

The sister group of Aculeata (Hymenoptera) – evidence from internal head anatomy, with emphasis on the tentorium

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Abstract

The Aculeata comprises some of the best known Hymenoptera. Traditionally, their sister group has been considered to be the Ichneumonoidea; however, recent phylogenetic analyses contradict this hypothesis. We evaluate three potential candidates for the sister group of aculeate wasps: Ichneumonoidea, Evanioidea and Trigonaloidea. This is addressed by investigating the internal head anatomy of representatives of the relevant taxa, specifically the tentorium, musculature and glands. One species each of the families Braconidae, Evaniidae, Gasteruptionidae, Aulacidae and Trigonidae, as well as Sphecidae and Sapygidae as representatives of Aculeata, and Ibalidae as outgroup is examined. 33 head anatomical characters are mapped on the three competing hypotheses. Aculeata + Evanioidea are corroborated by the presence of a secondary bridge, the presence of a subforaminal cup and the presence of one medial sulcus on the ventral head sclerotisation instead of two sublateral ones. Trigonaloidea + (Aculeata + Evanioidea) is corroborated by the presence of a bent cibarium. The presence of a hypopharyngeal gland, the backwards shift of the origin of the antennal muscles, the loss of the connection of the dorsal tentorial arms with the head capsule and the loss of ventral salivary dilators are retrieved as synapomorphies of Aculeata. Two hitherto unknown glands, a hypopharyngeal salivary gland in Sphecidae and Sapygidae and a hypopharyngeal-maxillary gland in Evaniidae, are described.

Key words

Evanioidea, Trigonaloidea, phylogeny, head musculature, glands, microCT.

1. Introduction

Aculeata or stinging wasps include some of the insect taxa with the highest ecological and economic impact such as ants and bees, in addition to other charismatic groups, e.g., gold wasps, velvet ants and spider wasps. They fill vital ecological roles as predators and pollinators, often to the benefit of humankind, although their medical impact is usually detrimental. Furthermore, the occurrence of eusociality among Hymenoptera is restricted to Aculeata, having evolved multiple times within the group (e.g. DANFORTH 2002). Though a lot is known about this fascinating group, the fundamental question of

identifying Aculeata's closest relatives has not been answered satisfactorily.

Three hypotheses have emerged repeatedly in recent analyses of hymenopteran phylogeny:

1. Aculeata + Ichneumonoidea. Traditionally, Aculeata have been regarded as the sister group of the Ichneumonoidea, one of the most diverse superfamilies of parasitoid wasps. Two morphological characters, the presence of ovipositor valvelli and distinct propodeal articulating processes, were suggested by RASNITSYN (1988) as synapomorphies in his analysis which, though intuitively

tive, can be regarded as a milestone in the reconstruction of hymenopteran phylogeny. However, VILHELMSSEN et al. (2010) found the presence of propodeal articulating processes to be widespread among the Apocrita, not restricted to just Aculeata and Ichneumonidae. RONQUIST et al. (1999) performed a formal cladistic reanalysis of Rasnitsyn's dataset and found moderate support for the ichneumonoid-aculeate relationship, as it was retrieved under implied weighting, but not among the equally weighted most parsimonious trees. Additional moderate support was provided by an early molecular analysis based on 16S rRNA (DOWTON & AUSTIN 1994). Furthermore, VILHELMSSEN et al. (2010) retrieved Aculeata + Ichneumonidae in their analyses based on morphological data, but again solely under implied weighting. Under equal weighting and with higher K values (K=25) the Aculeata were placed as sister group to the remaining Apocrita except Stephanoidea.

2. Aculeata + Evanioidea. The Evanioidea comprise three families united by having the metasoma inserted high on the mesosoma, but which are otherwise highly divergent morphologically and biologically: the Aulacidae are parasitoids of wood-dwelling insects, the Gasteruptiidae nest parasites of solitary bees and the Evanioidea emerged as the sister group of Aculeata in the most comprehensive analysis of hymenopteran relationships to date (SHARKEY et al. 2012). This analysis was performed by the Tree of Life project: morphological characters and molecular data were compiled from all sources available at the time, and analyzed using a combined approach. However, only the molecular data supported Aculeata + Evanioidea in SHARKEY et al. (2012). Additional molecular support was found in a subsequent analysis of 120,000 sequences from 80,000 sites that were extracted from GenBank (PETERS et al. 2011).

3. Aculeata + Trigonaloidea. The Trigonaloidea are another small superfamily containing only the Trigonalidae with less than 100 species worldwide (CARMEAN & KIMSEY 1998). Most of them are highly specialized hyperparasitoids of other parasitoid Hymenoptera (WEINSTEIN & AUSTIN 1991). In molecular analyses by HERATY et al. (2011) and KLOPFSTEIN et al. (2013) the Trigonaloidea were retrieved as the sister group of the aculeates. Again, morphological support is missing.

In the present study we use characters from the internal head anatomy to test these hypotheses. Head characters have proven to be informative on higher phylogenetic levels in previous studies in other holometabolous orders (e.g. BEUTEL et al. 2009; DRESSLER & BEUTEL 2010; RANDOLF et al. 2014), while in apocritan Hymenoptera this is a hitherto underexplored character complex. A few head anatomical studies have been done for basal Hymenoptera, either on the complete head anatomy of selected species (MATSUDA 1957; BEUTEL & VILHELMSSEN 2007) or with focus on specific regions of the head (VILHELMSSEN 1996, 1999, 2011). Thorough studies of the head also exist for Braconidae: ALAM (1951) and, more recently, KARLSSON & RONQUIST (2012). Platygasteridae were treat-

ed by MIKO et al. (2007) and POPOVICI et al. (2014), the latter being limited to the labiomaxillary complex but examined with confocal laser scanning microscopy which excellently illustrates the internal anatomy in great detail. Finally RONQUIST & NORDLANDER (1989) provided an extensive description of the skeletal morphology of the basal cynipoid *Ibalia rufipes* Cresson, 1879, which serves as an outgroup taxon for our analyses.

The best-examined aculeate taxon is, unsurprisingly, the honeybee (*Apis mellifera* Linné, 1758). SNODGRASS' (1910) pioneering comprehensive study of honeybee anatomy is a good starting point. For head anatomy, YOUSSEF (1971) provided a detailed topography of the cephalic musculature and nervous system and also a first attempt to homologize hitherto described head anatomical structures in Hymenoptera. A detailed investigation of the honeybee tentorium has been performed by ERICKSON & SHENG (1984), and it is also covered in BERRY & IBBOTSON (2010) and PORTO et al. (2016). Besides bees, there are a couple of classical detailed anatomical studies of other aculeates, JANET (1900, 1905) on ants (*Myrmica rubra* [Linné, 1758]) and DUNCAN (1939) on vespids (*Vespula pensylvanica* [de Saussure, 1857]) which are still unsurpassed in their level of detail.

Head anatomical data for the three evanoid families and for Trigonaloidea are provided in the present study for the first time.

2. Material and methods

2.1. Specimens examined

To evaluate the putative sister groups of the Aculeata, we examined one ichneumonoid, one trigonaloid, and one representative of each of the three evanoid families, in addition to two aculeates and an ibaliid as outgroup. A detailed list of the material is given in Table 1. The specimens were chosen based on the taxon sample of the Hymenopteran Tree of Life Project (SHARKEY et al. 2012). For each species one microCT scan, one sagittal and one cross section were acquired except for *Doryctes erythromelas*, where no microCT scan was obtained. For morphological investigations the specimens were killed in 90% alcohol, and then fixed in alcoholic Bouin's fluid for 3 hours. The voucher specimens are deposited in the Hymenoptera Collection of the Natural History Museum Vienna.

2.2. Histological sections

In order to better allow the resin to infiltrate the specimen, the head was carefully cut open with a scalpel on both sides at the eye region so that none of the structures studied were damaged. Subsequently the heads were embedded in Araldite. Semithin histological sections (2 µm)

Table 1. List of studied material.

