



Structure of mandibles in relation to trophic niche differentiation in a tropical millipede community

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Abstract

Isotopic composition of nitrogen in 19 species of Diplopoda from a tropical monsoon forest (Cat Tien National Park, southern Vietnam) which supports one of the most diverse millipede faunules globally (no less than 36 species from 17 families and 11 orders) forms a wide continuum of $\delta^{15}\text{N}$ values ranging from -2.4 to $+6.8\%$. This suggests a trophic niche differentiation among species. Variation in mouthpart structure could presumably reflect the different foods consumed by species representing at least higher taxa (families and orders). The fine structure of the mandibles in ten sympatric, mostly even syntopic species of Diplopoda does differ considerably between the higher taxa, but neither at the generic nor species level. Neither clear-cut trends in nor evident morphological patterns of, nor significant correlations between the structure of mandibles in Diplopoda species that have different isotopic compositions of nitrogen and presumably exploit different food resources, have been revealed.

Keywords

Diplopoda, ecology, mandible, stable isotopes, seasonal tropical forest, Vietnam

Introduction

Biological diversity of nearly all animal taxa, including Diplopoda, peaks towards the Equator. A range of hypotheses have been proposed to explain this phenomenon (Chown and Gaston 2000, Hawkins 2001, Willig et al. 2003). However, the communities of soil saprophagous animals, which form a large part of total biodiversity in

tropical forests, are only rarely taken into account (De Deyn and Van der Putten 2005, Stork and Grimbacher 2006).

Ecological theory suggests that the maintenance of high species diversity levels requires ecological niche separation of different species (Levine and Hille Ris Lambers 2009, Purves and Turnbull 2010). This can be segregation in time or in space, as well as in the food types used by the species. The diversity of above-ground animals in the tropics is likely related to the diversity of plants (Hill and Hill 2001, Willig et al. 2003), but saprophagous soil animals are less strongly co-adapted to their food sources, often showing no or only a weak positive correlation between the diversity of soil decomposers and that of plants (Hooper et al. 2000, Donoso et al. 2010). Diplopoda are typical soil decomposers, and are generally regarded as “primary destructors” of plant debris (Wardle 2002). Only relatively few species can consume green leaves, soil, tissues of dead and even living animals (Srivastava and Srivastava 1967, Hoffman and Payne 1969, Crawford 1992, Hopkin and Read 1992, Hashimoto et al. 2004, Ebreget al. 2005, Golovatch and Kime 2009). Recent advances in the use of stable isotope analysis revealed a complex structure of saprotrophic animal communities in temperate forests (Pollierer et al. 2009). Our preliminary data on the isotopic composition of tropical millipedes also suggest that individual species can occupy distinct trophic niches (Semenyuk and Tiunov 2011).

In millipedes, the main physical processing of the ingested food items is believed to occur in the mouth cavity (Köhler and Alberti 1990). Most of the Diplopoda have a gnawing mouth apparatus with the mandible as the main chewing device. Mandibles consist of an entire or composite base and a moveably separated gnathal lobe. The gnathal lobe is subdivided into several morphological and functional parts: external and internal teeth, pectinate lamellae, an intermediate area and a molar plate, the latter sometimes with an anterior fringe. External and internal teeth are believed to be used to separate pieces of food from the substrate and to cut them into smaller fragments. Pectinate lamellae consist of a number of small teeth which are likely to crush food particles. The density of these teeth probably determines the size of the fragments that enter the gut, increasing the efficiency of digestion. The molar plate squeezes out liquid components of crushed plant or microbial cells, as hypothesized by Köhler and Alberti (1990).

We presumed that variation in food types consumed by different species can be reflected in mouthpart structure. The aim of this study was to compare the mandibles of ten millipede species belonging to several higher taxa and differing in the isotopic composition of nitrogen in their tissues.

Methods

Millipedes and their potential food sources were collected in May–June 2008 in the Cat Tien National Park, Dong Nai Province, southern Vietnam (11°21'–11°48'N; 107°10'–107°34'E). The park covers an area of about 74,000 ha, lying at the foot of the central Vietnamese highlands, about 130 km northeast of Ho Chi Minh City.

