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SURFACE ULTRASTRUCTURE OF LABIAL AND MAXILLARY CUSPULES IN EIGHT SPECIES OF THERAPHOSIDAE (ARANEAE)

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ABSTRACT. Surface ultrastructure of labial and maxillary cuspules was studied in eight species of seven different genera of Theraphosidae. Cuspule ornamentation was observed through SEM images and comparisons were made among labial and maxillary cuspules of different species and different zones of each cuspule. Ornamentation patterns were different on the anterior face of the cuspule with respect to the posterior face. A significant correlation analysis between cuspule size and body size was found. The systematic use and the probable functions of the cuspules are discussed.

Keywords: Oral cuspules, cuspule ultrastructure, theraphosids

Labial and maxillary cuspules are globular to conical sclerotized features on the inner ventral corner of the maxillae and on the median-anterior side of the labium. They are exclusively found in mygalomorph spiders (Raven 1980, 1985). The number and distribution of cuspules has been used in mygalomorph systematics by several authors including Raven (1978, 1980, 1985, 1994), Griswold (1985), Snazell & Allison (1989), Goloboff (1993), Griswold & Ledford (2001), Pérez-Miles (1992, 2000) and Pérez-Miles et al. (1996), but studies on cuspule microstructure are scarce. Maxillary cuspule microstructure has been studied in Microstigmatidae (Griswold 1985), Barychelidae (Raven 1994) and in the theraphosid *Aphonopelma seemanni* (F.O.P.-Cambridge 1897) by Cutler & Vuilliomenet (2001). There are no explicit descriptions of the microstructure of labial cuspules although Raven (1994) suggested that they are similar to maxillary ones. In the present study, the surface ultrastructure of labial and maxillary cuspules were examined by SEM in eight theraphosid species corresponding to seven different genera and three different subfamilies (Aviculariinae, Ischnocolinae and Theraphosinae). This is a first approach to test the systematic value of such features in Theraphosidae. The possible mechanical, glandular and sensorial functions of the cuspules are discussed.

METHODS

Males of eight theraphosid species representing three subfamilies were studied including the Aviculariinae: *Iridopelma hirsutum* Pocock 1901; the Ischnocolinae: *Oligoxystre argentinense* (Mello-Leitão 1941) and the Theraphosinae: *Acanthoscurria suina* Pocock 1903, *Eupalaestrus weijenberghi* (Thorell 1894), *Grammostola iheringi* (Keyserling 1891), *Grammostola mollicoma* (Ausserer 1875), *Homoeomma uruguayense* (Mello-Leitão 1946), *Plesiopelma longisternale* (Schiapelli & Gerschman 1942). Seven individuals of *A. suina* and five of *E. weijenberghi* were additionally studied to estimate intraspecific variation. Body size was estimated from the carapace length of each individual measured dorsally with an ocular micrometer. One maxilla and the labium of each individual were removed for the observation of cuspules in a scanning electron microscope (SEM). Cuspule maximum width was measured from SEM images. Cuspules were counted using a stereoscopic microscope with an ocular reticule in fields of 1 mm^2 taken randomly from the labium and maxilla with at least 6 fields counted from each piece. Mean cuspule density was used as an estimator of the total number of cuspules. Nonparametric correlations were done using Spearman R test, means were compared by the Student's t test with restrictions for the variance. All individuals studied, including voucher specimens, were deposited in the Arachnological collection of the Facultad de Ciencias, Montevideo, Uruguay.

RESULTS

Shape, size and density.—Cuspules are placed in groups on the anterior median zone of the labium and on the inner ventral corner of the maxillae (Figs. 1–7). They are implanted approximately perpendicular with respect to body surface (venter of labium and maxillae). Labial and maxillary cuspules are similar (Figs. 8–11), globular-conical, short or more elongated, thick and reddish brown. Some cuspules showed a slight constriction in the middle of their length. Two faces could be recognized: anterior (oral, Fig. 8) and posterior (Fig. 9). Cuspules are inserted in circular sockets where the anterior edge is higher than the posterior edge (Fig. 9). General shape shows a similar pattern in most species with only slight differences (Figs. 8–23). No pores were found on the cuspule surface on any of the species studied. Cuspule size ranged from 39.6–107.8μm Table 1. A significant correlation between cuspule maximum diameter and body size was found in the labium ($r = 0.89$; $P < 0.05$) and also in the maxillae ($r = 0.97$; $P < 0.05$). We did not find significant correlation between body size and the number of labial and maxillary cuspules ($r = -0.60$, $P = 0.48$; $r = -0.32$, $P = 0.48$, respectively).

