Clypeal excision in *Tapinoma* FÖRSTER, 1850 ants is adaptive (Hymenoptera: Formicidae)

With 3 figures and 1 table

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**Summary**

Evidence is presented that the median clypeal excision in the dolichoderine ant genus *Tapinoma* FÖRSTER, 1850 is a rare adaptive trait improving the protrusion of mouthparts for better exploitation of food or water sources located in narrow cleft spaces. The problem of getting access to food from, for example, narrow tubes of nectaries becomes more serious with increasing worker head width. A regression analysis of species-specific means in 16 Westpalaearctic *Tapinoma* species shows that the relative depth of clypeal excision grows significantly with head width in the interspecific comparison (p<0.001). Similar relations are also indicated on the intraspecific level for all species with the regression functions being significant on the p<0.025 level. The clypeal cleft allows a sliding of the glossa and dorso-median crests of the labial galeae in dorsofrontal direction.

**Key words**

Functional morphology, adaptive phenotypic trait, foraging biology, morphometry

**Introduction**

Ant taxonomists may ask themselves if some of the interspecifically variable phenotypical characters used for species delimitation are under selection or neutral. There is no theory, for example, which difference in fitness could result if there are five or fifteen setae on pronotum of a *Formica* ant. One can certainly imagine...
that a regularly honey-combed or irregularly rugulose microsculpture on the vertex of a Cardiocondyla ant should influence mechanical stability of the cuticle and adhesion of particles or chemicals in a different way. Yet, can it make an adaptive or functional difference if there is a deeper or shallower clypeal excision in a Tapinoma worker while over 99% of the ant species worldwide do not show such a structure at all? The only function clypeal cleft seemed to have was not for ants: it was used in about a dozen of taxonomic papers from EMERY (1925) to SEIFERT (2012) as an informative character for species delimitation.

Rare and accidental observations often pave the road to awareness. Among some 1600 mounted Tapinoma workers in the collection of Senckenberg Museum of Natural History, there were two workers belonging to species of the Tapinoma nigerrimum (Nylander, 1856) complex that died in a posture with protruded mouthparts and opened mandibles. In one specimen, the glossa — a median, strongly rippled part of the labium (see figures 2-5 and 2-7 in HÖLDDOBLER & WILSON 1990) — exactly fitted into the clypeal cleft (Fig. 2). There was some shrinking of the organ due to drying, the glossa is a little broader in its natural condition and the labium is much more extended, but basically the photo shows what should happen in living ants.

It is easily intelligible that a deep clypeal excision allows a farther dorsofrontal protrusion of the glossa and labium and allows a bigger amplitude of dorsoventral movements of these organs. Tapinoma ants use a variety of food sources (XERDA et al. 1989, VERHAEGHE et al. 1992, SEIFERT 2007) among these are liquids to be imbibed from narrow cleft spaces. A typical problem represents the extraction of nectar from diverse forms of tube-, funnel- or spur-shaped nectaries strongly narrowing towards the base. Such structures are developed in several plant families (HEGI 1957, 1966, 1979). The problem grows the larger the foraging ant is. A blocked broad-headed worker can only try to protrude its mouthparts as far as possible to get access to a liquid at the bottom of a microspace. As a consequence, large Tapinoma ants should adaptively develop not only absolutely but also relatively deeper clypeal excisions. This paper intends to check this hypothesis on the interspecific and intraspecific level based on morphometric data in Westpalaeartic Tapinoma species.

Material and Methods


The following measurements were taken in fully dried, mounted workers.

| CW | maximum cephalic width |
| CL | maximum cephalic length between points A and B |
| ExCly | Maximum depth of anteromedian clypeal excision |

Measuring was done under use of polarized-coaxial light illuminators and the high-resolution stereomicroscopes Wild M10 equipped with a 1.6x apochromatic objective and a Leica M165C equipped with a 2.0x apochromatic objective at magnifications of 120 to 240x (CW) and 320 to 350x (ExCly). The mean measuring error was estimated as 2.1 µm in CW and 0.6 µm in ExCly. The relative depth of clypeal excision is described as the per cent ratio of ExCly/CL.