The climate is tropical monsoon with two distinct seasons: a rainy season from late April to November and a dry season from December to March. The mean annual temperature is close to 26°C, with rather small seasonal fluctuations. The mean annual rainfall is about 2,450 mm, the most rainy months being August and September (400–450 mm per month), when much of the park area is inundated. In contrast, there is almost no precipitation from January to March. The elevations vary between 120 and 220 m a.s.l. The relief is hilly with numerous small rocky outcrops and lowlands, the latter usually flooded for several weeks during the rainy season. Lowlands are especially characteristic of the eastern part of the area bordering the Dong Nai River. Sampling plots were selected in that area. Soils are mostly loamy, black ferrallitic, formed on basalt bedrock. The carbon content of the upper mineral soil typically varies from 3 to 8%; the pH is close to 5.5 in well-drained areas, but often decreases below 4.5 in wet depressions. Along the Dong Nai River, the soils are formed on sandy river sediments.

The vegetation of the National Park is very diverse and includes over 150 tree species, of which *Lagerstroemia calyculata* (Lythraceae) associated with Dipterocarpaceae, Fabaceae and Datisceae often dominates the upperstorey and canopy (Vandekerckhove et al. 1993, Blanc et al. 2000). Most of the upper canopy trees are deciduous and shed foliage during the dry season. At the end of the dry season (April), a substantial amount of litter (up to 800–1000 g m⁻²) accumulates on the soil surface. However, with the onset of the rainy season this litter is quickly consumed by termites and other soil macroinvertebrates.

Diplopoda were collected by hand-sorting of soil and litter at five permanent plots (Anichkin et al. 2007, Belyaeva and Tiunov 2010). These plots represent the commonest ecosystems in the eastern part of the Park. At each plot, eight soil samples (50 × 50 cm) were taken, separated to leaf litter layer, upper 2 cm of mineral soil, and deeper soil layer down to 10 cm. Besides millipedes, predatory centipedes (Chilopoda) were collected. In addition, we collected diplopods from tree trunks, epiphytes and decaying logs, including those lying also beyond the sampling plots. Adult animals were determined to the lowest possible taxonomic level, often to species, and dried at 60°C. Potential food sources of millipedes were represented by green leaves, leaf litter of dominating tree species (*L. calyculata*, *Tetrameles nudiflora*, *Ficus* sp., *Dipterocarpus alatus*, *Afzelia xylocarpa*), humified soil and sporocarps of saprotrophic litter fungi. Material was dried at 60°C and ground to fine powder before isotopic analyses.

Samples for isotopic analyses contained about 0.5 mg of dry animal tissue or 1.5–3 mg of dry plant or soil material. The isotopic composition of nitrogen (¹⁵N/¹⁴N) was determined with a Finnigan Delta V Plus isotope ratio mass spectrometer (Thermo, USA), coupled with a Flash 1112 elemental analyzer (Thermo, USA). Stable isotope abundance was expressed using the conventional δ notation with $\delta^{15}\text{N} (\text{‰}) = \left[\frac{R_{\text{sample}} - R_{\text{standard}}}{R_{\text{standard}}} \right] \times 1000$, where R_{sample} and R_{standard} represent the ¹⁵N/¹⁴N ratios of the sample and standard, respectively. Atmospheric N₂ served as a primary standard. IAEA reference materials (USGS 40, USGS 41) were used for calibration. Acetanilide

(Merck, Darmstadt) was used as a laboratory standard to correct drift (measured after every 10 samples). An analytical error of $\delta^{15}\text{N}$ determination was less than $\pm 0.2\text{‰}$ (SD, eight repeated measurements of USGS 40). In total, 19 millipede species were analyzed.

Mandibles of ten species were extracted from alcohol-preserved animals, dried, mounted and examined using a Cam Scan MV2300 scanning electron microscope (Tescan, Brno).

Results

The Diplopoda community of Cat Tien consists of at least 36 species from 17 families and 11 orders (Table 1).

Millipedes were found predominantly in leaf litter and at the soil/litter interface. Large-sized species, such as *Thyropygus carli*, *Orthomorpha* sp. 1, *Sphaerobelum* sp.,

Table 1. Taxonomic structure of the Cat Tien millipede community.