Intra-specific variation in cuspule width was less than 10% in *A. suina* (mean 46.01 ± 3.46 SD, $n = 7$) and in *E. weijenberghi* (mean 50.7 ± 3.22 SD, $n = 5$) and no significant differences were found between sexes in these species (t = 1.017, $P > 0.30$; t = 0.246, $P > 0.80$, respectively). We found significant differences in cuspule width between these species (t = 3.52, $P < 0.01$).

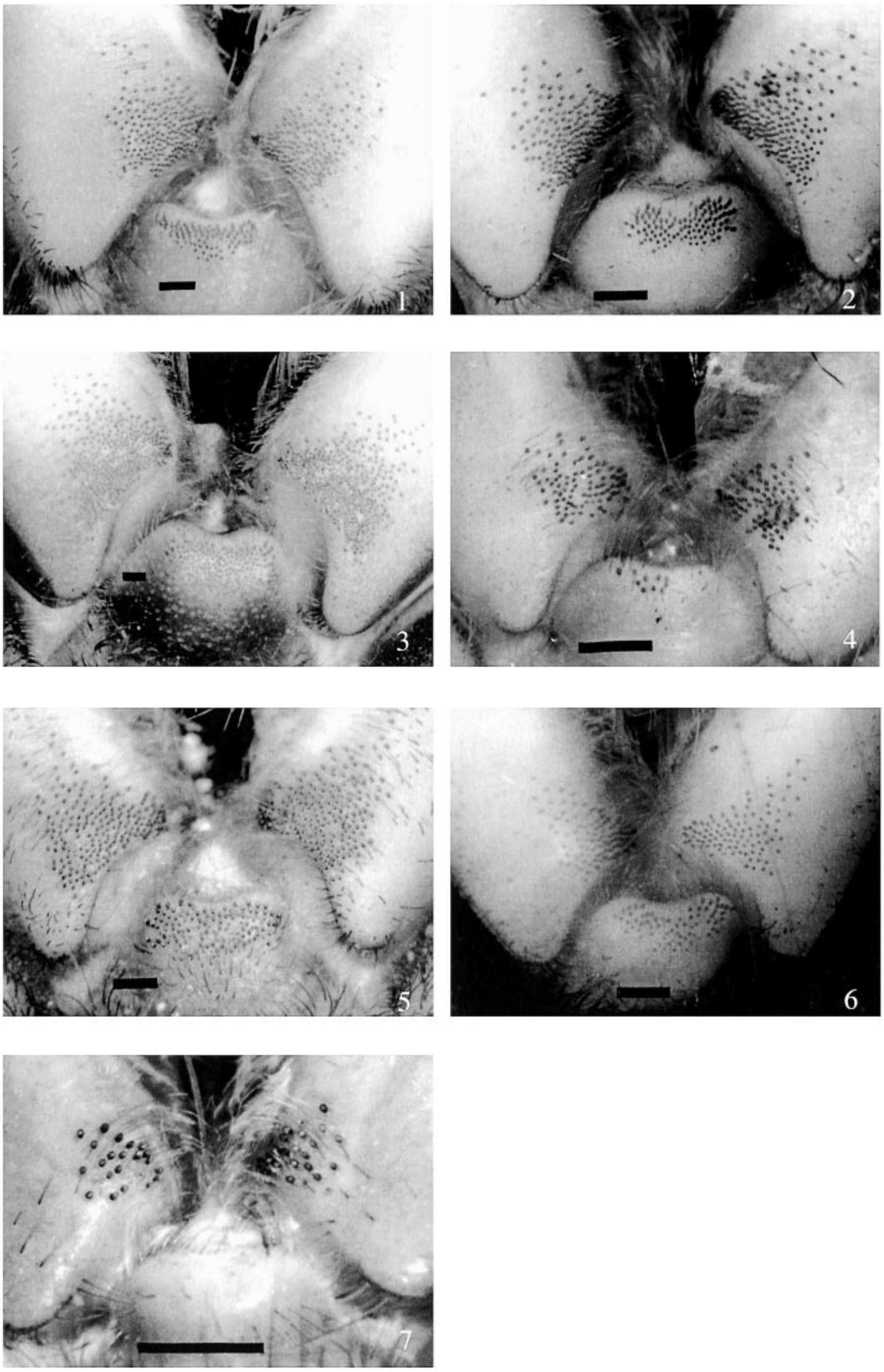
Cuspule ornamentation.—The surface of the labial cuspules is completely covered by ridges. The general pattern of ridges resembles the shape of a finger print in most species. Ornamentation of the anterior face differs from the posterior face. The disposition of ridges also differs in different zones of each face, comparing basal, median and apical zones. The general morphology and ornamentation of the cuspule is similar in all species studied, with the exception of dimensions. Slight variations among cuspule morphology and ornamentation in the same individual are similar to intra-specific and interspecific variations in the species studied.