Family	Species	Sex	MicroCT	Sagittal histol. sections	Cross histol. sections	Label data
Aulacidae	<i>Pristaulacus strangaliae</i> Rohwer, 1917	f	Morphosource file #M8283	×	×	USA, West Virginia, Hardy Co. [unty], 16.VI–1.VII.[20]04, [Malaise Trap, D.R. Smith]
Braconidae	<i>Doryctes erythromelas</i> (Brullé, 1846)	f, m	not microCT scanned	×	×	USA, West Virginia, Hardy Co. [unty], 3mi[les] NE Mathias, 38°55'N 78°49'W, 16.–29.vii.2004, Malaise Tr[ajp, D. Smith]
Evaniidae	<i>Evaniella semaeoda</i> Bradley, 1908	m	Morphosource file #M8281	×	×	USA, V[irgini]A, Prince William Co.[unty], Bull Run M[oun]t[ai]n., Jackson Hollow, camp ground area, 38°52.8'N 77°41.4'W, 8–21 July 2011, Mal.[aise] trap # 1, D.R. Smith
Gasteruptionidae	<i>Gasteruption tarsatorius</i> (Say, 1824)	f	Morphosource file #M8282	×	×	USA, V[irgini]A, Prince William Co.[unty], Bull Run M[oun]t[ai]n., Jackson Hollow, camp ground area, 38°52.8'N 77°41.4'W, 25 June–7 July 2011, Mal.[aise] trap # 3, D.R. Smith
Ibaliidae	<i>Ibalia rufipes</i> Cresson, 1879	f	Morphosource file #M8285	×	×	From Fredrik Ronquist, no other data
Sapygidae	<i>Sapyga pumila</i> Cresson, 1880	f, m	Morphosource file #M8280	×	×	USA, Ut[ah], Cache Co[unty], reared VIII. [20]04, [James P.] Pitts
Sphecidae	<i>Pison chilense</i> Spinola, 1851	f, m	Morphosource file #M8279	×	×	Chile, Reg[ion] IV, Limari Prov.[ince], FrayJorge Nat.[ional] P[ar]k, 190 m, 30.6448°S 71.6572°W, Irwin Parker, 1.–8.V.[20]04
Trigonalidae	<i>Orthogonalys pulchella</i> (Cresson, 1867)	m	Morphosource file #M8284	×	×	USA, V[irgini]A, Essex Co.[unty], 1 mi[le] SE Dunnsville, 21.V.–3.VI.1998, Malaise trap, David R. Smith

were made with a diamond knife on a Reichert Ultracut Ultramicrotome (University of Vienna, Core Facility Cell Imaging and Ultrastructure Research) and stained with 0.1% toluidine blue. The sections were imaged with a Nikon Eclipse 80i microscope coupled with a Nikon DS-Fi1 camera and studied with the software Amira 5.4 (FEI Visualization Sciences Group, Mérignac Cedex, France). For the figures the images were processed with Adobe Photoshop 7.0 and plates were compiled in Adobe Illustrator CS 11.0.0. The histological sections are deposited in the Hymenoptera Collection of the Natural History Museum Vienna (for details see Table 1).

2.3. Imaging, MicroCT and 3D-reconstruction

Following METSCHER (2009) the specimens were stained with a 1% iodine solution and scanned in 95% ethanol with an Xradia MicroXCT x-ray microtomography system (University of Vienna, Department of Theoretical Biology) with a tungsten or rhodium source at 40–80 kV and 4–8 W. The images were reconstructed using the software provided with the microCT system. The microCT data were reconstructed with 2×2 pixel binning to reduce noise and file size, and reconstructed volume images were exported as TIFF image stacks. The image stacks are available for download at Morphosource (<http://morphosource.org>; P205: The sister group of Aculeata (Hymenoptera) – evidence from internal head anatomy). The media file details for each specimen are given in Table 1. The software Amira 5.4 (Fig. 5) and 6.0 (Figs. 2–4) was used for 3D-visualization and analysis of the data. The structures were labelled manually and reconstructed using the Amira *Arithmetics* tool for selective volume renderings (following KLEINTEICH et al.

2008; Fig. 2). The images were processed with Adobe Photoshop 7.0 and plates were compiled in Adobe Illustrator CS 11.0.0. Drawings were made in Adobe Illustrator CS 11.0.0.

2.4. Phylogeny

The character matrix was assembled in Mesquite 2.74 (MADDISON & MADDISON 2015). In addition to the taxa studied the following species were scored from literature: *Macroxyela ferruginea* (Say, 1824) (Xyelidae) from BEUTEL & VILHELMSSEN (2007); *Filacus pluricinctus* (Norton, 1862) (Tenthredinidae) from MATSUDA (1957; as *Macrophya pluricincta*); *Vespula pensylvanica* from DUNCAN (1939); *Apis mellifera* from YOUSSEF (1971). The characters of VILHELMSSEN (2011) that were informative in the context of the studied taxa were included as characters 28–33. The characters were mapped on the phylogenetic hypotheses from RASNITSYN (1988), SHARKEY et al. (2012) and KLOPFSTEIN et al. (2013) pruned to match our taxon sample using Winclada 1.00.08 (NIXON 2002). The matrix is available as Electronic Supplement file 1.

2.5. Terminology

The classification of musculature follows WIPFLER et al. (2011). For other structures we follow the Hymenoptera Anatomy Ontology (YODER et al. 2010; HYMENOPTERA ANATOMY CONSORTIUM 2015). Scientific terms used in the manuscript were extracted from the Hymenoptera Anatomy Ontology (HAO) using the “Analyze” tool (SELTSMANN et al. 2016) with the respective definitions and references and are available as Electronic Supplement file 2.

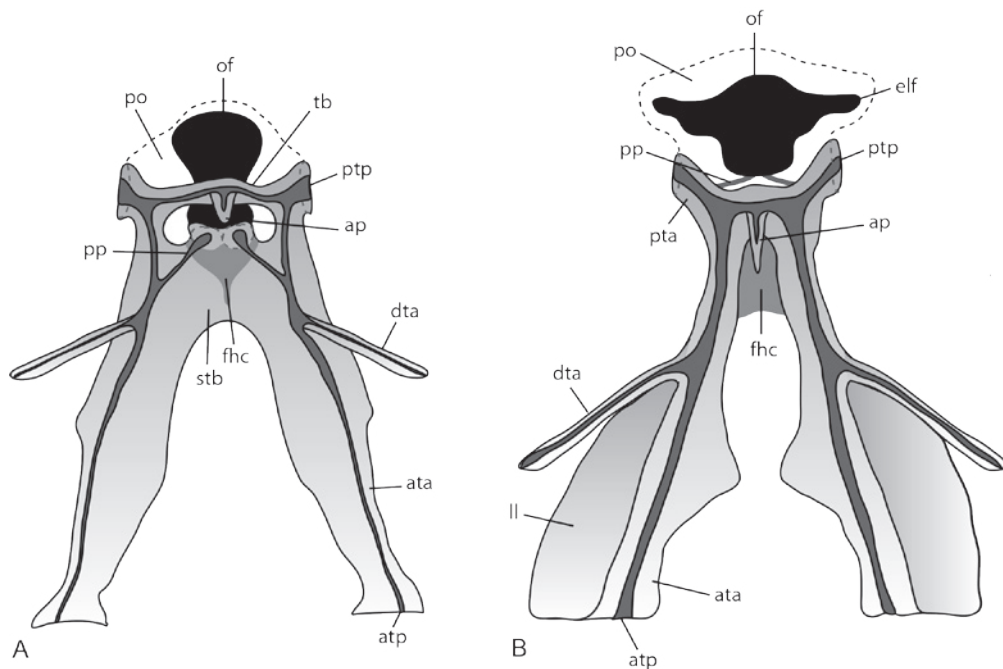


Fig. 1. Drawing of the tentorium of **A:** *Evaniella semaeoda* and **B:** *Doryctes erythromelas* (based on a reconstruction). — **Abbreviations:** ata – anterior tentorial arm, ap – anterior process, atp – anterior tentorial pit, dta – dorsal tentorial arm, elf – elongated lateral flange, fhc – area fused with head capsule, II – lateral lamella, of – occipital foramen, po – postocciput, pp – posterior process, pta – posterior tentorial arm, ptp – posterior tentorial pit, stb – secondary tentorial bridge, tb – tentorial bridge.

