Sexual Dimorphism in the Mandible Shape of *Neospondylis upiformis* (Coleoptera: Cerambycidae)

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**Abstract**

Sexes of adult Cerambycidae (Coleoptera) are usually discriminated by the greater length of male antennae. However, in Spondylidinae, adult antennae are short and the difference between sexes is negligible and difficult to appraise. Only two species belong to this subfamily in North America, one of these being *Neospondylis upiformis* (Mannerheim), a species rarely caught in eastern North America. Unexpectedly, we collected numerous specimens of *Neospondylis upiformis* on Anticosti Island, Quebec, which appears as a hotspot for this species in eastern Canada. We show that sexual dimorphism in the mandible shape of *N. upiformis* (Mannerheim) can be used to discriminate sexes. Females have robust mandibles with a sharp cutting inner edge while males have thin mandibles and a well-rounded inner edge. There was no overlap between sexes in all measures done on mandibles, showing that mandible shape was a reliable criterion for sexing *N. upiformis*. We also tested previously reported criteria using antennae, as well as other characteristics such as body size, and show that they can hardly discriminate between sexes in *N. upiformis*. We also present illustrations of male and female genitalia, which is rarely available for Cerambycidae.

**Keywords**

*Neospondylis upiformis*, Cerambycidae, Sexual Dimorphism, Mandible, Genitalia

**1. Introduction**

Sexual dimorphism is widespread among animals [1]. In insects, it often allows determining sex more easily and avoids the tedious task of dissecting genitalia. The criterion most often used to discriminate between sexes in adult Ceramby-
cidae (Coleoptera) is the greater length of male antennae [2] [3]. However, this criterion is difficult to use for certain groups such as Spondylidinae, a subfamily in which adult antennae are short, rarely reaching the base of the pronotum [4]. Only two species belong to this subfamily in North America, one of these being *Neospondylis upiformis* (Mannerheim), a species commonly captured in western North America, but which is uncommon in eastern Canada [4] [5] [6] [7] [8] [9]. Unexpectedly, numerous specimens of this longhorned beetle were collected between 1993 and 2007 on Anticosti Island, Quebec, which appears as a hotspot for this species in Eastern Canada [9].

Few studies have addressed the biology and life-history of *N. upiformis*. The most prominent report comes from Alberta in western Canada, where larvae were found in white spruce roots up to 50 cm below ground and more than a meter away from the stump, where some pupae were located [10]. The author also reported that adults are “somewhat adapted for digging, having unusually large mandibles and terminal lamellae on the fore tibiae” [10]. While examining *N. upiformis* adult mandibles, we observed that certain specimens had thick and robust mandibles with a sharp cutting inner edge, while others had much thinner mandibles with a well-rounded inner edge. We dissected genitalia of a subset of specimens and confirmed that each mandible shape was characteristic of a particular sex.

In this paper, we present data showing that 1) mandible shape is a reliable criterion for rapidly sexing adult *N. upiformis*, 2) previously reported criteria using antennae can hardly discriminate between sexes in *N. upiformis*, and 3) other characteristics such as body size cannot be used for sexing this species.

2. Materials and Methods

We used 12-funnel Lindgren traps to survey the xylophagous beetles of Anticosti Island in 1993 [9]. Among the beetles collected, we identified over 250 specimens of *N. upiformis* using available taxonomic keys [4] [5]. Using fine forceps and insect pins, we extracted the genitalia of 11 specimens, under a stereomicroscope. The specimens were randomly selected, alternating between the two groups characterized by different mandible shapes. The genital structures were cleaned in 70% ethanol and mounted in Canada balsam on small plastic slides pinned with the specimens from which they were extracted (*Figure 1*). Photographs were taken using a Canon EOS Digital Rebel XT/350D camera mounted on a Tessovar Zeiss stereomicroscope and controlled by ZoomBrowser EX software. Images were managed with Corel PaintShop Pro software. Using fine forceps, we also extracted the mandibles of these 11 specimens to take measurements. Dissections were stopped after 11 specimens as it represented 5% of available pinned specimens and there was a perfect fit between mandible shape and genitalia for sexing *N. upiformis* adults.