In a general pattern, the anterior face (Figs. 8, 10, 12, 14, 16, 18, 22) has parallel longitudinal ridges on the basal half and parallel transverse ridges on the apical half (which are continued by the circular ridges in the posterior face). In this face the longitudinal ridges are fused to the transversal ridges in several points of contact. The posterior face of the cuspules show longitudinal and diagonal ridges in the basal half; the central zone shows small loose ridges that resemble a whirl or more or less parallel ridges (Figs. 9, 11, 13, 15, 17, 19, 20, 21, 23). The periphery of the apical zone has circular to oval concentric parallel ridges. The intra-specific study shown that in *A. suina*, the interdistances between two ridges were approximately 1.2 μm in labial cuspules and 1.7 μm ± 0.29 SD in maxillary cuspules. No significant differences were found in the interdistances between sexes (t = 1.76, $P > 0.10$). *Eupalaestrus weijenberghi* has both faces of cuspules similar to *A. suina*. The interdistances between two ridges were 1.2 μm in labial cuspules and 1.6 μm ± 0.27 SD in maxillary cuspules. No significant differences were found in the interdistances between sexes (t = 1.07, $P > 0.30$). When we compared the interdistances of ridges between *A. suina* and *E. weijenberghi*, no significant differences were found (t = 0.30, $P > 0.70$).