1. <i>Alloproctoides</i> aff. <i>dawydoffi</i> (Attems)	Family Lophoproctidae	Order Polyxenida
2. <i>Termitodesmus</i> sp.	Family Termitodesmidae	Order Glomeridesmida
3 & 4. <i>Zephronia</i> spp. 1 & 2	Family Zephroniidae	Order Sphaerotheriida
5. ? <i>Prionobelum</i> sp.		
6. <i>Sphaerobelum</i> sp.		
7. <i>Hyleoglomeris</i> sp.	Family Glomeridae	Order Glomerida
8. <i>Siphonophorella</i> sp.	Family Siphonophoridae	Order Siphonophorida
9. <i>Pseudodesmus</i> sp.	Family Andrognathidae	Order Platydesmida
10. <i>Metopidiotrix</i> sp.	Family Metopidiotrichidae	Order Chordeumatida
11. <i>Thyropygus carli</i> (Attems)	Family Harpagophoridae	Order Spirostreptida
12. <i>Plusioglyphiulus ampullifer</i> Golovatch et al.	Family Cambalopsidae	
13. <i>Apeuthes</i> sp.	Family Pachybolidae	Order Spirobolida
14. <i>Nepalmatoiulus</i> sp.	Family Julidae	Order Julida
15. <i>Eutrichodesmus</i> sp.	Family Haplodesmidae	Order Polydesmida
16. <i>Niponiella</i> sp.	Family Cryptodesmidae	
17. <i>Cryptocorypha hoffmani</i> Golovatch et al.	Family Pyrgodesmidae	
18. <i>Pseudocatapyrgodesmus pulcher</i> Golovatch et al.		
19. <i>Skotodesmus vietnamicus</i> Golovatch et al.		
20. <i>Desmoxytes pilosa</i> (Attems)	Family Paradoxosomatidae	
21. <i>Desmoxytes cattiensis</i> Nguyen et al.		
22–24. <i>Orthomorpha</i> spp. 1, 2, 3		
25–28. “ <i>Tylopus</i> ” spp. 1, 2, 3, 4		
29. <i>Helicorthomorpha holstii</i> (Pocock)		
30. <i>Anoplodesmus anichkini</i> Golovatch & Semenyuk		
31. <i>Touranella cattiensis</i> Golovatch & Semenyuk		
32. <i>Nedyopus dawydoffiae</i> (Attems)		
33–35. Unassigned spp. 1, 2, 3		
36. “ <i>Martensodesmus</i> ” sp.	Family Opisotretidae	

Apeuthes sp., "*Tylopus*" sp. 1, *Desmoxytes* spp. and *Helicorthomorpha holstii*, were collected mainly from the litter surface. Smaller species like *Alloproctooides* aff. *dawydoffi*, Fuhrmannodesmidae spp. and "*Martensodesmus*" sp. occurred mostly in mineral soil, as did the juvenile Paradoxosomatidae. Sphaerotheriida species were largely absent from the soil samples, with only *?Prionobelum* sp. collected from tree trunks and suspended soil having been analyzed.

The isotopic composition of nitrogen ($\delta^{15}\text{N}$) of leaf litter, saprotrophic litter fungi and soil organic matter averaged $0.2 \pm 0.2\text{‰}$, $1.5 \pm 0.3\text{‰}$, and $4.5 \pm 0.5\text{‰}$, respectively (Fig. 1). Most of the millipede species were enriched in ^{15}N relative to leaf litter. However, the $\delta^{15}\text{N}$ values of different Diplopoda varied widely and ranged from -2.3‰ (*Touranella cattiensis*) to $+6.8\text{‰}$ (*Plusioglyphiulus ampullifer*), the overall range of $\delta^{15}\text{N}$ values exceeding 9‰ (Fig. 1). A similarly wide range of $\delta^{15}\text{N}$ values, reflecting a di-

