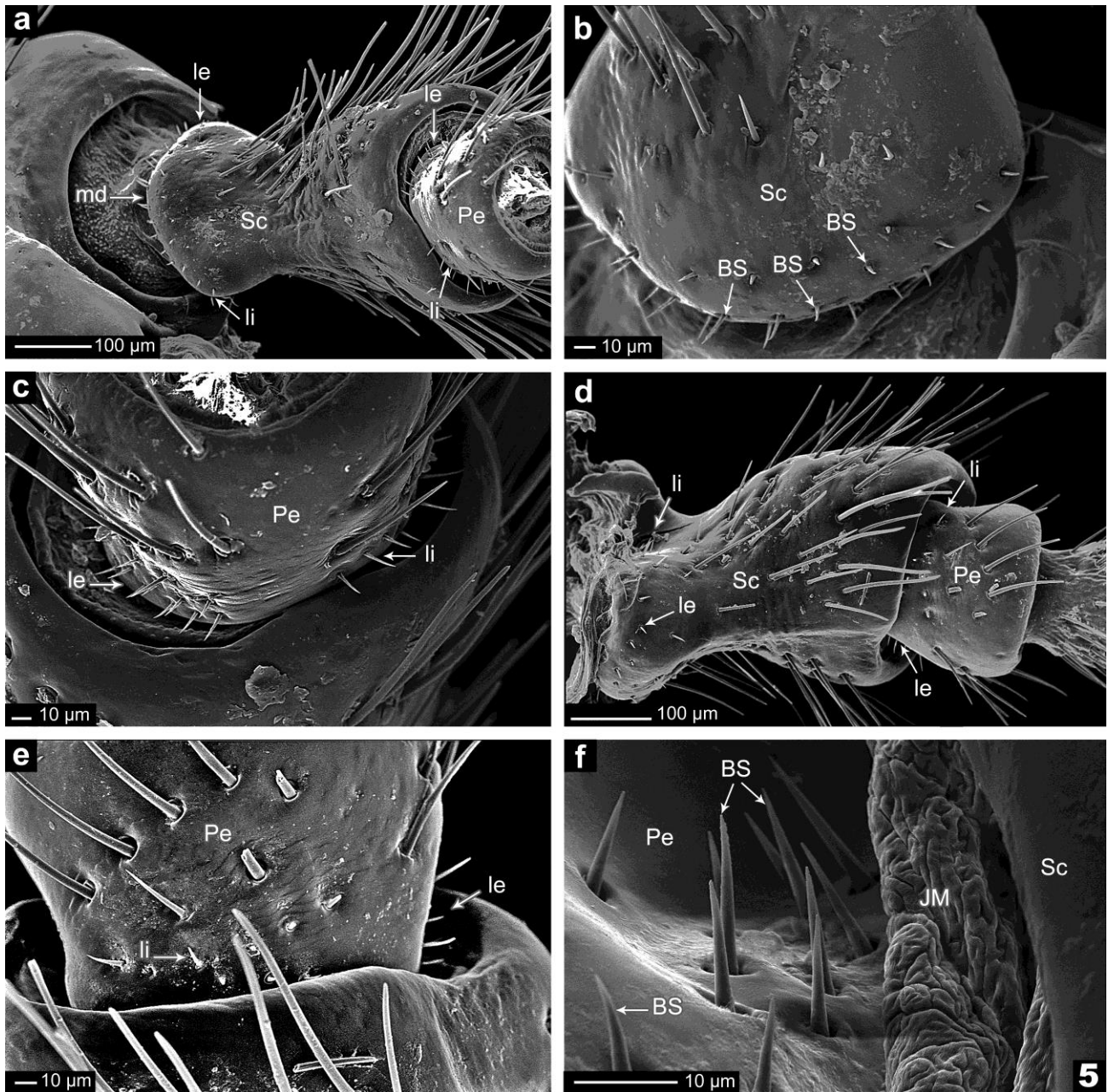


Figure 5. *Drilus mauritanicus*, female antenna. Böhm sensilla; **a**. dorsal view of scape (Sc) and pedicel (Pe) showing clusters of Böhm sensilla : medio-dorsal (md), latero-external (le) and latero-internal (li); **b**. detail of the medio-dorsal cluster of scape; BS, Böhm sensilla; **c**. detail of the latero-external and latero-internal clusters of pedicel; **d**. ventral view of scape and pedicel showing clusters of Böhm sensilla : latero-external and latero-internal ; **e**. detail of the clusters of pedicel ; **f**. detail of Böhm sensilla BS; JM, joint membrane.

Uniporous sensilla chaetica C2 are distinguished from sensilla C1 by their constant length (73-75 µm), a basal diameter of 5 µm, a squat appearance, a tendency to bend at half length and a blunt tip (Fig. 6 c, d). The terminal pore is always difficult to observe in SEM. Sensilla C2 occur only on the flagellomeres (antennomeres A3-A10). On A3-A5, they are both located in the middle of the segment (3-4 sensilla) and distally on each side (1-2 sensilla) (Fig. 3a, c). From A6 to A10, there are only 2 distal sensilla one on each side (Fig. 3 d-h). Their number, as calculated on the ventral face of an antenna from A3 to A10, is: 4, 3, 5, 2, 2, 2, 2, 2 = 22. No dorsal sensilla are present from A3 to A5.

Sensilla chaetica C3 are long sensilla (100-110 µm) with a bifurcate or trifurcate tip, and a basal diameter of 5 µm

present on some antennomeres. They are rare, no more than 2 sensilla per flagellomere (Fig. 6e-h).

Sensilla basiconica (all types) are present on all the flagellomeres (A3-A10). On the ventral face, the sensilla basiconica of A3 are concentrated on the upper outer edge (Fig. 3) and 1 or 2 isolated sensilla are also present but always in the distal region. On A4 and A5, they tend to scatter. On A6-A9, they come together again in the upper outer edge. Finally on A10, there are 5 sensilla, 4 distal and one median. Their number on the ventral face of antennomeres A3-A10, as counted for a given individual, is 14, 15, 18, 10, 8, 9, 11, 5 = 90 (Fig. 3), while the dorsal face bears 13, 11, 9, 7, 9, 8, 6, 2 = 65 sensilla.