The protrusion movements of the mouthparts were simulated in dead ethanol-stored worker ants by pulling with a fine forceps.

Results and Discussion

Tab. 1 shows the results of morphometric investigations. A regression of the species-specific means of clypeal depth index ExCly/CL against head width CW (Fig. 1) shows for fifteen species a highly significant positive correlation according to the function

\[
\text{ExCly/CL} = 17.452 \times CW - 5.918 \quad (r=0.8160, p<0.001, n=16).
\]

All species with mean CW < 0.7 mm show a clypeal excision index smaller than 5.5% and the excision is extremely reduced in the nanitic T. pygmaeum. Ten out of eleven species with mean CW > 0.7 mm show indices larger than 7.9%. The only deviation is T. festae — an East Mediterranean species with completely unknown biology. The inclusion of mean values of two species with very low sample size in this regression is not suspected to provide a wrong picture in the interspecific comparison. The mean value of clypeal cleft index of 0.84% in Tapinoma pygmaeum based on only five measured specimens from three sites is confirmed by the available descriptions of this ant which report an extremely shallow or absent clypeal excision in an exceptionally small ant (ESPADALER 1977, CASENT0280679 in antweb.org).
Tab. 1: Morphometric data of 16 West Palaearctic species of *Tapinoma*. Given are the species-specific means of cephalic width CW, the clypeal excision index ExCly/CL and the slope A, intercept B, linear correlation coefficient R and significance level P of regressions of clypeal excision index against cephalic width.

<table>
<thead>
<tr>
<th>Species</th>
<th>n</th>
<th>CW [mm]</th>
<th>ExCly/CL [%]</th>
<th>slope</th>
<th>intercept</th>
<th>R</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>pygmaeum</em></td>
<td>5</td>
<td>0.4345</td>
<td>0.82</td>
<td>-0.15</td>
<td>0.884</td>
<td>0.0279</td>
<td>n.s.</td>
</tr>
<tr>
<td><em>kinburni</em></td>
<td>7</td>
<td>0.5487</td>
<td>2.79</td>
<td>-4.517</td>
<td>5.263</td>
<td>0.5028</td>
<td>n.s.</td>
</tr>
<tr>
<td><em>madeirens</em></td>
<td>54</td>
<td>0.6490</td>
<td>4.58</td>
<td>2.639</td>
<td>2.863</td>
<td>0.2394</td>
<td>0.082</td>
</tr>
<tr>
<td><em>subboreale</em></td>
<td>74</td>
<td>0.6653</td>
<td>4.79</td>
<td>1.410</td>
<td>3.855</td>
<td>0.1782</td>
<td>n.s.</td>
</tr>
<tr>
<td><em>israelis</em></td>
<td>29</td>
<td>0.6729</td>
<td>5.47</td>
<td>5.253</td>
<td>1.939</td>
<td>0.6047</td>
<td>0.001</td>
</tr>
<tr>
<td><em>tauridis</em></td>
<td>29</td>
<td>0.7115</td>
<td>8.56</td>
<td>3.472</td>
<td>6.088</td>
<td>0.3229</td>
<td>0.087</td>
</tr>
<tr>
<td><em>erraticum</em></td>
<td>125</td>
<td>0.7220</td>
<td>7.97</td>
<td>6.613</td>
<td>3.200</td>
<td>0.7150</td>
<td>0.000</td>
</tr>
<tr>
<td><em>spec. BALC</em></td>
<td>88</td>
<td>0.7474</td>
<td>9.15</td>
<td>6.890</td>
<td>4.002</td>
<td>0.6362</td>
<td>0.000</td>
</tr>
<tr>
<td><em>festae</em></td>
<td>32</td>
<td>0.7842</td>
<td>3.69</td>
<td>1.878</td>
<td>2.219</td>
<td>0.396</td>
<td>0.025</td>
</tr>
<tr>
<td><em>phoenix</em></td>
<td>82</td>
<td>0.8203</td>
<td>10.13</td>
<td>3.733</td>
<td>7.071</td>
<td>0.3398</td>
<td>0.002</td>
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<tr>
<td><em>simrothi</em></td>
<td>102</td>
<td>0.8250</td>
<td>12.14</td>
<td>4.762</td>
<td>8.214</td>
<td>0.5428</td>
<td>0.000</td>
</tr>
<tr>
<td><em>spec. DARI</em></td>
<td>119</td>
<td>0.8421</td>
<td>9.30</td>
<td>3.033</td>
<td>6.758</td>
<td>0.4796</td>
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<tr>
<td><em>karavajevi</em></td>
<td>4</td>
<td>0.9214</td>
<td>11.40</td>
<td>-4.430</td>
<td>15.484</td>
<td>0.6788</td>
<td>n.s.</td>
</tr>
<tr>
<td><em>magnum</em></td>
<td>255</td>
<td>0.9241</td>
<td>8.58</td>
<td>1.979</td>
<td>6.756</td>
<td>0.3216</td>
<td>0.000</td>
</tr>
<tr>
<td><em>ibericum</em></td>
<td>72</td>
<td>0.9842</td>
<td>9.96</td>
<td>2.163</td>
<td>7.828</td>
<td>0.4153</td>
<td>0.000</td>
</tr>
<tr>
<td><em>nigerrimum</em></td>
<td>69</td>
<td>1.0050</td>
<td>9.91</td>
<td>0.093</td>
<td>9.815</td>
<td>0.0935</td>
<td>n.s.</td>
</tr>
</tbody>
</table>