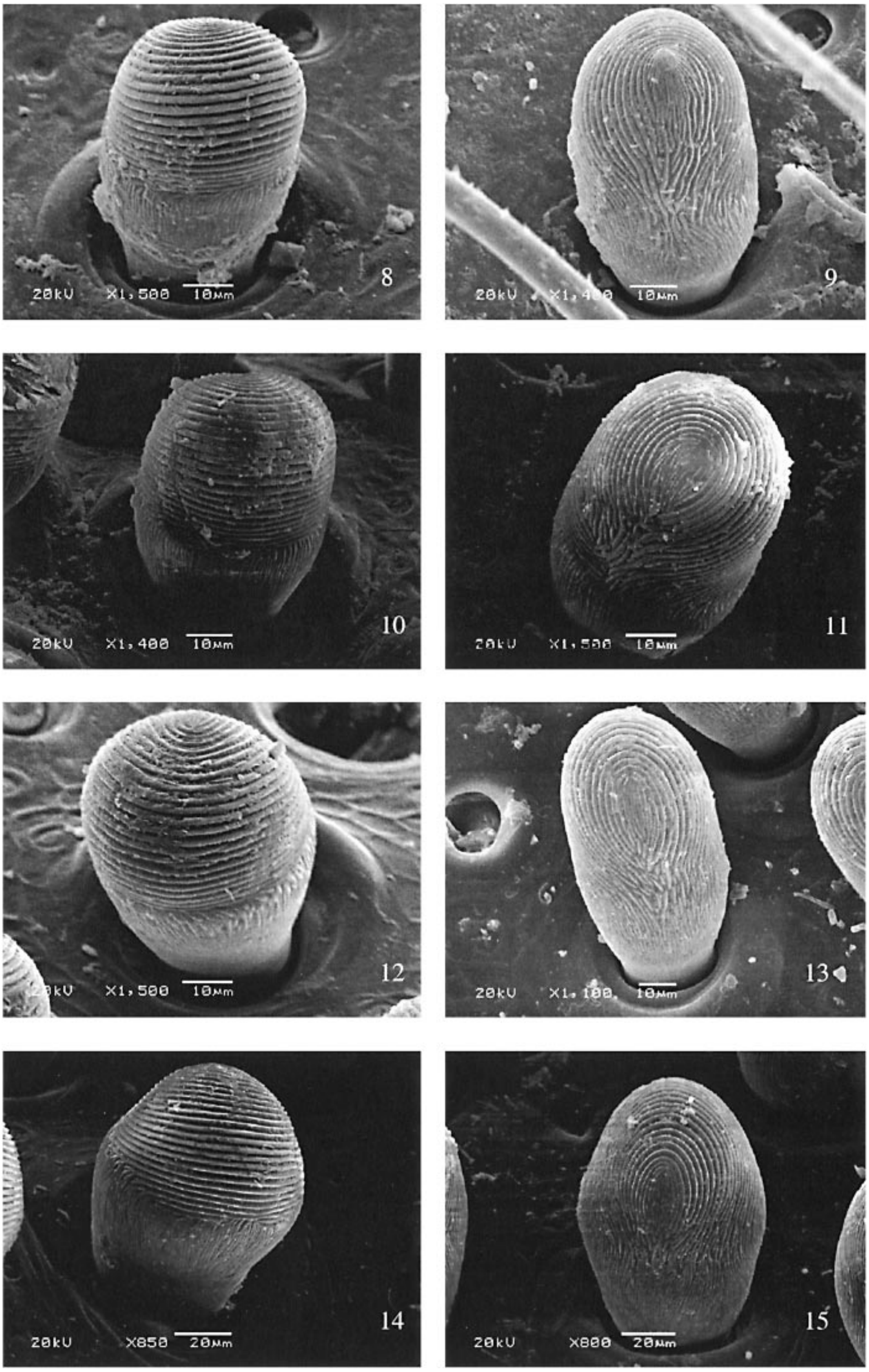
Interdistances between two ridges (in labial and maxillary cuspules respectively) in the other species studied were as follows: in *G. iheringhi* 2.4 μm and 1.8 μm; in *G. mollicoma* 2.3 μm and 2.5 μm; in *H. uruguayense* 1.3 μm and 1.5 μm; in *P. longisternale* 1 μm and 1.3 μm; in *I. hirsutum* 1.6 μm and 1 μm. *Oligoxystre argentinense* lacks labial cuspules, on coxal cuspules the interdistance between two ridges was 1.2 μm.

DISCUSSION

Raven (1994) found that maxillary cuspule size is independent on adult size in Barychelidae. He found several discrete cuspule sizes related to the number of cuspules (in species with numerous cuspules, cuspules are small). In contrast, in the theraphosids studied, we found significant correlations between both maxillary and labial cuspule size with spider