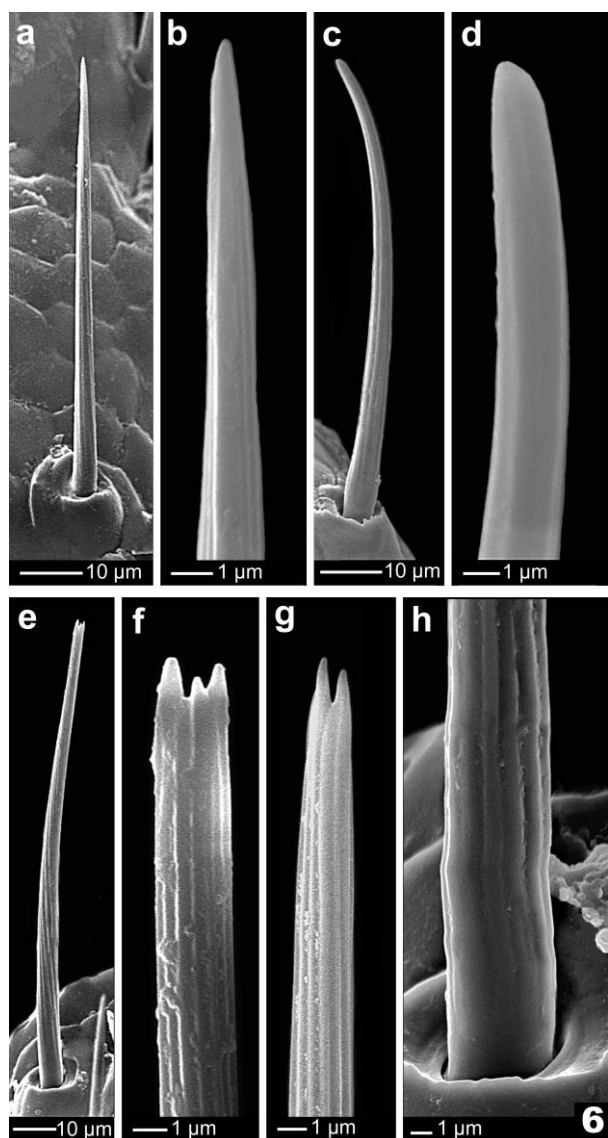


Figure 6. *Drilus mauritanicus*, female antenna. **a.** aporous sensillum chaeticum C1; **b.** tip of C1; **c.** uniporous sensillum chaeticum C2; **d.** tip of C2; **e.** trifurcate sensillum chaeticum C3; **f.** tip of C3; **g.** **h.** tip and base of bifurcate sensillum C3.

4 types of sensilla basiconica are observed:

Sensilla *B1* (12.7-13.4 µm long, 3.5-3.8 µm basal diameter) are slender and blunt-tipped, smooth, without visible pores in SEM, inserted in a dome-shaped base (8.3 µm on the outer diameter). They are the most numerous sensilla basiconica (Fig. 7a, b). For the females that have just been fecundated, the upper half of these sensilla is often covered with a scatter of tiny filaments (Fig. 7a).

Sensilla *B2* are similar to previous sensilla but they are longer (17.4-18.3 µm long, 3.3-3.4 µm basal diameter) and therefore appear more slender than sensilla *B1* (Fig. 7a, c). Certain sensilla also possess small filaments (Fig. 7d). Sensilla *B2* are rare: no more than 2 on the ventral face and one on the dorsal face.

Sensilla *B3* are conical pegs, 6.5-7.7 µm long, with a base measuring 3.0-3.2 µm in diameter and are inserted in a slightly convex circular disk 5 µm in diameter (Fig. 7f). The distal extremity is more or less regularly grooved without a

terminal pore (Fig. 7g). There are a maximum of 3 sensilla per flagellomere (Fig. 7f).

Sensilla *B4* are small pegs (9.2-9.5 µm long, 2.5-2.8 µm in basal diameter) surrounded by a basal collar of 6.5 µm in outer diameter (Fig. 7e). There is no more than one sensillum among the other sensilla basiconica.

Sensilla of the membrane at the apex of the distal adult-type antennomere

The membrane at the apex of the 10th (or 11th) antennomere bears three types of sensilla: a very large multiporous sensillum basiconicum LB, a sensillum styloconicum and a sensillum basiconicum *B5* (Fig. 8a).

The *large* multiporous sensillum basiconicum has a cone-shape 43 µm, 34.5 µm, and 27 µm long, variable according to individuals and 21 µm, 17.5 µm, 10 µm in basal diameter, respectively (Fig. 8a); it is directly fixed to the joint membrane without the intermediary of a stand but edged by a slender basal rim. Its wall is entirely perforated by pores whose density is 12-15 pores/µm² (Fig. 8b). Sensillum styloconicum and sensillum basiconicum *B5* are situated side by side between the large sensillum basiconicum LB and the 11th antennomere (Fig. 8a). Sensillum styloconicum *St* comprises a stylus (8.0 µm high, 4.0 µm basal diameter) and a sensory cone, 2.0 µm high. Sensillum basiconicum *B5* is slender with a sharp tip (18.6 µm long, 2.2 µm basal diameter).

Sensilla of the larval-type antennomere

According to antennae, the larval-type antennomere is either the 11th or the 12th antennomere (Fig. 4). The sensilla of the larval-type antennomere show various sensillum types from one antenna to another.