Mandibles were cleaned in ethanol and once dried, they were glued to a rectangular card point, exposing their dorsal side. Each mandible was photographed,
image files were conserved and various measures were taken using the ImageJ software. This software provided measures (concavity) of the area beneath the cutting edge and beneath the groove between mesal teeth (Figure 2), which are useful to show sexual dimorphism but which would be difficult to use in laboratory. We thus added linear measurements for this purpose. We drew a line between the apical incisor of the mandible and the proximal tip of the mesal tooth and then measured mandible thickness at its widest point and the corresponding area beneath the inner cutting edge (Figure 2). The ratio A/B (thickness/curvature) expresses mandible shape for both sexes (see Figure 2). All remaining specimens were sexed according to the mandible shape criterion.

In order to test other criteria for sexing *N. upiformis*, we used an electronic graduated ocular (Wild MMS 235) mounted on a stereomicroscope. First, we measured the length of the ultimate and penultimate antennal segments on 25 males and 25 females collected on Anticosti Island in 1993. It allowed to test the criteria proposed by Linsley that the ultimate segment is nearly twice as long as the penultimate one in males, while it is only 1½ longer in females [4]. We also measured the body length, from the frons to the tip of the abdomen of each specimen collected on Anticosti Island in 1993 (n = 251).

The various measurements made on mandibles, antennae (ratio ultimate/penultimate segments) and body length were compared between males and females using ANOVAs followed by Tukey’s all pairwise comparison tests (post-hoc analysis). The *lm* function from the *stats* package in R was used (R Core Team 2014).

3. Results and Discussion

Specimens showing robust mandibles with a sharp cutting inner edge were all females (n = 5), while those with thin mandibles and a well-rounded inner edge were all males (n = 6). There was only slight intra-sex variation in all measures done on mandibles and no overlap between sexes (Table 1), making mandible
Figure 2. Female and male mandibles of *Neospondylis upiformis* (Mannerheim) and measurements taken for comparing sexes.

Table 1. Comparison of three measurements taken on mandibles of *Neospondylis upiformis* males (n = 6) and females (n = 5) collected on Anticosti Island in Quebec, Canada, in 1993.

<table>
<thead>
<tr>
<th></th>
<th>Cutting edge concavity*</th>
<th>Mesal tooth concavity*</th>
<th>Thickness/curvature* (a/b)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean ± SD</td>
<td>Range</td>
<td>Mean ± SD</td>
</tr>
<tr>
<td>Male</td>
<td>0.55 ± 0.06</td>
<td>0.30 - 1.00</td>
<td>0.086 ± 0.008</td>
</tr>
<tr>
<td>Female</td>
<td>0.13 ± 0.02</td>
<td>0.07 - 0.26</td>
<td>0.005 ± 0.001</td>
</tr>
</tbody>
</table>

*See Figure 2. For each variable, ANOVA followed by Tukey’s pairwise comparison; P < 0.001.

shape highly reliable as a criterion for sexing *N. upiformis*. For instance, the basal molar area of the mandible varied between sexes, males showing a bilobed mesal tooth separated by a deep groove from the base of the mandible, while the groove and the mesal tooth were strongly blunted in females, giving a more robust appearance to female mandibles (Figure 2). This can easily be appraised by looking at the area delimited by the inner cutting edge of the mandible and a line drawn between the apical incisor and the proximal tip of the mesal tooth. Because of the stronger curve of the inner cutting edge of the male mandible, this area was significantly larger in males than in females (Table 1). Moreover, the mesal tooth area was also significantly larger in males than in females (Table 1; Figure 2). Consequently, the ratio between mandible thickness and the space beneath the inner cutting edge of the mandible was significantly larger in females than in males (7.2 vs 1.7; Table 1; Figure 2).

The structures on sternite VII usually makes it possible to discriminate between sexes in Cerambycidae [11]. This sternite is generally elongated and rounded at its apex, and often bear pits and carena that vary between sexes. However, in *N. upiformis*, the sternite and tergite VII, even if they are easily visible, are similar for both sexes and do not make it possible to discriminate between males and females without examining the internal genital structures (Figure 3). Indeed, it is not suggested to use genitalia for sexing cerambycids, as the genital segments are rarely everted when they die [12], and *N. upiformis*
Figure 3. Seventh tergite and sternite and abdomen tip of female and male Neospondylis upiformis (Mannerheim).

does not differ from other species in this regard. Photographs of the various structures of male genitalia (Figure 4) confirm previously published drawings [13] but also illustrate how the median lobe is inserted into the tegminal ring to form the aedeagus. In fact, the aedeagus is formed by the combination of the median lobe with the tegmen, which consists of the two parameres (or lateral lobes) connected to the tegminal struts by the tegminal ring. Female genitalia and the spermatheca are also shown [14] (Figure 4).