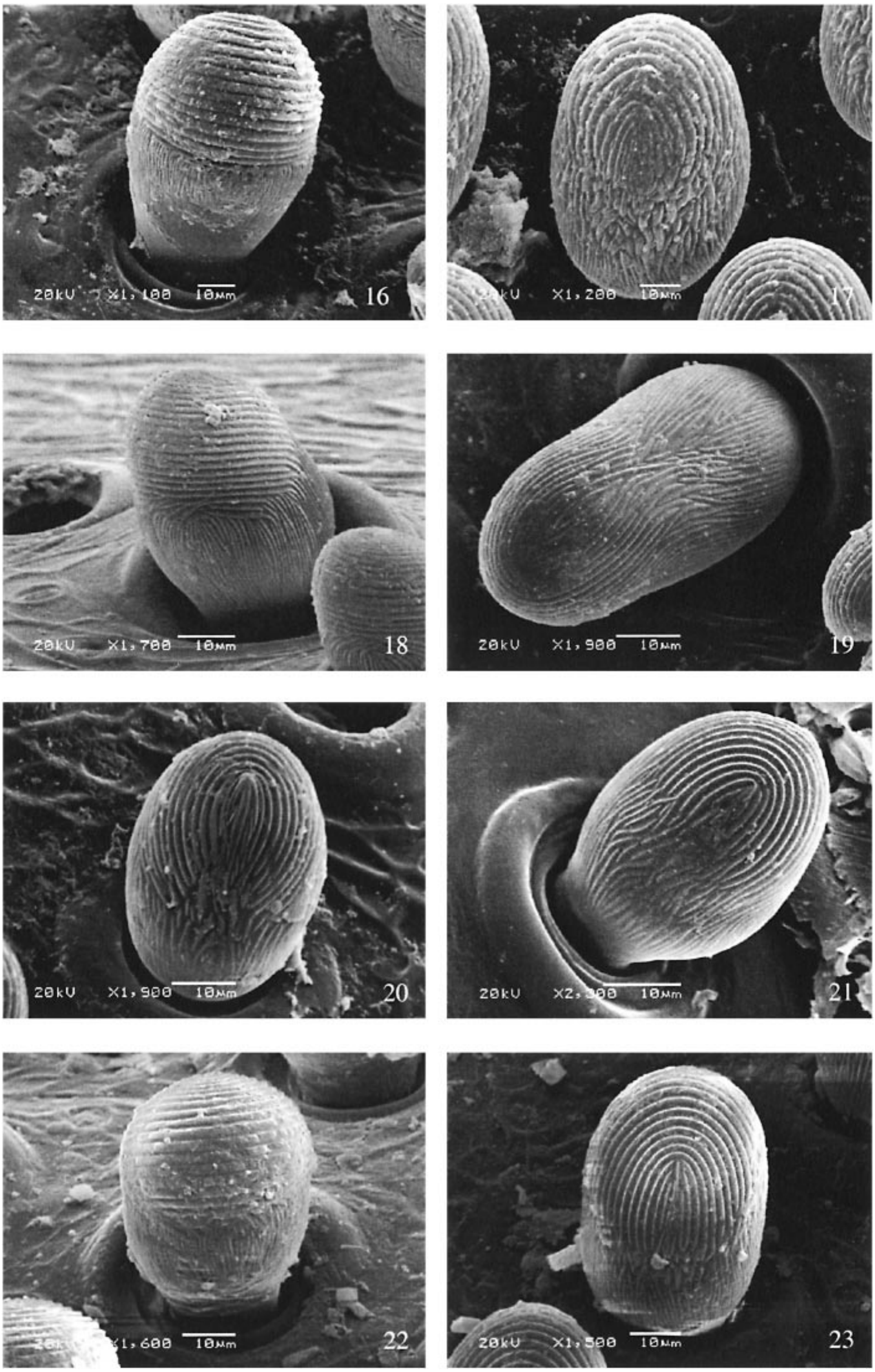
Figures 1–7.—Oral region of the species studied showing position of maxillary and labial cuspules. 1. *Acanthoscurria suina*. 2. *Eupalaestrus weijenberghi*. 3. *Grammostola mollicoma*. 4. *Homoeomma uruguayense*. 5. *Plesiopelma longisternale*. 6. *Iridopelma hirsutum*. 7. *Oligoxystre argentinense*. (Scale = 0.5 mm).



Figures 8–11.—Cuspules of *Acanthoscurria suina* male. 8, 9. Maxillary cuspules. 8. Anterior view. 9. Posterior view. 10, 11. Labial cuspules. 10. Anterior view. 11. Posterior view.

Figures 12–13.—Maxillary cuspule of *Eupalaestrus weijenberghi*. 12. Anterior view. 13. Posterior view.

Figures 14–15.—Labial cuspule of *Grammostola iheringi*. 14. Anterior view. 15. Posterior ventral view.