On the dorsal face, 6 sensilla chaetica *C2* are located at the tip, the 3 apical sensilla are the longest ones (54.5-68.2 µm), but the 3 subapical are of variable length (36.4, 59.1 µm). They are all shorter than the identical sensilla of the other antennomeres but their apical location ensures their privileged function (Fig. 9a). A sensillum basiconicum of *type B2*, 14.5 µm long, is found towards the inner edge and 3 sensilla basiconica *B6* are concentrated on the outer edge (Fig. 9a). The latter sensilla (10.8-13.6 µm long, 3.4 µm in basal diameter) are smooth, sharp-tipped pegs, regularly curved and inserted on the antennal integument without socket (Fig. 9b). A similar sensillum, but of greater length (17.3 µm long, 4.6 µm basal diameter) is apical (Fig. 9c). Wall-pores are sometimes observed on certain sensilla *B6*. A sensillum chaeticum *C1* is present on the outer edge (Fig. 9c).

On the ventral face of the antennomere

Three sensilla basiconica *B7* are grouped on the inner edge of the antennomere (Fig. 10a). They are directly inserted into the antennal integument. They have the shape of a more or less regular cone 4-6 µm in height and 4-5 µm in basal diameter. A terminal pore is sometimes visible (Fig. 10b).

Four sensilla basiconica *B8* (Fig. 10a, c) are located in the vicinity of the latter. This sensillum type is made up of a small peg 2.5 µm long placed at the summit of a large dome 5.1 µm in diameter and 2.5 µm in height. There are 4

sensilla B8 at the tip of antennomere (Fig. 9c, 10a). Sometimes 2 sensilla B4 similar to the B4 of antennomeres of adult-type replace 2 of the 4 latter sensilla B8 (Fig. 9c).

Two sensilla basiconica B9 of pyramidal shape (2.8 μm in height, 3.4-4.0 μm in basal diameter) are often present among the latter sensilla, one near the sensilla B7, the other near the sensilla B8 (Fig. 10a, c). The sensilla B9 are sometimes absent (Fig. 9c).

A sensillum basiconicum B10 is always present between sensilla B7 and B8 (Fig. 9c, 10a, c). It is a blunt-tipped cylindrical peg, 7.2-8.5 μm in length, and 2.0-2.3 μm in basal diameter: the diameter varies little up to the apex (1.6-1.7 μm). The base is surrounded by a thick collar (4.1 μm in outer diameter, 1.6 μm in height).

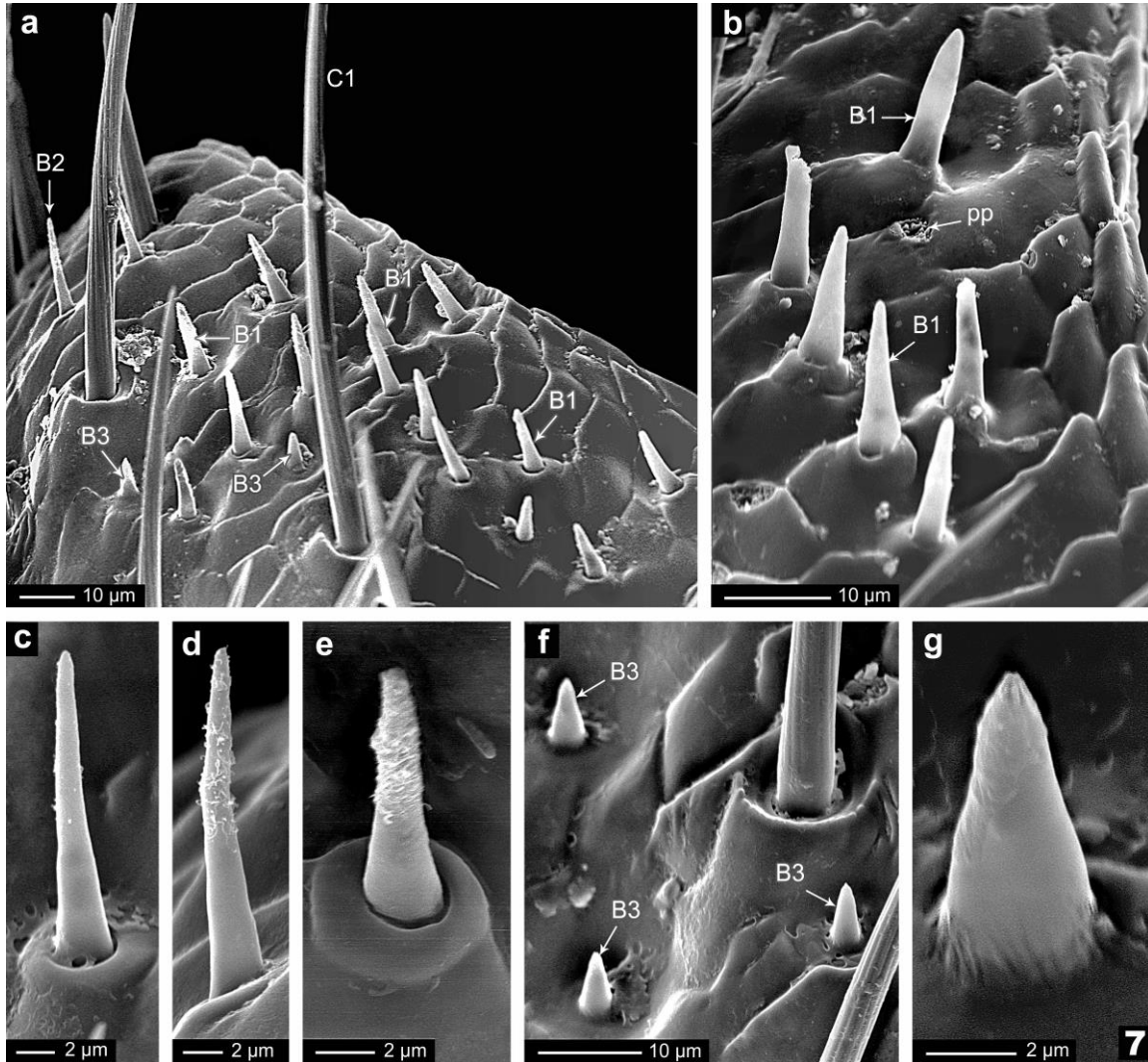


Figure 7. *Drilus mauritanicus*, female, sensilla basiconica of antennomeres 3-10. **a.** sensilla basiconica of three types (B1, B2, B3) grouped together on the upper outer edge of the ventral face of antennomere A6; **b.** general view of 6 sensilla basiconica B1; pp, perforated plaque; **c.** **d.** sensilla basiconica B2; **e.** sensillum basiconicum B4; **f.** cluster of 3 sensilla basiconica B3; **g.** sensillum basiconicum B3.