3. Results

3.1. Tentorium

The tentorium (Figs. 1–4) is the internal skeleton of the head. The basic structure consists of anterior and posterior tentorial arms, which are tubular invaginations from the anterior and posterior side of the head capsule respectively, and dorsal tentorial arms which are extensions of the anterior arms (Fig. 1). The points of invagination are the anterior and posterior tentorial pits. A transverse tentorial bridge connects the anterior and posterior tentorial arms.

3.1.1. Anterior tentorial arms. In Hymenoptera the anterior tentorial arms are always well developed and mostly equipped with lamellate extensions which serve as muscle attachment sites. The anterior arms have prominent lateral lamellae in *Ibalia* (Fig. 2A: ll) and *Doryctes* (Fig. 1B: ll) extending between the anterior tentorial pits and the dorsal tentorial arms. In *Orthogonalys* (Fig. 2B: dll) and *Evaniella* (Fig. 1A: dll) there are lateral lamellae which are bent upwards. In *Pison* (Fig. 2E: vll) and *Sapyga* (Fig. 2F: vll) the lamellae are oriented ventrolaterally and restricted to the area adjacent to the anterior tentorial arms reaching only about half-way to the dorsal arms. Likewise, median lamellae can be developed. They are similarly formed in *Orthogonalys*, *Gasteruption* (Fig. 2D: ml) and *Pristaulacus* (Fig. 2C: ml), having similar width to the tubular part of the anterior arm and extending from a point just posterior of the dorsal arms to the

anterior tentorial pits. In *Doryctes* and *Sapyga* triangular median lamellae are present just anterior to the dorsal arms.

3.1.2. Secondary tentorial bridge. A secondary tentorial bridge sensu MICHENER 1944 (Fig. 1A: stb) is often formed posteriorly between the ventral parts of the anterior tentorial arms. The secondary tentorial bridge is present in all studied Evanioidea and Aculeata (Figs. 1, 2: stb) while no such structure is present in *Orthogonalys* and *Ibalia*. In *Doryctes* the anterior arms merge with the inwardly bent head capsule (Fig. 1B: fhc). In *Evaniella*, *Gasteruption*, *Pison* and *Sapyga* a postgenal ridge is developed and connected with the ventral surface of the secondary tentorial bridge.

3.1.3. Dorsal tentorial arms. In all studied species dorsal tentorial arms are present (Figs. 1, 2). They extend to the anterior part of the head capsule in *Ibalia*, *Doryctes*, *Orthogonalys* and Evanioidea, connecting to it close to the antennal fossae. There is usually no external indication of the attachment points. In *Pison* and *Sapyga* the dorsal arms are weakly developed and do not connect with the head capsule (Fig. 2E,F). The dorsal arms arise at various distances along the anterior arms: slightly posterior to mid-length of the anterior arms in *Ibalia* (Fig. 2A), quite far posteriorly at the level of the anterior end of the secondary tentorial bridge in *Evaniella*, *Pison* and *Sapyga* (Figs. 1A, 2E,F), around mid-length of the anterior arms in *Pristaulacus* and *Doryctes* (Figs. 1B, 2C), and even further anteriorly in the anterior halves of the anterior arms in *Gasteruption* (Fig. 2D).

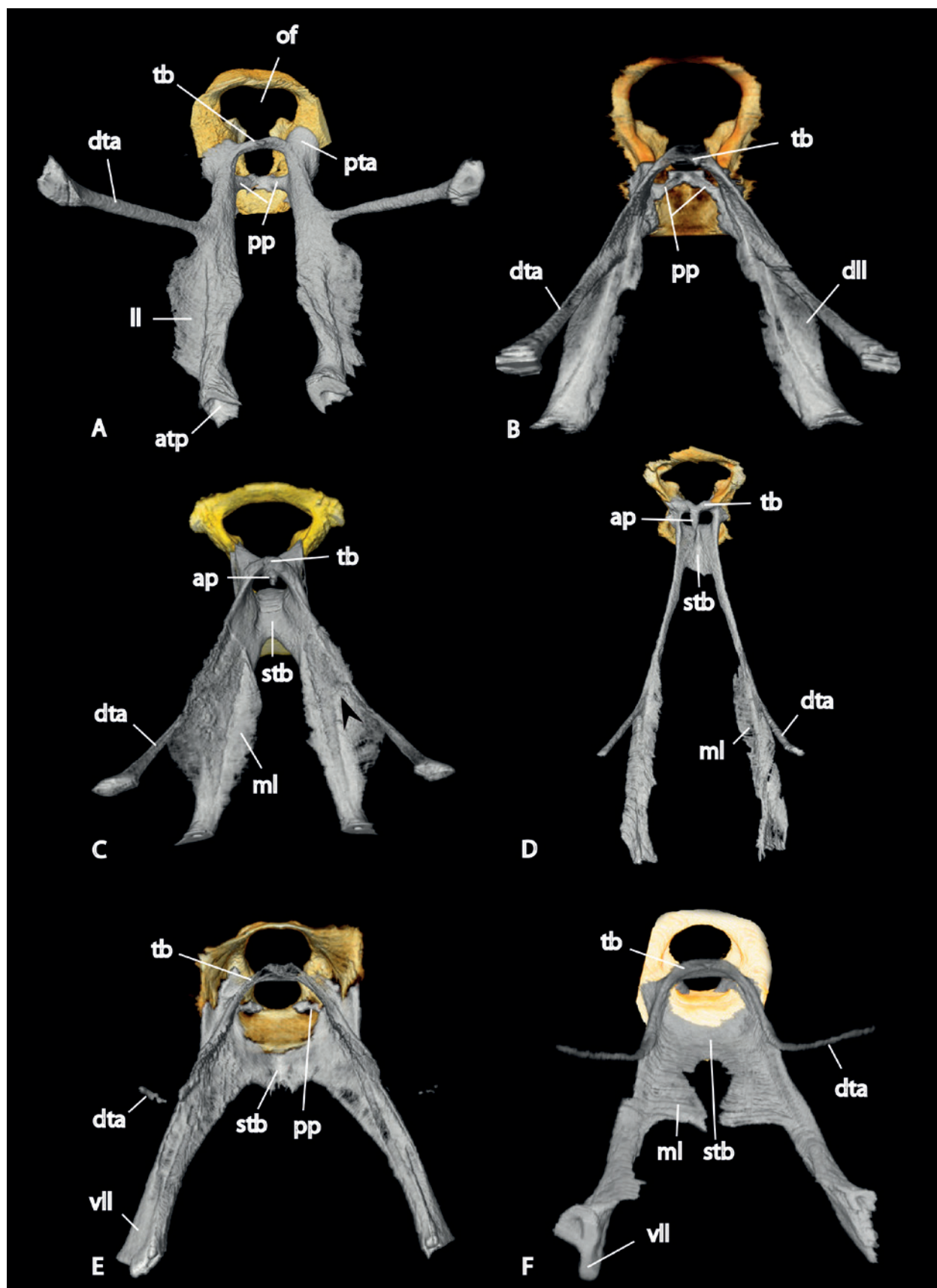


Fig. 2. Volume rendering of tentorium and occipital foramen. **A:** *Ibalia rufipes*; **B:** *Orthogonalys pulchella*; **C:** *Pristaulacus strangaliae*; **D:** *Gasteruption tarsatorius*; **E:** *Pison chilense*; **F:** *Sapyga pumila*. — **Abbreviations:** ap – anterior process, atp – anterior tentorial pit, dll – dorsolateral lamella, dta – dorsal tentorial arm, ll – lateral lamella, ml – median lamella, of – occipital foramen, pp – posterior process, pta – posterior tentorial arm, stb – secondary tentorial bridge, tb – tentorial bridge, vll – ventrolateral lamella; arrow in 2C indicates point of origin of dta.