Figures 16–17.—Maxillary cuspule of *Grammostola mollicoma*. 16. Anterior view. 17. Posterior view.
Figures 18–19.—Labial cuspule of *Plesiopelma longisternale*. 18. Anterior view. 19. Posterior view.
Figure 20.—Labial cuspule of *Homoeomma uruguayense*, posterior view.
Figure 21.—Maxillary cuspule of *Oligoxystre argentinense*, posterior view.
Figures 22–23.—Labial cuspule of *Iridopelma hirsutum*. 22. Anterior view. 23. Posterior view.

Table 1.—Sizes (single cuspules) and density of cuspules in eight species of theraphosid spiders.

Taxa	Length (μm)		Width (μm)		Density of cuspules (number/mm²)		Density of ridges (number/10μm)	
	Labial	Maxillary	Labial	Maxillary	Labial	Maxillary	Labial	Maxillary
Theraphosinae								
Acanthoscurria suina	58.3	61.3	40.8	38.7	3.0 ± 1.5	4.0 ± 4.2	9	7
Eupalaestrus weijenberghi	71.2	74.3	41.5	39.3	3.8 ± 1.8	6.3 ± 3.9	7–9	10
Grammostola iheringi	98.5	107.8	70.2	69.8	4.5 ± 1.3	4.5 ± 1.1	6	6
Grammostola mollicoma	74.1	72.5	46.2	50.0	2.2 ± 0.9	2.7 ± 1.6	5	5
Homoeomma uruguayense	43.0	40.9	31.1	28.5	7.0 ± 4.3	6.0 ± 4.2	9	10
Plesiopelma longisternale	53.8	71.3	29.1	38.0	10.7 ± 3.0	7.7 ± 7.0	11	8
Aviculariinae								
Iridopelma hirsutum	53.7	69.7	36.8	33.9	4.5 ± 2.3	4.9 ± 3.2	7	13
Ischnocolinae								
Oligoxystre argentinense	—	39.6	—	27.8	—	4.8 ± 1.7	—	10

size. No significant correlation was found between cuspule number and cuspule size.

Two models of ornamentation were described in the maxillary cuspules of the Microstigmatidae (Griswold 1985): one presenting deep grooves and the other with many fine shallow grooves, the former considered as synapomorphic of clade ‘‘c’’ of Griswold (1985). Raven (1994) suggested the study of cuspule ridge interdistances (0.5–1 μm or 3–5 μm) to distinguish between two patterns in Nemesiidae. The interdistances of cuspule ridges found in the theraphosid species studied have intermediate values (0.9–2.5 μm) between Raven’s groups and their aspect fits with Griswold’s (1985) second model (‘‘many fine shallow groves’’).

The differences in ornamentation found between the anterior and the posterior faces of the cuspules is here reported for the first time in Theraphosidae. However, these differences in ornamentation are probably also present in Microstigmatidae and Barychelidae considering the figures given by Griswold (1985:6, figs. 17–18) and Raven (1994:303–310, figs. 3–10) respectively. A unique cuspule description from a theraphosid species was done by Cutler & Vuilliomenet (2001) in *Aphonopelma seemani*. In our opinion this description corresponds to the posterior face.

No strong differences were found in cuspule morphology or ornamentation among the genera and species studied. This, together with the similarity in other families, could reflect that cuspules are an early synapomorphy at the level of the Mygalomorphae as was indicated by Raven (1980) and could be interpreted as a conserved feature through the evolution of several mygalomorph taxa. We therefore suggest these structures have limited systematic value.

The probable functions of the cuspules in theraphosids could be mechanical, sensorial and glandular. Cutler & Vuilliomenet (2001) suggest a glandular or sensory function for the cuspules of *A. seemani* on the basis of a pore observed on the apical region of the cuspules, that could be interpreted as a sensory pit or secretory gland. We did not observe any pore on labial nor maxillary cuspules. Considering the oral inclination of the cuspules, their ornamentation and their unique presence in mygalomorphs with paraxial chelicerae, a mechanical function seems probable. Cuspules could help in prey retention by opposing the backward force of the chelicerae. The ornamentation of the apical half of the anterior face with transverse ridges could be related to particle retention near the mouth.

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