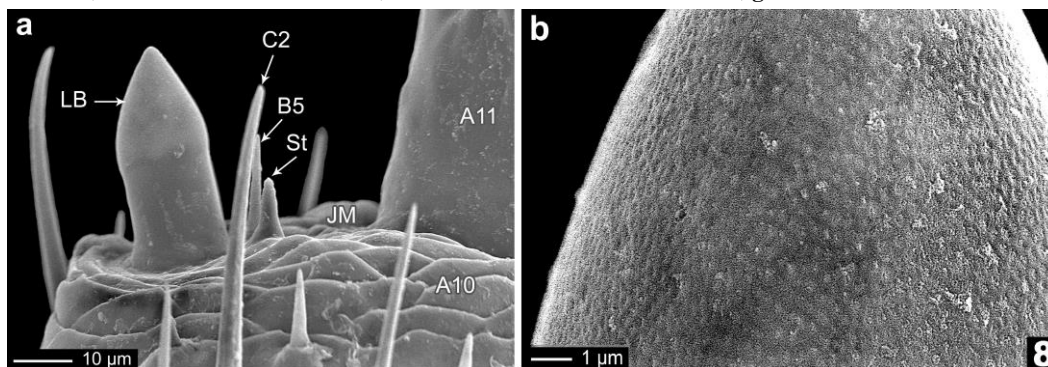


Figure 8. *Drilus mauritanicus*, female, sensilla of the joint membrane (JM) between A10 and A11. **a.** large multiporous sensillum basiconicum LB, sensillum styloconicum St, sensillum basiconicum B5; **b.** wall pores of sensillum basiconicum LB; A10, A11, 10th and 11th antennomeres; C2, uniporous sensillum chaeticum.

A flattened sensillum *basiconicum* B11 in the form of an elongated triangle (6.8 μm long, 2.0 μm in basal diameter) is located near the sensillum B10 in a more distal position (Fig. 9c, 10a, 10d). Whereas all the other sensilla are located on

the inner edge of the antennomere, the sensillum B12 alone is located on the outer edge (Fig. 10a). It is a small peg, 1.5–2.7 μm long, surrounded at the base by a collar of 5.4 μm in outer diameter.

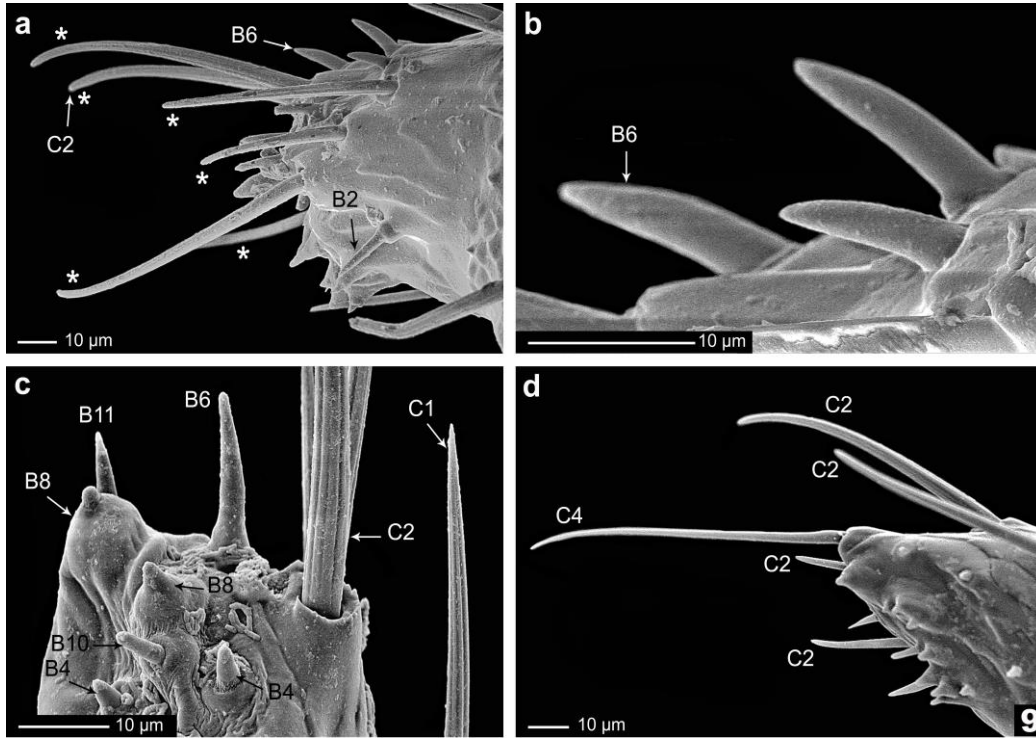


Figure 9. *Drilus mauritanicus*, female, sensilla on the apex of the 12th antennomere, **a**, dorsal face, uniporous sensilla chaetica C2 (asterisk), sensilla basiconica B2 and B6; **b**, group of sensilla B6; **c**, ventral face, sensilla chaetica C1 and C2, sensilla basiconica B4, B6, B8, B10, B11; **d**, ventral face, sensillum chaeticum C4 and sensilla C2.