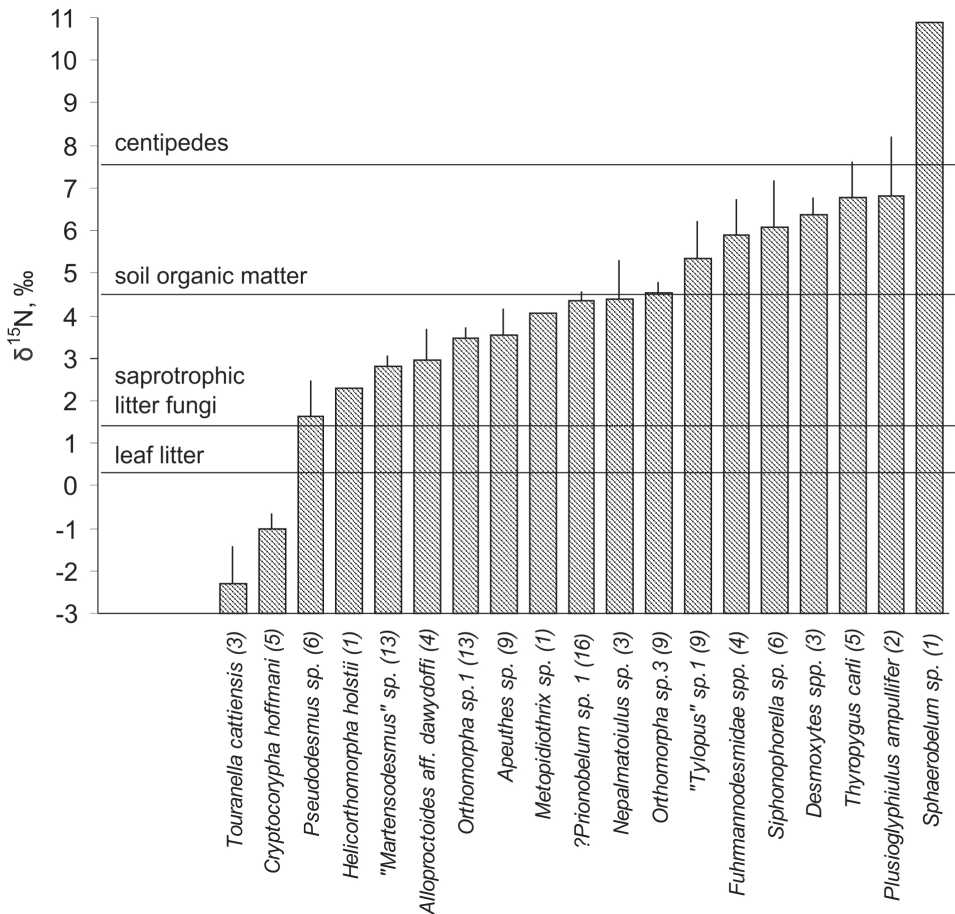


Figure 1. Variation in $\delta^{15}\text{N}$ values of 19 Diplopoda species from Cat Tien National Park (means + SE, number of specimens analysed is given in brackets). Horizontal lines show the mean $\delta^{15}\text{N}$ values of leaf litter, saprotrophic litter fungi, soil organic matter and predatory centipedes.

versity of trophic niches occupied, was revealed in other species-rich groups of litter-dwelling arthropods, e.g. collembolans (Chahartaghi et al. 2005) or oribatid mites (Schneider et al. 2004).

The fine structure of the mandibles of the Diplopoda studied varied considerably between orders and, to a lesser extent, families (Table 2), i.e. well according to the known structural patterns (Ishii 1988), but did not show any clear correlation with the $\delta^{15}\text{N}$ values in millipede tissues. Pectinate lamellae are well-developed in all species, only in *T. carli* is this structure relatively small (Fig. 3: 3). In *Pseudodesmus* sp., one of the two representatives of Colobognatha analyzed, the molar plate seems to be strongly reduced, if not missing (Fig. 2: 1).

The mandible of all species studied shows well-developed external and internal teeth. The internal teeth, which are possibly used to separate food particles from the