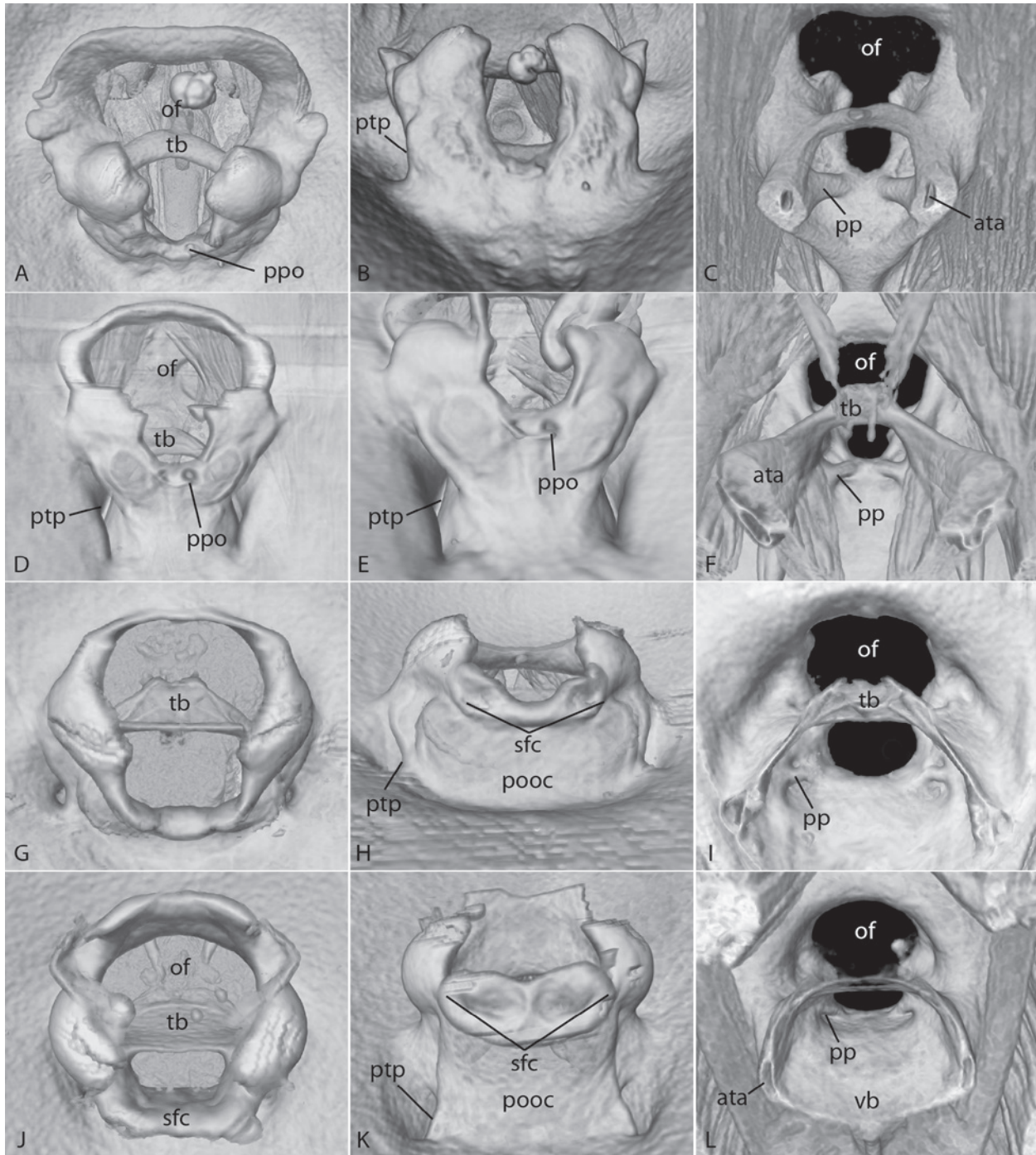


Fig. 3. Volume rendering of occipital foramen. **A–C:** *Ibalia rufipes*; **D–F:** *Orthogonalys pulchella*; **G–I:** *Pison chilense*; **J–L:** *Sapyga pumila*. **A,D,G,J** posterior view; **B,E,H,K** posteroventral view; **C,F,I,L** anterior view from the inside of the head capsule. — **Abbreviations:** ata – anterior tentorial arm, of – occipital foramen, pooc – postocciput, pp – posterior process, ppo – opening of posterior process, ptp – posterior tentorial pit, sfc – subforaminal cup, stb – secondary tentorial bridge, tb – tentorial bridge.

3.1.4. Tentorial bridge. In all studied species the tentorial bridge has an anterior process (Fig. 1: ap) that serves as attachment point for the anterior tentoriobuccal muscle (Obu5). The tentorial bridge varies considerably in length: It is shorter than the diameter of the anterior arms in *Ibalia*, *Orthogonalys*, *Gasteruption*, approximately equals the diameter of the anterior arms in *Evaniella*, *Pristaulacus*, *Pison*, *Doryctes* and is distinctly longer than the diameter of the anterior arms in *Sapyga*.

3.1.5. Posterior tentorial arms. The posterior arms are short and stout in all studied Hymenoptera. The posterior tentorial pits are located lateral to the occipital foramen in all studied species except *Orthogonalys* where they are slit-like elongated and reach below its ventral margin (Figs. 3, 4: ptp).