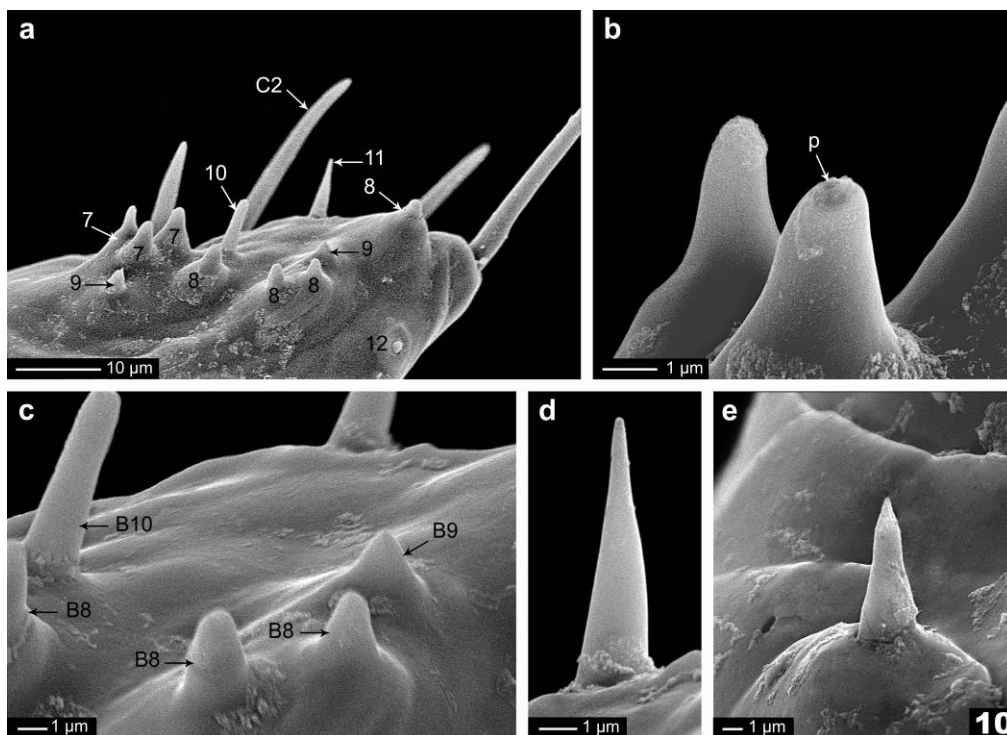


Figure 10. *Drilus mauritanicus*, female; sensilla on the ventral face of the 12th antennomere, **a**, distal part with sensilla basiconica of subtypes 7, 8, 9, 10, 11, 12; **b**, detail of sensillum B7 with terminal pore (p); **c**, detail of sensilla basiconica of subtypes 8, 9, 10; **d**, sensillum basiconicum B11; **e**, sensillum basiconicum B13.

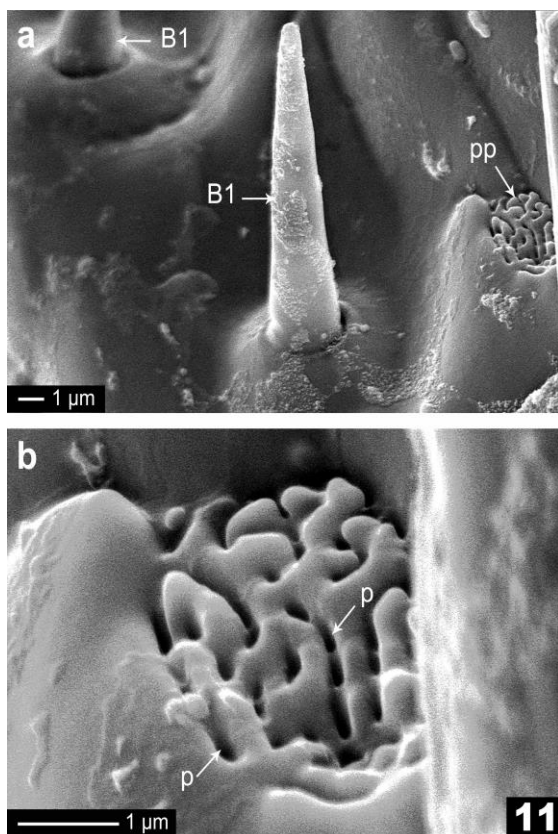


Figure 11. *Drilus mauritanicus*, female; **a**. perforated plate pp on the distal adult-type antennomere; **b**. detail of perforated plate; B1, sensillum basicicum type 1; p, pore.

Towards the base of the antennomere is a *sensillum B13* which resembles a sensillum B4 (6.6 µm long, 2.5 µm in basal diameter) inserted in a dome-shaped base (5.0 µm in height, 8.4 µm in basal diameter) (Fig. 10e).

Aporous sensillum chaeticum C4 is sometimes observed (Fig. 9d) at the distal end of the antennomere. It resembles a sensillum C1 but it is longer (64 µm) and less rigid.

Perforated plates are frequently found on the distal adult-type antennomere towards the middle of the segment: one isolated and two others located near the sensilla basiconica B1 (Fig. 11a, b). The circular, sponge-like area around the pores is 2.7-3.0 µm in diameter and is perforated by about 25 pores which are either round (0.1 µm in diameter) or linear or again sinuous (0.4 µm in length) (Fig. 10b). They can also be found on other antennomeres such as A6 (Fig. 7b). They are always reduced in number, at most 3 per antennomere.

DISCUSSION

The length of the 10th antennomere, twice as long as that of the 9th, has suggested to different authors that it is made up of two segments (Cros 1926, Faucheux & Agnas 2011, Faucheux & Kunderata 2014). Cros points out that « chez la femelle de *D. mauritanicus*, le onzième article est de l'ordre de grandeur du précédent ». The number of segments has already been subject to controversy in *D. flavescens* as regards the number of visible antennomeres which appears to vary, according to the individuals, from 9 to 10 (Schmitz 1909). In *Drilus concolor* Ahrens, 1812, Rosenberg (1909) mentions 11 antennomeres in the female. Cros (1926) who observed 18 females obtained from breeding was convinced

that the females of *Drilus mauritanicus* all possess antennae of 11 visible antennomeres, all of which were perfectly developed, to which is added a 12th surmounting the 11th.