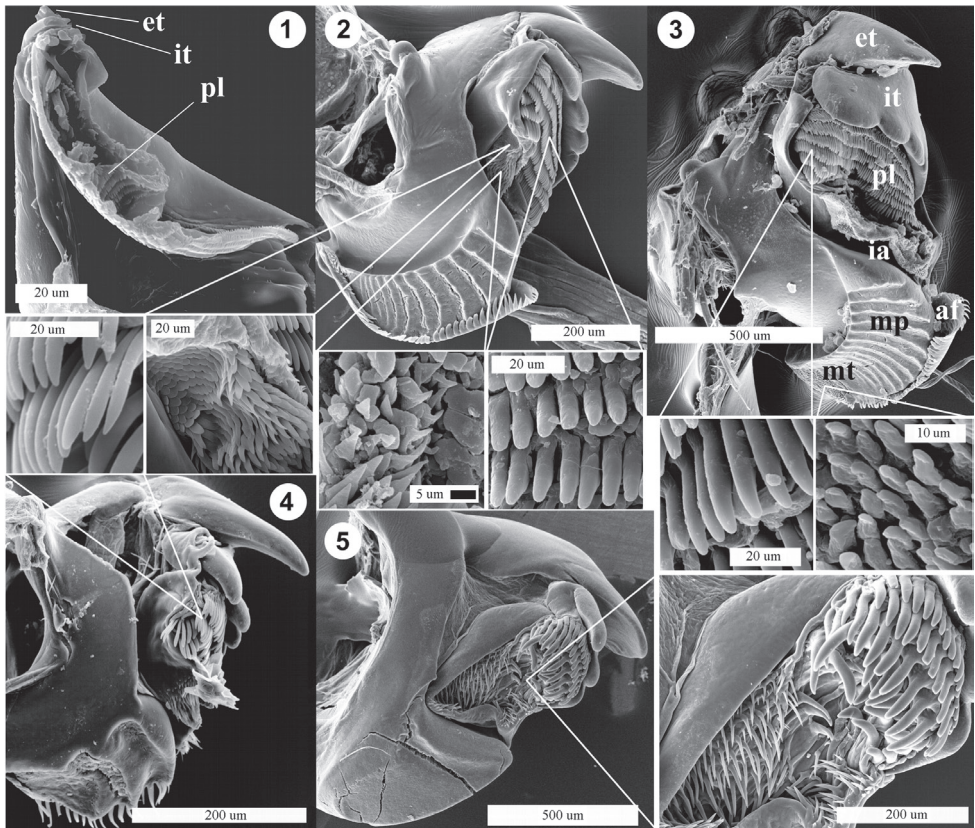


Figure 2. Mandibles of Diplopoda species with $\delta^{15}\text{N} < 4.5\text{‰}$. **1** *Pseudodesmus* sp. (abbreviations: et – external tooth, it – internal tooth, pl – pectinate lamellae) **2** *H. holstii* (with two different parts of the intermediate area and pectinate lamellae teeth in a high-resolution inset) **3** *Orthomorpha* sp. I (with pectinate lamellae teeth and molar tufts, abbreviations: et – external tooth, it – internal tooth, pl – pectinate lamellae, ia – intermediate area, af – anterior fringe, mp – molar plate, mt – molar tuft) **4** *Nepalmatoiulus* sp. (with pectinate lamellae) **5** *?Prionobelum* sp. (with pectinate lamellae teeth).

Table 2. Summarized characteristics of the mandibles and $\delta^{15}\text{N}$ values in the studied Diplopoda species.

	Body length, mm	Number of internal teeth	Number of teeth rows on pectinate lamellae	Approx. density of teeth in pectinate lamellae	Character of molar plate	Presence of molar tuft at posterior end of molar plate	$\delta^{15}\text{N}$ values, mean \pm SE, ‰
<i>Pseudodesmus</i> sp.	4–18	-	7	225 per 100 μm^2	-	-	1.6 \pm 0.9
<i>H. holstii</i>	4–30	4	6	6 per 100 μm^2	Stairs-like	Yes	2.3
<i>Orthomorpha</i> sp. 1	4–45	4	6	72 per 10,000 μm^2	Stairs-like	Yes	3.5 \pm 0.3
<i>Nepalmatoiulus</i> sp.	4–35	4	4	200 per 10,000 μm^2	Large-scale stairs	?	4.4 \pm 0.9
? <i>Prionobelum</i> sp.	up to 15	3	7	15 per 10,000 μm^2	Flat	No	4.3 \pm 0.2
" <i>Tylopus</i> " sp. 1	4–34	4	6	70 per 10,000 μm^2	Stairs-like	Yes	5.3 \pm 0.9
<i>Desmoxytes</i> sp.	5–18	4	6	95 per 10,000 μm^2	Stairs-like	Yes	6.4 \pm 0.4
<i>T. carli</i>	7–140	4	6	42 per 10,000 μm^2	Large-scale stairs	No	6.8 \pm 0.9
<i>P. anpullifer</i>	5–45	5	6	250 per 10,000 μm^2	Notched	No	6.8 \pm 1.4
<i>Sphaerobelum</i> sp.	up to 43	3	5	6 per 10,000 μm^2	Flat	No	10.9

substrate, are somewhat better developed in the species having higher $\delta^{15}\text{N}$ values (Fig. 3). The molar plates of various species show different types of surface, i.e. with dense stairs-like structures, or molar processes in terms of Ishii and Tamura (1996), as observed in our Paradoxosomatidae (Figs 2: 2, 3 and 3: 1, 2), with sparse stairs-like molar processes/ribs, as seen in the juliforms *T. carli* and *Nepalmatoiulus* sp. (Figs 2: 4 and 3: 3), or smooth, as evidenced by the sphaerotheriidans *?Prionobelum* sp. and *Sphaerobelum* sp. (Figs 2: 5 and 3: 5). The mandible of the small *Pseudodesmus* sp. seems to have no molar plate, but pectinate lamellae are long and evident (Fig. 2: 1). This species