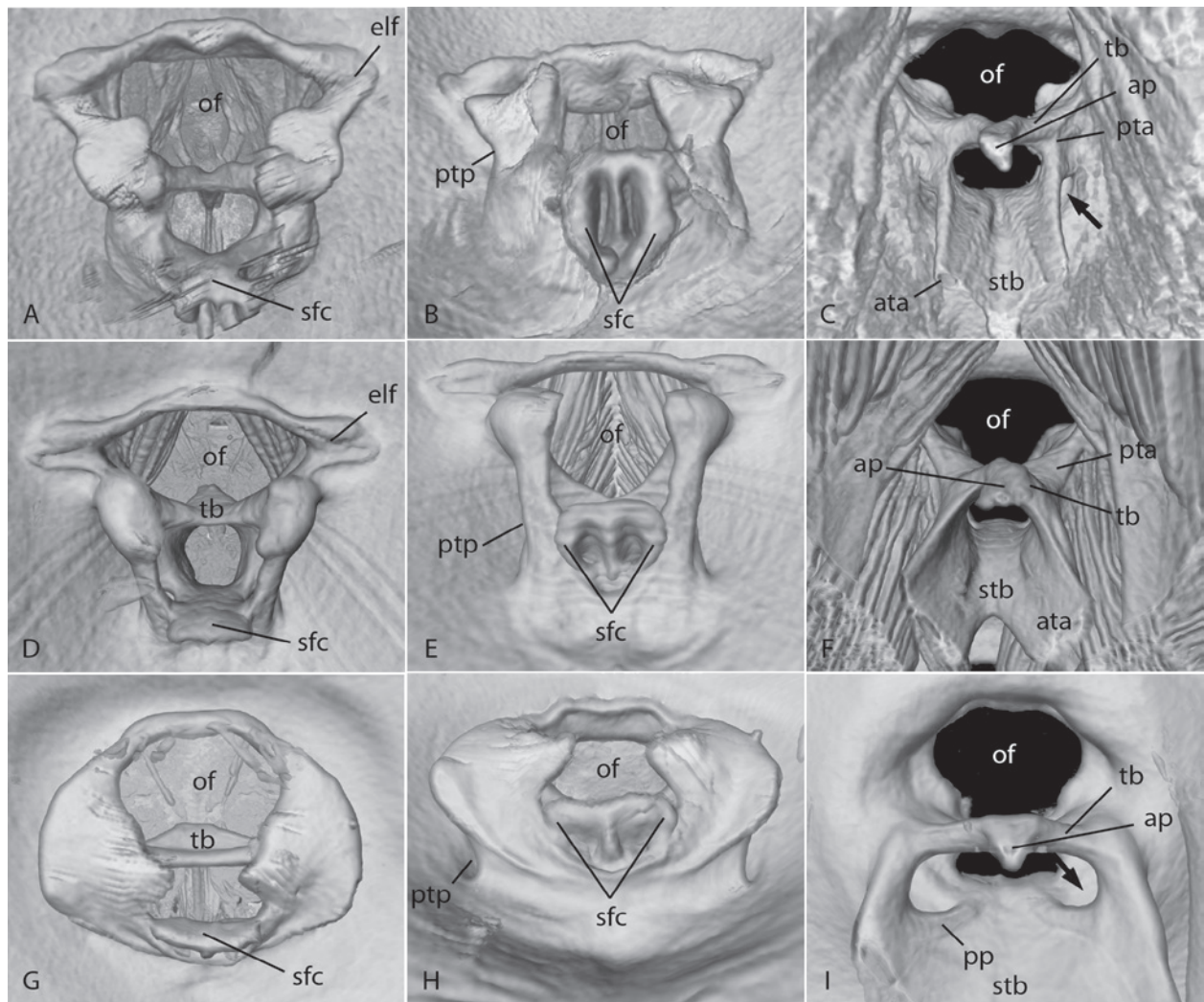


Fig. 4. Volume rendering of occipital foramen of Evanioidea. **A–C:** *Gasteruption tarsatorius*; **D–F:** *Pristaulacus strangaliae*; **G–I:** *Evaniella semaeoda*. **A,D,G** posterior view; **B,E,H** posteroventral view; **C,F,I** anterior view from the inside of the head capsule. — **Abbreviations:** ap – anterior process, ata – anterior tentorial arm, elf – elongated lateral flange, of – occipital foramen, pp – posterior process, pta – posterior tentorial arm, ptp – posterior tentorial pit, sfc – subforaminal cup, stb – secondary tentorial bridge, tb – tentorial bridge; arrows indicate separation of tentorium and head capsule lateral of the postoccipital apodeme.

3.1.6. Posterior processes. The posterior tentorial processes of the tentorium are paired tubular evaginations of the posterior tentorium. They originate on the inner surface of the anterior tentorial arms in *Ibalia* and Evanioidea, and on the posterior tentorial arms near the pits or even on the cranial wall in *Doryctes*, *Orthogonalya*, *Pison* and *Sapyga* (Figs. 3, 4: pp). The processes are similar in diameter to the dorsal tentorial arms, being well-developed in *Ibalia* and Evanioidea, and distinctly thinner in *Pison* and *Sapyga*. In Evanioidea the posterior processes delimit the secondary tentorial bridge posterolaterally and fuse with the ventral margin of the occipital foramen. Between this contact area and the posterior tentorial pits the tentorium is not in contact with the head capsule (Fig. 4C,I: arrow). In *Pison* and *Sapyga* the posterior margin of the tentorium is fused with the ventral margin of the occipital foramen all the way between the posterior tentorial pits (Fig. 3I,L).

3.2. Postocciput

The upper margin of the occipital foramen is arched in all species studied. Its dorsolateral corners are extended into lateral flanges in *Doryctes*, *Gasteruption* and *Pristaulacus* (Figs. 1B, 4A,D: elf) while they are rounded in the rest. The occipital foramen is distinctly narrower ventrally of the occipital condyles in *Ibalia*, *Orthogonalya*, *Doryctes*, *Gasteruption* and *Pristaulacus*; the tapering is indistinct in *Evaniella*, *Pison* and *Sapyga*, giving the foramen nearly a dumbbell-shape (Figs. 3C,F,I,L, 4C,F,I: of). On the ventral margin of the foramen the attachment site for the profurcopostoccipital muscles forms a subforaminal cup sensu BERRY & IBBOTSON (2010) in Evanioidea and the aculeates (Figs. 3H,K, 4B,E,H: sfc). In Evanioidea it is entirely formed by the posterior ends of the posterior processes, in *Pison* and *Sapyga* the distinctly smaller posterior processes terminate within the

structure. The postocciptut is extended into a collar ventrally in *Pison* and *Sapyga* (3H,K: pooc).

3.3. Glands

The described glands consist of glandular units with two cell types: a gland cell, called terminal cell (class III gland cells sensu NOIROT & QUENNEDEY 1974) and an associated duct cell, the so called intercalary cell, which forms the cuticular canal by which the secretion is dispensed. The terminal cell lies at the proximal end of the canal. The part of the canal reaching into the terminal cell is called the receiving canal while the remaining part of the canal is the conducting canal. It is either directly linked with the cuticula or opens into a duct that collects and excretes the glandular secretion.

3.3.1. Hypopharyngeal gland (Figs. 6D, 7A). A paired hypopharyngeal gland is present in *Pison* and *Sapyga*. It consists of a compact organ formed by secretory units of terminal cells and intercalary cells emptying into a duct which opens into the hypopharyngeal wall. It represents a gland type 2 sensu CRUZ-LANDIM & COSTA (1998).

3.3.2. Hypopharyngeal salivary gland (Figs. 6D, 7B). Additionally, in *Pison* and *Sapyga* an unpaired gland is found in the hypopharyngeal lobe. It is a compact roundish organ and consists of terminal cells which are located in the hypopharyngeal lobe, and intercalary cells ending in a short collecting canal which opens into the salivarium just anterior to the insertion of the hypopharyngosalivariar muscle (0hy12).

3.3.3. Hypopharyngeal-maxillary gland (Fig. 7C,D). In *Evaniella* the hypopharyngeal-maxillary gland is paired and consists of two groups of terminal cells on each side: one is positioned ventrally of the hypopharyngeal wall near the functional mouth, the other is found further posteriorly near the insertion point of the craniocardinal muscle (0mx1) on the cardinal process. The intercalary cells of both groups drain the secretion through pores in the membrane in the conjunctiva connecting the head capsule to the maxilla.

3.3.4. Mandibular gland (Fig. 7E–G). The mandibular gland is morphologically quite diverse. It always consists of terminal cells arranged around a secretion reservoir which opens into the oral cavity between the mandible and the clypeus. The gland is located frontolaterally between the clypeus and antennal base in *Gasteruption*, *Evaniella*, *Pristaulacus*, *Pison*, *Sapyga* and *Ibalia*, and close to the base of the mandible in *Orthogonalys* and *Doryctes*. In *Sapyga* the gland is bifid and the second lobe is located laterally in the postgenal region; the reservoirs of both lobes merge before opening through a common excretory duct at the base of the mandibles. In *Sapyga*, *Pison*, *Evaniella*, *Orthogonalys* and *Ibalia*, the secretory cells are densely arranged, in *Pison* and *Evaniella* lining

the reservoir anteriorly, in *Orthogonalys* mainly posteriorly, and in *Ibalia* and *Sapyga* surrounding the reservoir on all sides. In *Gasteruption*, *Pristaulacus*, and *Doryctes* the terminal cells are not clustered but scattered around the reservoir.

3.3.5. Glossal gland (Figs. 6B,C, 7G). A glossal gland consisting of terminal cells and intercalary cells opening through pores in the anterior glossal sclerites is present in *Gasteruption*, *Evaniella*, *Orthogonalys*, and *Doryctes*, absent in *Pison*, *Ibalia* and *Pristaulacus* and probably absent in *Sapyga* (there are ducts in the anterior glossal sclerite but no associated secretory cells can be recognized).

3.3.6. Galeal gland (Fig. 7H). Terminal cells are found in the anterior part of the maxilla, at the base of the galea and the palpus of *Orthogonalys* as well as in the galea of *Gasteruption*. The excretory canaliculi and the opening of this gland could not be identified.

3.4. Musculature

For details on each taxon see Table 2.

3.4.1. Antennal muscles (Fig. 5). All four tentoriocapal muscles (0an1–0an4) are present in the studied specimens, and they are in the same position relative to each other; differences are found in their position on the anterior tentorial arms: They originate along the entire length of the anterior arms in *Evaniella* (Fig. 5C), *Orthogonalys* and *Pristaulacus*, only anterior to the dorsal arms in *Gasteruption*, *Doryctes* (Fig. 5B) and *Ibalia* (Fig. 5A), and only on the posterior half of the anterior arms in *Pison* (Fig. 5D) and *Sapyga*. Furthermore, they can be situated more medially or laterally depending on the position of the antennal foramina relative to the tentorium.