There are no literature data available to compare with the mean index of 11.4% calculated from four *Tapinoma karavajevi* workers but this data point is near to the trend line over all species (Fig. 1).

The within-species relations confirm a positive allometry of clypeal cleft index. All thirteen species with a sample size > 25 workers show positive allometries. Nine of these functions are highly significant, two are weakly significant and one not significant (Tab. 1). The weakly positive slope and insignificance in *T. nigerrimum* is explained by an aberrant population in southern France.

Fig. 1: Plotting of intraspecific mean of clypeal excision index ExCly/CL against intraspecific mean of cephalic width in workers of 16 West Palaearctic *Tapinoma* species.

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Simulating the movements in living ants by pulling mouthparts in dead, ethanol-stored specimens by a fine forceps led to the following conclusions. The cleft allows a protrusion of mouthparts into a more dorsofrontal direction. The glossa may slide through the cleft during the initial phase of this movement (Fig. 2) and the dorso-median crests of the labial galeae (marked with black alignment in Fig. 3) during a later phase. During maximum protrusion in frontal direction, the tip of the glossa exceeds the tips of the half-opened mandibles.

These data support the hypothesis that the depth of the clypeal excision is modified in most *Tapinoma* species in an adaptive way to allow also broad-headed workers an exploitation of food sources from narrow cleft spaces. This solution appears less time- and energy-consuming than opening cleft spaces by force as it was observed, for example, in *Myrmica ruginodis* Nylander, 1856 which bites a hole in the bottom of the spur in *Viola* flowers to get access to the nectar (Seifert 2007). Furthermore, a non-destructive exploitation saves the plant and extends the time interval for use of a nectar source.

While the functional morphology and principal advantage of a clypeal cleft is immediately intelligible from the mechanics of movement, it remains unclear how frequent the ants are confronted in nature with situations where this structure is really needed. Narrow bases of corolla tubes or tenuous flower spurs containing nectar are found in several plant families and some plant genera develop inside the flower special nectary leaves strongly narrowing towards the base (Hegi 1957, 1966, 1979). However, it seems that nectararies with a very small basal lumen causing a blockade for ants with head widths of > 800 μm are not frequent and the absence of a clypeal cleft in the vast majority of ants with a similar food selection and similar body size (such as *Lasius*) suggests a rather low fitness advantage of a clypeal cleft. The advantage could be more significant when water has to be extracted from impenetrable clefts. *Tapinoma* ants frequently live in strongly xerothermous habitats high above the ground water table and it may be important to get access to the last hidden residues of water. In the absence of any reasonable counter-hypothesis, I assume that the clypeal excision is a rare and special adaptive trait that evolved in a clade of Dolichoderine ants and is positively allometric at least in *Tapinoma*.

**Acknowledgements**

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References