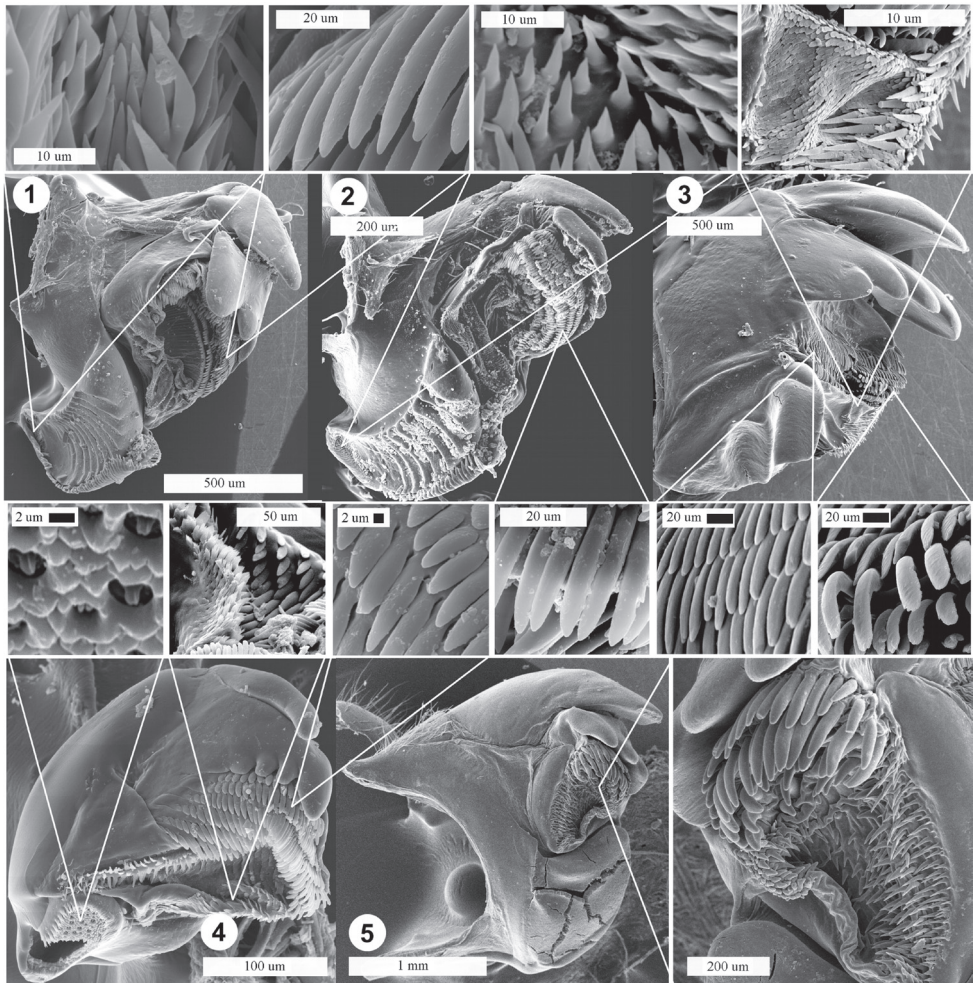


Figure 3. Mandibles of Diplopoda species with $\delta^{15}\text{N} > 4.5\text{‰}$. **1** “*Tylopus*” sp. 1 (with molar tufts and pectinate lamellae teeth high-zooming inset) **2** *Desmoxytes* sp. (with molar tufts and pectinate lamellae teeth) **3** *T. carli* (with part of intermediate area and two different kinds of pectinate lamellae teeth: straight conical and curved lamellar) **4** *P. ampullifer* (with tongue-liked structures on molar plate, intermediate area and teeth of pectinate lamellae) **5** *Sphaerobelum* sp. (with pectinate lamellae).

mainly occurs under the bark of dead wood and, like perhaps any Colobognatha, can be presumed to be a suctorial feeder.