The ratio between the length of the ultimate and penultimate antennal segments was significantly different between males and females (Table 2), but the ratio was smaller (1.60) for males than that previously reported by Linsley [4] (2.0). Indeed, there was an overlap in measures between the sexes (range of 1.47 - 1.73 for males vs 1.29 - 1.56 for females), showing that this criterion does not always allow discrimination between sexes. Moreover, this criteria is difficult to appraise visually (Figure 5). Also, the Linsley criteria that antennae reach or slightly exceed the base of elytra in males, while they do not exceed the base of the pronotum in females [4] is difficult to use for sexing adult N. upiformis because the antennae of pinned specimens are not oriented toward the elytra and the head is rarely well-aligned with the rest of the body (Figure 1). Finally, even if females were significantly larger than males (Table 2), this criterion cannot be used for discriminating sexes as there is a large overlap in body length of males and females (Figure 6).

4. Conclusion

The evolution of sexual dimorphism has often been interpreted as arising from sexual selection but dimorphism in mouthparts could be the only unequivocal evidence for an evolution through intersexual niche partitioning [1]. Sexual dimorphism in mandible shape could thus result from differences in the ecological needs of males and females. In cerambycidae beetles, females often dig a cavity into the bark in which they lay their eggs [15]. As N. upiformis larvae have been
Figure 4. Genital structures of female and male *Neospondylis upiformis* (Mannerheim).

Figure 5. Female and male antennae of *Neospondylis upiformis* (Mannerheim).
Figure 6. Body length of males and females *Neospodylis upiformis* (Mannerheim) collected on Anticosti Island, Quebec, Canada, in 1993.

Table 2. Ratio between the ultimate and penultimate antennal segments (n = 25 for each sex) and body length (n = 116 and 135 for males and females, respectively) of *Neospodylis upiformis* collected on Anticosti Island, Quebec, Canada, in 1993.

<table>
<thead>
<tr>
<th>Ultimate/penultimate antennal segment</th>
<th>Body length (mm)</th>
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<tbody>
<tr>
<td></td>
<td>Mean ± SD</td>
</tr>
<tr>
<td>Male</td>
<td>1.60 ± 0.01&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>Female</td>
<td>1.46 ± 0.02&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
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<sup>a</sup>ANOVA followed by Tukey's pairwise comparison; P < 0.001. <sup>b</sup>ANOVA followed by Tukey's pairwise comparison; P = 0.01.

found in tree roots and collars [10], females may use their robust mandibles to dig into soil to reach tree roots for laying eggs. This could explain why mandibles of *N. upiformis* are scoop-shaped. Besides, in chrysomelid beetles, it has been suggested that enlarged mandibles might be used by males as clasping organs during copulation [16]. It could also be the case for the curved mandibles of
male *N. upiformis* but direct observation of their mating behaviour is needed to confirm such hypothesis. Meanwhile, mandible shape appears as a reliable criterion for rapidly sexing *N. upiformis*, at least for Anticosti Island (Figure 7). As *N. upiformis* is uncommon in eastern North America, specimens examined in this study all came from one location, an island, where particular conditions may have led to specific adaptations. Therefore, the importance of geographic variation should be further verified with other specimens. For instance, pronounced differences in mandibles and ligula were observed for *Spondylis buprestoides* collected in Turkey and Italy [13]. A first look at specimens collected from western Canada showed that the two types of mandible shape were also present, as was the case for the few other specimens collected elsewhere in Quebec.

**Acknowledgements**

We thank Mario Fréchette from the Ministère de l’Agriculture, des Pêcheries et de l’Alimentation du Québec for the identification of *N. upiformis*. We are grateful to Isabelle Lamarre from the Canadian Forest Service of Natural Resources Canada (CFS-NRCan) for improving the language and editing the manuscript and to Jean-Michel Béland from CFS-NRCan for his help in extracting, mounting, photographing and measuring mandibles, and for the statistical analysis.

**Conflicts of Interest**

The authors declare no conflicts of interest regarding the publication of this paper.

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