Our results show that the female antenna of *D. mauritanicus* is composed of 10 or 11 visible antennomeres of imaginal type and of an 11th or 12th rudimentary antennomere of larval type and not necessarily of 12 segments as Cros claimed in 1926. The last antennomere of imaginal type is a special case because it possesses a distal hollow (joint membrane) comprising structures observed in the larval antenna (large multiporous sensillum basicicum, and small sensilla). These results have been confirmed on the 4 individuals (8 antennae) studied. We have obtained two little females from breeding (length: 21mm, 25 mm) and two larger ones (length: 31 mm, 35 mm); the small ones possessed 11 antennomeres, and the large ones 12 antennomeres. Further observation is necessary to ascertain whether the number of antennomeres is really related to the size of the females.

Comparison with the male antenna

Figure 12 allows us to compare the morphology of the antenna in the larva, the adult female and the adult male. The larval antenna has already been observed (Faucheux 2014) as has the male antenna which is pectinate and 11-segmented (personal observations).

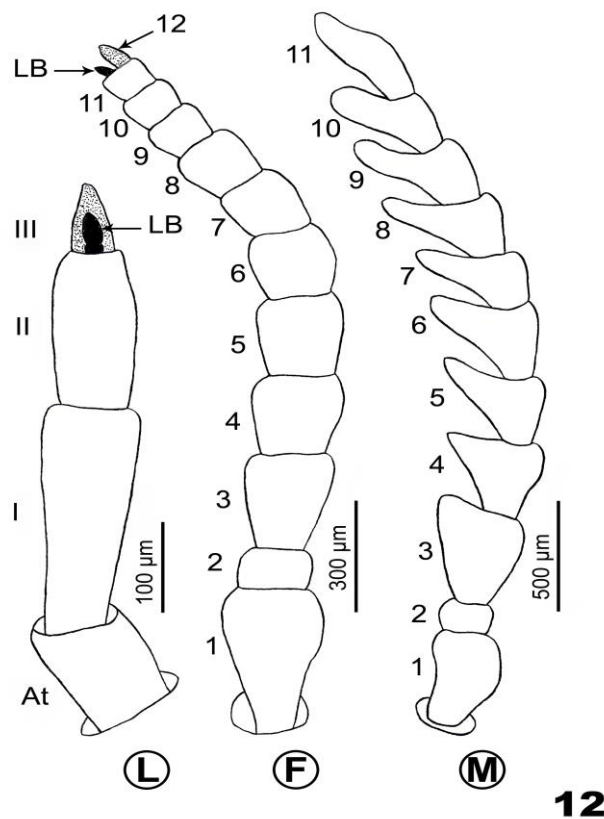


Figure 12. *Drilus mauritanicus*, diagrammatic representation of antennae of larva (L), female adult (F), male adult (M). I-III, larval antennomeres; 1-11, male or female antennomeres; 12, larval-type antennomere of female; At, antacorium; LB, large multiporous sensillum basicicum.

The flagellum sensilla common to the two sexes are the sensilla chaetica C1, the sensilla chaetica C2, the sensilla basiconica B1, B2 and B4. Sensilla B3 and B5, present in the female, have not been observed in the male antenna;

Aporous sensilla chaetica C1 function as tactile mechanoreceptors enabling the beetle to determine the position of the antennae with respect to its surroundings (Altner 1977, Zacharuk 1985, Faucheux 1999). Merivee *et al.* (1999) reveal in electrophysiological results obtained in the Elateridae Elaterinae *Agriotes obscurus* (Linnaeus, 1758) and *Limonium aeruginosus* (Olivier, 1790) that sensilla C1 are sensitive to mechanical stimuli.

Sensilla chaetica C2 have been called “sensilla trichodea” or “sensilla trichodea of type 1” in Elateridae Elaterinae (Merivee *et al.* 1997, 1998, 1999), sensilla trichodea type 1 in *Tetrigus lewisi* Candèze, 1873 (Ren *et al.* 2014). Not observable in SEM on the female antenna of *D. mauritanicus*, the terminal pore is described from similar sensilla in *Ips sexdentatus* Boern, 1776 and *Ips pini* (Say, 1826) by Faucheux (1989, 1994). Ren *et al.* (2014) have shown that the hair shaft possessed a thick wall, two lumen of which one has dendritic branches, and one lymph lumen without dendrite. Taking into account their external morphology, their ultrastructure, their low numbers and their localization, the sensilla C2 which are «TP sensilla» (Altner 1977) or «uniporous sensilla» (Zacharuk 1985, Faucheux 1999) are both mechanoreceptive and chemoreceptive. These sensilla have been shown by means of electrophysiological methods to be contact chemoreceptors in the male elaterid *A. obscurus* (Merivee *et al.* 1998).

The comparison between the numbers and percentages of the antennal sensilla of both sexes throws light on the functions of the sensillum types (Faucheux & Agnas submitted). This must take into account the respective lengths of the male (3.0-3.2 mm) and female antennae (2.0-2.2 mm). The number of tactile sensilla chaetica C1 is 1317 sensilla per antenna in the male and 370 in the female. Although the latter are fewer in the female, they nevertheless perform an important function because the female, in contact with the ground, receive permanent mechanical stimuli, whereas the winged male is in contact with the substratum only when it alights on plants. The uniporous sensilla chaetica C2, with a gustatory function, though they exist in different numbers in the male (49) and the female (28) nevertheless reveal considerable possibilities in both sexes.

Aporous sensilla chaetica C3, present on female antennae are absent from male antenna but resemble the thorny sensilla chaetica with fingers-shape tip C1 of the larval antenna of *D. mauritanicus*.