The mandibles of *P. ampullifer* differ significantly from those of the other species in showing a very small external tooth while the molar plates have unusual crater-like structures with tongues (Fig. 3: 4); these may have a sensory function. The pectinate lamellae are enlarged, which can indicate consumption of soft food or a filtering type of nutrition (Enghoff 1985). In the Cat Tien National Park, this species was often found in shallow caverns between stones, where moist decaying remains of plant and animal origin can accumulate. Consumption of this food, rich in microorganisms, might lead to elevated $\delta^{15}\text{N}$ rates in the tissues of *P. ampullifer*.

Discussion

The $\delta^{15}\text{N}$ values of animals are known to increase by 2–3.5‰ from one trophic level to the next one (Post 2002, Vanderklift and Ponsard 2003). In addition, an increase in the $\delta^{15}\text{N}$ values in soil animals can indicate the use of humified soil organic matter (Tiunov 2007). Our data fully confirm these observations; the $\delta^{15}\text{N}$ values of soil organic matter were ca 4.3‰ higher relative to plant litter, whereas predatory centipedes were enriched in ^{15}N by about 7.5‰ compared to litter. The $\delta^{15}\text{N}$ values of millipede tissues formed a relatively uniform continuum. However, a wide range of $\delta^{15}\text{N}$ values suggests a consistent difference in the diet of species which have significantly different isotopic compositions of nitrogen (Scheu and Falca 2000, Pollierer et al. 2009).

Among the species examined, all five basic morphotypes were present, i.e. polyxenoid, glomeroid, platydesmoid, polydesmoid and juloid (Golovatch and Kime 2009). Despite this high morphological and taxonomic diversity, which might have also resulted from dwelling in various habitats, the Diplopoda species of Cat Tien failed to show clear-cut spatial differentiation patterns both between the forest plots and litter/soil strata. However, litter and the uppermost soil are extremely heterogeneous environments by themselves and certainly offer a wealth of microhabitats to be used by different species or even their developmental stages.

The structure of the mouthparts of litter-dwelling millipedes seems to influence their assimilation rates. The density and relative size of pectinate lamellae teeth may correlate not only with the crushing efficiency of the mandibles, but also with body size (Köhler and Alberti 1990, Köhler et al. 1991). The mandibles of smaller species show the highest density of pectinate lamellae teeth and probably a better efficiency of food assimilation. Considering that the Cat Tien diplopod faunule, one of the richest globally (Golovatch 1997), encompasses species from 17 families and 11 orders, of which representatives of as many as 13 families and nine orders have been analyzed here, a comparative analysis of mandibular structures in relation to possible functional roles the taxa play in the ecosystem would be an interesting objective. This is especially

important in relation to the isotopic evidence for the use of different food resources by different species.

The mandibles of the millipede orders have long been known to differ considerably in structure (Ishii 1988). In other words, the mandibles tend to show most of the important morphological characters at the ordinal or even higher levels only. The Polydesmida is currently perhaps the sole order where stable differences in structure of the molar plate have hitherto been found in as many as eight families studied in this respect (Ishii and Tamura 1996). However, a few semi-aquatic, mostly troglobitic species of Pyrgodesmidae (Adis et al. 1998), Polydesmidae (Adis et al. 1997), both in Polydesmida, as well as some Mediterranean Julida (Enghoff 1985), show the mouthparts modified into a highly disjunct brooming or filtrating apparatus.

Generally speaking, the structure of millipede mandibles can well be presumed as being related to specializations for different kinds of food in species having different isotopic signatures. The fine structure of the mandibles of the Diplopoda studied here did vary considerably, especially well so between orders and, to a lesser extent, families (Figs 2 and 3; Table 2). Nevertheless, the variation in the mandibular structure of particular species having different $\delta^{15}\text{N}$ values fails to support their separation into well-structured trophic guilds. The same seems true for the patterns of spatial distribution of species, both local and between-habitat.

Conclusion

As a result, our studies show neither clear-cut trends in nor evident morphological patterns of, nor significant correlations between the structure of mandibles in Diplopoda species that have different isotopic compositions of nitrogen and presumably exploit different food resources. There is certain variation in mandibular structure of individual higher taxa, but in general the mouthparts are relatively uniform at the lower taxonomic levels. This is confirmed by both species of Zephroniidae (Sphaerotheriida), as well as in all Paradoxosomatidae (Polydesmida) under study.

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