3.4.2. Mandibular muscles. The craniomandibular muscles (0md1, 0md3) are well developed; the origin of M. craniomandibularis externus is slightly variable in whether it reaches the postgena or not. The craniomandibular muscles in *Doryctes* are unusually weakly developed and embedded in fat tissue. Two tentoriomandibular muscles (0md6, 0md8; Fig. 8B) are present in *Evaniella*, *Orthogonalys*, *Pison* and *Sapyga*; only one of them (0md8) is developed in *Gasteruption*.

3.4.3. Maxillary muscles (Figs. 5, 8). M. craniolacinialis (0mx2) is present only in *Orthogonalys*. One muscle consistently inserts at the cardostipital suture; it is homologized with M. tentoriocardinalis (0mx3) (Fig. 5: 0mx3, Fig. 8E). M. tentoriostipitalis anterior (0mx4) is divided into two components separated from each other by more than the width of one component in *Pison*, *Evaniella*, *Orthogonalys* and *Sapyga* (Fig. 5C,D). In *Sapyga* the origin of the anterior component is located on a premental-clypeal sclerite (“Segelhalter” sensu OSTEN 1982). In *Pison* the points of insertion of these two components

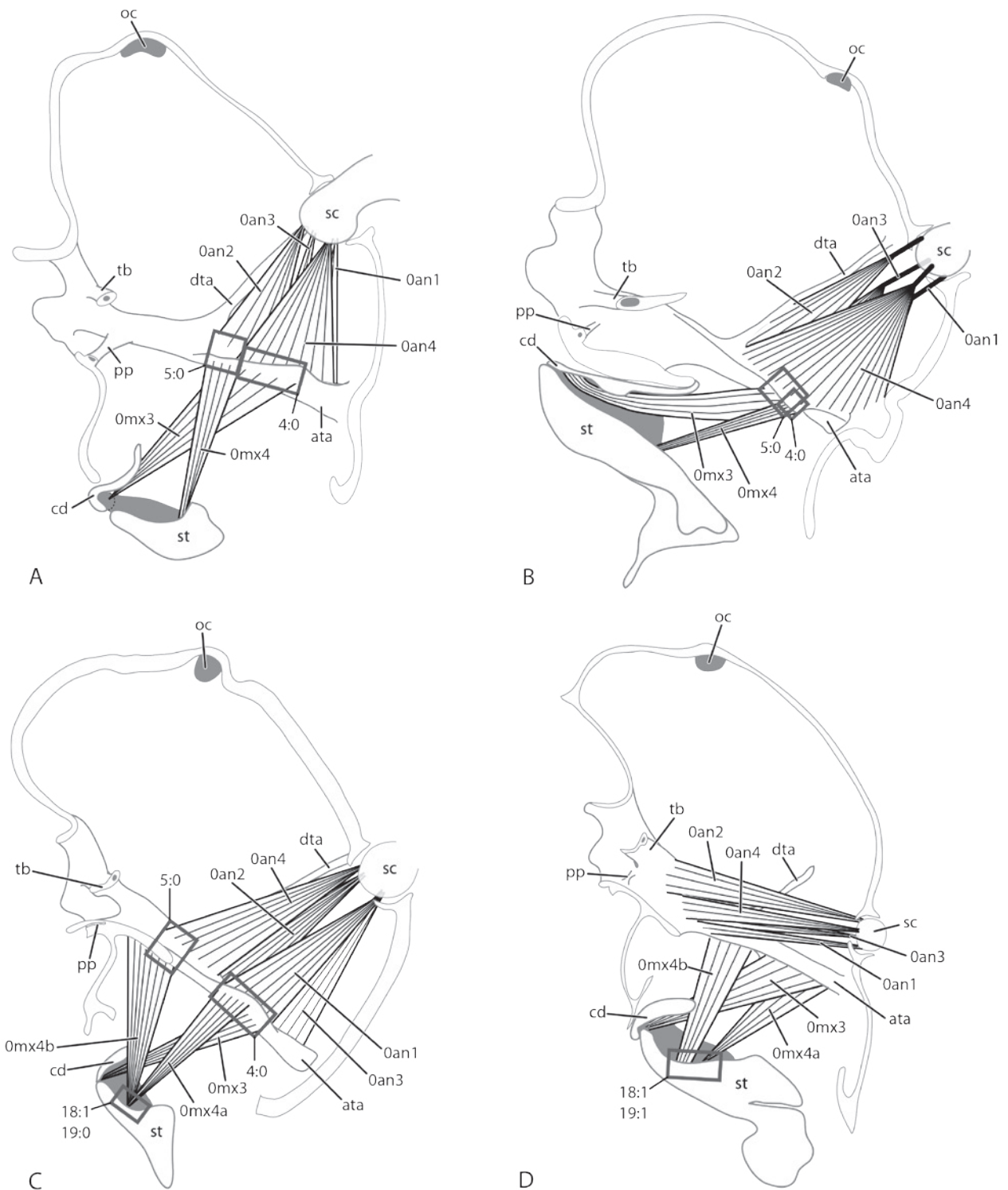


Fig. 5. Schematic drawings of a virtual sagittal section at the level of the lateral ocellus based on volume renderings and histological sections, illustrating the relative position of the antennal and the maxillary muscles on the tentorium. **A:** *Ibalia rufipes*; **B:** *Doryctes erythromelas*; **C:** *Evaniella semaeoda*; **D:** *Pison chilense*. — **Abbreviations:** ata – anterior tentorial arm, cd – cardo, dta – dorsal tentorial arm, oc – lateral ocellus, pp – posterior process, sc – scapus, st – stipes, tb – tentorial bridge; 0an1 – M. tentorioscapalis anterior, 0an2 – M. tentorioscapalis posterior, 0an3 – M. tentorioscapalis lateralis, 0an4 – M. tentorioscapalis medialis, 0mx3 – M. tentoriocardinalis, 0mx4 – M. tentoriostipitalis anterior; boxes indicate respective character states.

are separated as well, though both are on the medial stipitopital wall (Fig. 5D: 0mx4a, 0mx4b). M. stipitolacinialis (0mx6) is absent only in *Gasteruption*. M. stipitogalealis (0mx7) consists of two components with different origins

in *Pristaulacus*. Of the two stipitopalpal muscles the internal one (0mx10) is only present in *Evaniella* and *Orthogonalys*.