Sensilla basiconica have been reported on the antennae of numerous coleopterans. More specifically, the sensilla B1 and B2 of female antenna resemble the same sensilla in the male antenna of *D. mauritanicus* (Faucheux & Agnas,

submitted), sensilla B1 and B2 on the antennal flagellum of three Elateridae Elaterinae species such as *A. obscurus*, *L. aeruginosus* and *Melanotus villosus* (Fourcroy, 1785) (Merivee *et al.* 1997, 1998, 1999), and also B1 and B2 of the Elateridae Agrypninae *T. lewisi* Candèze, 1873 (Ren *et al.* 2014). Their surface on scanning electron micrographs appears to be smooth and not perforated. However, breaks of pegs show a thin wall compared to the sensillum lumen, and the presence of pores on the inner face of the wall in the two types on the male antennae of Drilini (Faucheux & Kundrata, submitted). Taking into account their ultrastructure, sensilla basiconica correspond to the «multiporous chemosensilla» (Zacharuk, 1980), “single-walled, wall pore sensilla” (Altner and Prillinger, 1980). These sensilla in the male reach great numbers (n = 4681), compared to those in the female (n = 130). Most of these sensilla (B1 and B2) in the male are probably sensitive to a female sexual pheromone facilitating copulation. The precise role of these olfactory sensilla in the female has not been determined.

Sensilla B3 in the female resemble sensilla B8 in the Drilini male antennae in which a terminal pore is sometimes visible and to which a gustatory function is attributed (Faucheux & Kundrata submitted).

Sensilla B4 of the female are identical to the sensilla B10 of *Drilus*, *Malacogaster*, and *Selasia* male antennae and also to “sensilla basiconica SB3” of *Xylotrechus grayii* (Chen *et al.* 2014), and the “sensilla auricillica” of *T. lewisi* (Ren *et al.* 2014). In this latter species, they have wall pores and consequently, they may be olfactory. The perforated plates are rare on the female antenna while on the male antenna, they are present on all flagellomeres and their number is close to that of the sensilla basiconica, (for example: 107 glands are found on the ventral surface of the terminal flagellomere) (Faucheux & Kundrata 2015). They correspond to putative aphrodisiac integumental glands. Their quasi absence in the female antenna strengthens this hypothesis.

Comparison with the antenna of the primary larva

Sensilla on the joint membrane of larva and female

The joint membrane situated at the distal part of the female antennomere 10 resembles the joint membrane located on the distal part of larval antennomere II (Fig. 13a, b). Both bear the large sensillum basiconicum (LB in female, B1 in larva), a sensillum styloconicum and a sensillum basiconicum (B5 in the female, B2 in larva), and another segment (A11 in the female, AIII in larva).

The sensillum styloconicum and the sensillum basiconicum are found between LB and A12 in the female, but are peripheral in the larva (Fig. 13a, b). The presence of the large multiporous sensillum basiconicum in the two antennae is without question the most interesting datum, the female sensillum being of slightly smaller dimensions than those of the larval sensillum.

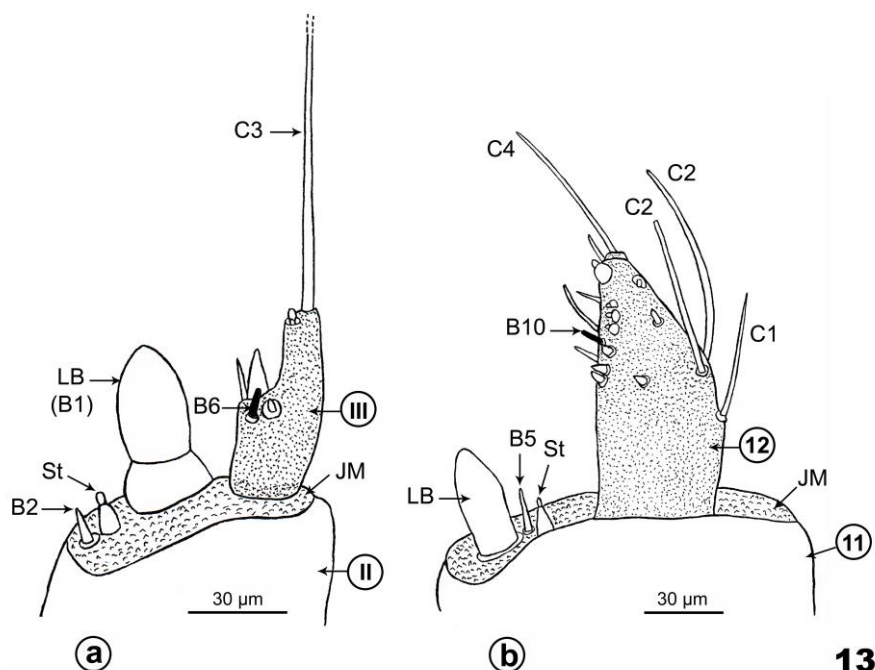


Figure 13. *Drilus mauritanicus*, diagrammatic representation of types and distribution of antennal sensilla, **a**, in the larva, on distal part of antennomere II and on antennomere III. At, antacorium; JM, joint membrane; LB (B1), large sensillum basiconicum; St, sensillum styloconicum; B2, B6, sensilla basiconica types 2, 6; C3, terminal sensillum chaeticum of type 3 (according to Faucheux 2014). **b**, in the female, on distal part of antennomere 11 and on antennomere 12; JM, joint membrane; LB, large sensillum basiconicum; St, sensillum styloconicum; B5, 10, sensilla basiconica types 5, 10; C1, C2, C3, C4, sensilla chaetica of types 1, 2, 3, 4. (Remark: B2 = B5 ; B6 = B10).

The large sensillum basiconicum of the female probably possesses the same structure and the same function as that of the larva. The high number of chemosensory neurons of this multiporous sensory organ suggests a possible ability of fine odour discrimination related to prey choice or host location (Giglio *et al.* 2008). The sensillum styloconicum and the sensillum B5 are possible olfactory receptors.

Sensilla of larval antennomere III and female larval-type antennomere

It is tempting to compare larval antennomere III and female larval-type antennomere 12 which occupy the same position on the joint membrane (Fig. 13). The number of sensilla is greater in the female (24) than in the larva (5) (Fig. 13). Only a few sensillum types are common to the two antennae: female B10 and larval B6, female B6 and larval B4, female C4 and larval C3. Sensilla B10 resemble larval sensilla B6 which possess a terminal pore and therefore probably have a gustatory function. Female sensilla B6 probably have an olfactory function. The female aporous sensillum chaeticum C4 occupies the same position as that of the larval aporous sensillum chaeticum C3 at the tip of the segment. A vibroreceptive function has been attributed to the larval sensillum. Although the sensillum in the female is shorter, a similar function can be proposed.

The other sensilla basiconica of the female are absent from the larval antenna. Sensilla B7 with a terminal pore can be considered as gustatory sensilla.

Sensilla B8 of female *D. mauritanicus* resemble “sensilla basiconica subtype 13” of male *Drilus concolor* Ahrens, 1812 (Faucheux, personal observations), “short

sensilla basiconica I” of *Psylloides affinis* (Paykull, 1788) (Ritcey & McIver, 1990) and “sensilla campaniformia” of *Xylotrechus grayii* (White, 1855) (Chen *et al.* 2014). The scarcity of these short sensilla basiconica, as well as their morphology, may give clues to their probable function. According to Chapman (1982), sensilla sensitive to stimuli which permeate the insect’s immediate environment, such as heat and humidity, are present in low numbers on the antennae. In the Coleopteran Coccinellidae *Epilachna varivestis* Mulsant, 1850, Fischer and Kogan (1986) reported that sensilla basiconica type II, whose morphology resembles sensilla basiconica I of *P. affinis*, sensilla basiconica B13 of *D. concolor*, and sensilla “B2” of female *D. mauritanicus* are often thermo- or hygroreceptors. Furthermore, sparsely occurring pegs on various other insects have been demonstrated to be hygrothermoreceptors (Tichy 1979, Yokohari 1981, Altner & Loftus 1985, Faucheux 1999).

Sensillum B13 is of identical type to the sensilla B8 present in the male Drilini *Drilus* sp., *Malacogaster* sp. and *Selasia* sp. (Faucheux, personal observations) and to the sensilla B4 of the male antenna of *D. mauritanicus* (Faucheux, personal observations). Like these sensilla, the sensillum B13 is probably a gustative receptor.

Other sensilla absent from the larva are present both on the female larval-type antennomere and the adult-type antennomeres: the sensillum chaeticum C1 and the sensilla chaetica C2. This shows that, albeit rudimentary, the female larval-type antennomere conserves tactile and gustatory functions. It is interesting to note that the bifurcate or trifurcate sensilla chaetica C3 of the female are absent from the male antenna (Faucheux, personal observations) but are present on the larval antenna.

What is the interest for the female to possess on its antennae structures present on the larva?

According to Cros (1926), *D. mauritanicus*, as concerns the females at least, take no food; he offered snails to the insects but they did not touch them. This also the opinion of Mielzinski (1824), Desmarests (1824) and Audouin (1824) concerning the females of *D. flavescens*. However, Lucas (1849) fed snails *Cepaea hortensis* (Müller, 1774) (= *Helix hortensis*) for eight days to a female of the Drilini *Malacogaster passerinii* Bassi, 1833. Concerning the latter species, having given a live snail to a female 10 days after its emergence, it broke the shell and emptied the occupant before ingesting it (Faucheux & Agnas 2008). Thus, the females of Drilini are capable of ingesting snails in certain circumstances. Perhaps they take food if they are not rapidly impregnated. Indeed, the observed life of female *D. mauritanicus* is between 14 and 19 days (Cros 1926). Mielzinski (1824) kept a female of *D. flavescens* alive for five weeks. The persistence of larval sensory structures on the antennae, in particular the “large olfactory sensillum basiconicum” would allow the female to have a predatory behaviour equal to that of the primary larva actively seeking its prey.

Comparison with other cases of neoteny in Insects

In certain colonies of termites, neotenic insects of both sexes can replace adult males and females and ensure the development of colonies. Since termites are heterometabolous insects, the antennae of larval instars resemble the antennae of adults and neotemics; there are no morphological differences between the neotenic insects and the adults which are distinguished only by the number of sensilla (Faucheux & Lebrun 1988 and unpublished data). In the coleopteran *Lampyris noctiluca* (Linnaeus, 1767) of which the family Lampyridae is close to that of the Elateridae, the neotenic female, larviform and wingless, possesses no supplementary antennomere at the tip of its antennae (pers. obs.). The persistence of larval characteristics on the antennae of neotenic females seems to be a characteristic specificity of the females of *D. mauritanicus* and probably of the Drilini as well.

CONCLUSION

The present study reveals the considerable sexual dimorphism concerning the antennae of *Drilus mauritanicus*. If the male antennae are typical of Coleopterans with 11 identical antennomeres, those of the female are atypical with the presence of a variable number of antennomeres (10 or 11) and, above all, that of a rudimentary supplementary antennomere. The number of olfactory sensilla basiconica of the male is 30 times superior to that of identical sensilla of the female (Faucheux, personal observations). The supplementary antennomere recalls the distal antennomere of the larva and its sensilla. The composite character of the female antenna is related to the neoteny of the adult female which possesses both adult characteristics (possibility of reproduction, existence of adult-type antennomeres) and larval characteristics (general shape of the body, absence of wings, presence of an antennomere of larval type). A

comparison with other females of Drilini would help to discover whether the neoteny produces the same results on the antennae. According to Cros (1930), the female of *M. passerinii* with its antennae comprising 7 segments, seems to possess its terminal antennomere “surmounted by a tiny eight segment in the shape of a cylindrical stick with a round tip”.

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