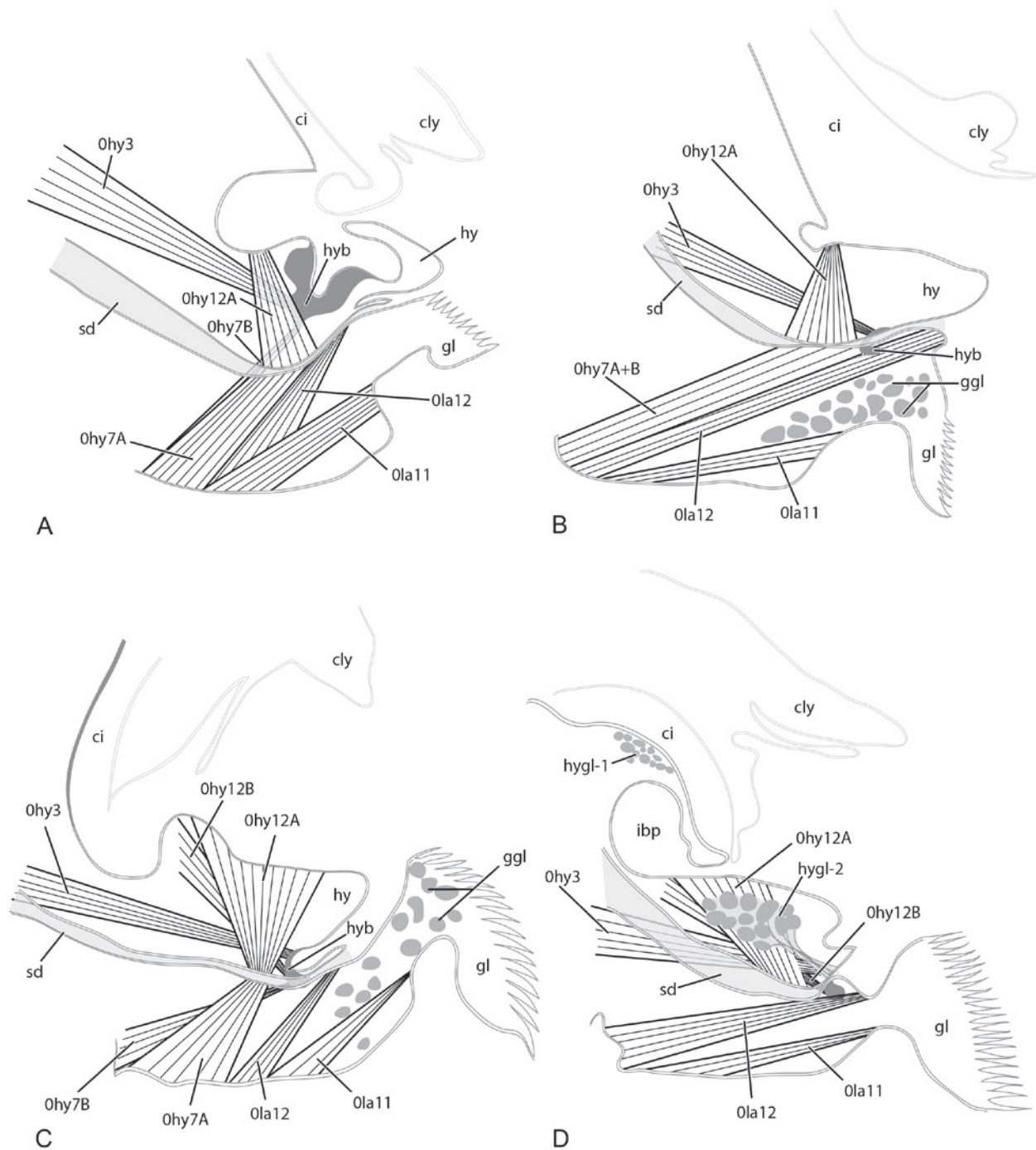
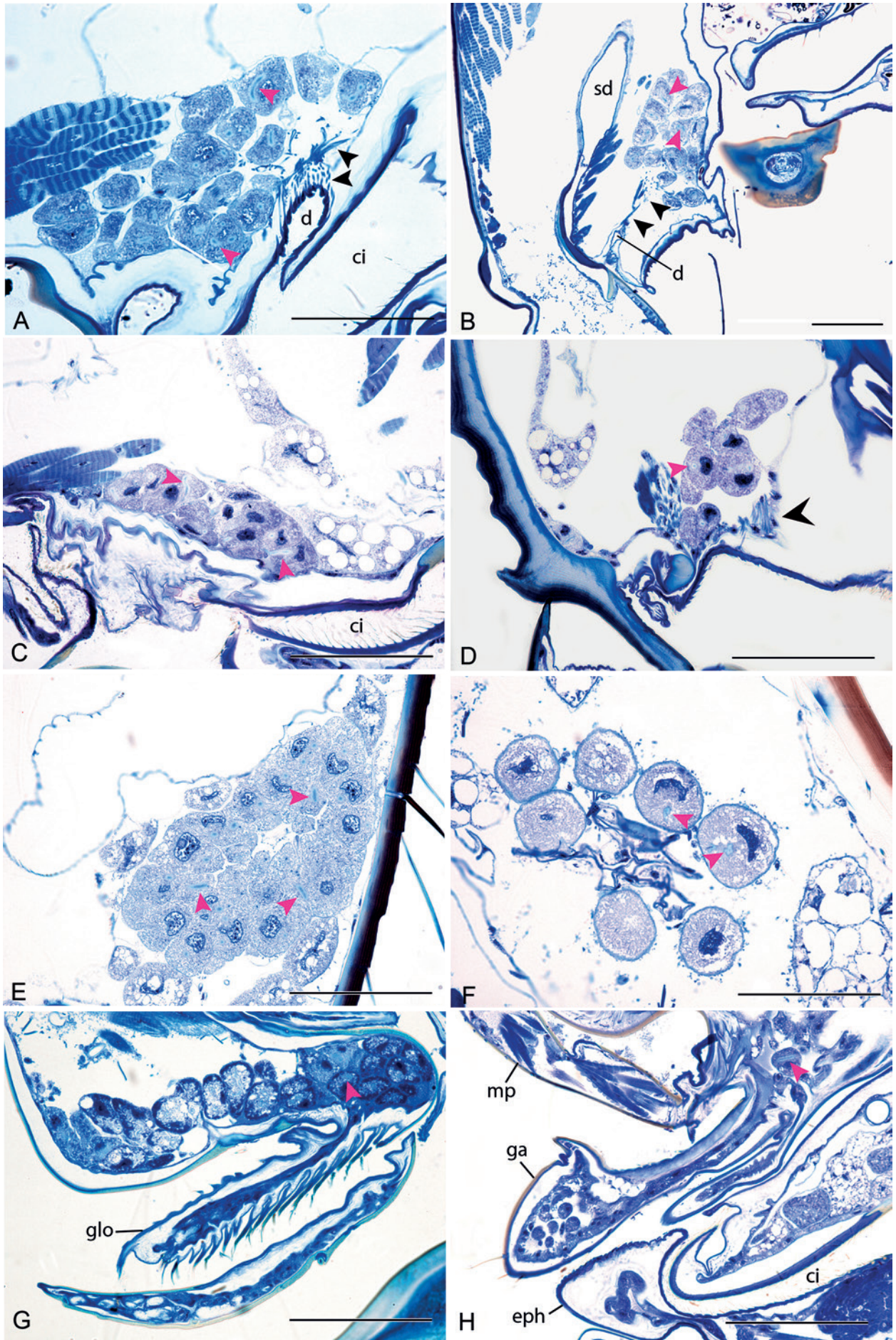


Fig. 6. Schematic drawings of a virtual sagittal section of the salivarial region based on histological sections. **A:** *Ibalia rufipes*; **B:** *Doryctes erythromelas*; **C:** *Evaniella semaeoda*; **D:** *Pison chilense*. — **Abbreviations:** ci – cibarium, cly – clypeus, ggl – glossal gland, gl – glossa, hy – hypopharyngeal lobe, hyb – hypopharyngeal button, hygl-1 – hypopharyngeal gland I, hygl-2 – hypopharyngeal gland II, ibp – infrabuccal pouch, sd – salivary duct; 0hy3 – M. tentoriohypopharyngalis, 0hy7A – M. praementosalivaris, 0hy7B – M. praementosalivaris (sclerite), 0hy12A – M. hypopharyngosalivaris, 0hy12B – M. hypopharyngosalivaris (sclerite), 0la11 – M. praementoparaglossalis, 0la12 – M. praementoglossalis.

→ **Fig. 7.** Sagittal histological sections of glands. **A:** *Pison chilense*: hypopharyngeal gland I; **B:** *Pison chilense*: hypopharyngeal salivary gland; **C:** *Evaniella semaeoda*: hypopharyngeal component of hypopharyngeal-maxillary gland; **D:** *Evaniella semaeoda*: maxillary component of hypopharyngeal-maxillary gland; **E:** *Pison chilense*: mandibular gland; **F:** *Pristaulacus strangaliae*: mandibular gland; **G:** *Orthogonalys pulchella*: glossal gland; **H:** *Gasteruption tarsatorius*: galeal gland. — **Abbreviations:** ci – cibarium, d – collecting duct, eph – epipharynx, ga – galea, glo – glossa, mp – maxillary palp, sd – salivary duct. Scale bars: 100 µm. Black arrows indicate the conducting canals of the intercalary cells; pink arrows indicate examples of the receiving canals in the terminal cells.



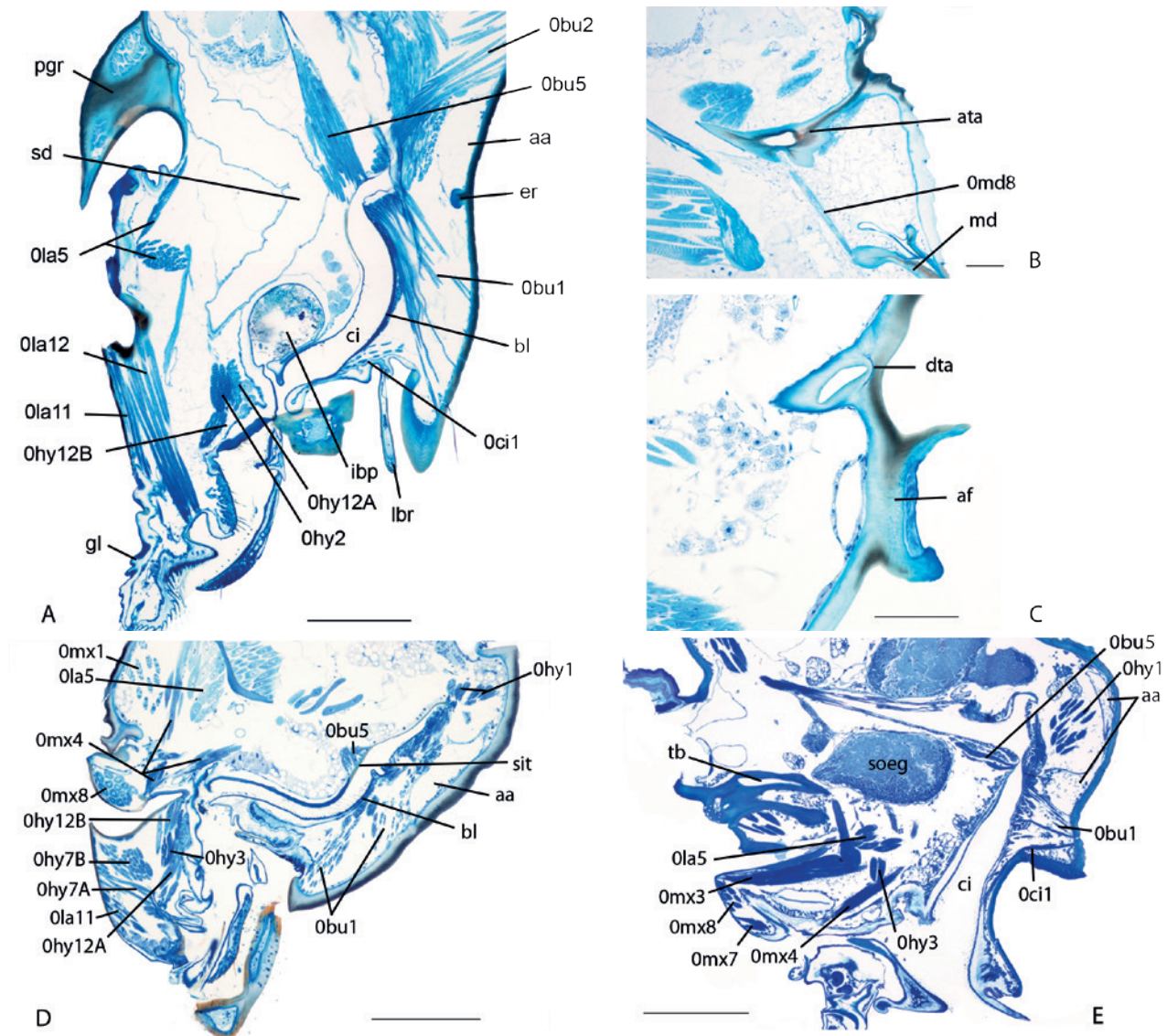


Fig. 8. Sagittal histological sections. **A:** *Pison chilense*; **B:** *Sapyga pumila*; **C:** *Orthogonalys pulchella*; **D:** *Evaniella semaeoda*; **E:** *Doryctes erythromelas*; A,D,E median section of the anterior head region, notice the bent cibarium in *P. chilense* and *E. semaeoda*; B detail, indentation of ata at insertion of M. tentoriomandibularis medialis inferior; C detail, continuous connection of dorsal tentorial arms and head capsule. — **Abbreviations:** aa – antennal ampulla, af – antennal foramen, ata – anterior tentorial arm, bl – buccal lobe, ci – cibarium, dta – dorsal tentorial arm, er – epistomal ridge, gl – glossa, ibp – infrabuccal pouch, lbr – labrum, md – mandible, pgr – postgenal ridge, ppt – prepharyngeal tube, sd – salivary duct, sit – sitophore, soeg – suboesophageal ganglion, tb – tentorial bridge; 0bu1 – M. clypeobuccalis, 0bu2 – M. frontobuccalis anterior, 0bu5 – M. tentoriobuccalis anterior, 0ci1 – M. clypeopalatalis, 0hy1 – M. frontooralis, 0hy3 – M. tentoriohypopharyngalis, 0hy7A – M. praementosalivaris, 0hy7B – M. praementosalivaris (sclerite), 0hy12A – M. hypopharyngosalivaris, 0hy12B – M. hypopharyngosalivaris (sclerite), 0la5 – M. tentoriopraementalis, 0la11 – M. praementoparaglossalis, 0la12 – M. praementoglossalis, 0md8 – M. tentoriomandibularis medialis inferior, 0mx1 – M. craniocardinalis, 0mx3 – M. tentoriocardinalis, 0mx4 – M. tentoriostipitalis anterior, 0mx7 – M. stipitogalealis, 0mx8 – M. stipitopalpalis externus. Scale bars: A, D, E 500 µm; B, C 100 µm.

3.4.4. Labial, hypopharyngeal and salivary muscles (Figs. 6, 8). M. tentoriopraementalis (0la5) has a second component with a distinctly different, anterior origin in *Pison* (Fig. 8A). In addition to M. hypopharyngosalivaris (0hy12A), a muscle leading to the nearby hypopharyngeal button is observed (0hy12B; Figs. 6 C,D, 8A,D). It is divided from M. hypopharyngosalivaris by M. tentoriohypopharyngalis (0hy3), and present in all studied species except *Ibalia* (Fig. 6A), *Doryctes* (Fig. 6B) and *Sapyga*. There is also a corresponding second

component of the ventral salivary musculature inserting on the hypopharyngeal button (0hy7B; Figs. 6A–C, 8D). The ventral salivary muscles (0hy7A and 0hy7B) are absent in *Pison* (Fig. 6D) and *Sapyga*.

3.4.5. Prepharyngeal and pharyngeal muscles (Fig. 8). The muscles of the digestive tract are quite variable. M. frontoepipharyngalis (0lb2), M. clypeopalatalis (0ci1) and M. tentoriobuccalis posterior (0bu6) are absent in some of the studied species, M. frontobuccalis posterior

Table 2. List of muscle origin and insertion. — *Abbreviations:* ata – anterior tentorial arm, atp – anterior tentorial arm, dta – dorsal tentorial arm, tb – tentorial bridge, pta – posterior tentorial arm, ptp – posterior tentorial pit.

Name of muscle	Insertion	Ibalia	Orthogonolys	Evaniella	Gasterupion	Pristaulacus	Doryctes	Pison	Sapyga	Remarks
M. tentorioscapalis anterior (0an1)	ventral margin of scapal base	ata, partly on lateral extension	ata	ata	ata, just posterior to atp	ata	on lateral extension of ata	ata, at mid-length	on median extension of ata	anteriormost originating antennal muscle
M. tentorioscapalis posterior (0an2)	dorsal margin of scapal base	ata, ant. to dta	ata, ant. to tb	ata, ant. to dta	ata, ant. to dta	ata, ant. to tb	on lateral extension of ata	ata, ant. to tb	ata, ant. to dta	posteriormost originating antennal muscle
M. tentorioscapalis lateralis (0an3)	lateral margin of scapal base	ata, partly on lateral extension	ata, at area of origin of dta	ata, at area of origin of dta	ata, ant. to dta	ata, at area of origin of dta	on lateral extension of ata	ata, at area of origin of dta	ata, ant. to dta	always posterior to 0an1
M. tentorioscapalis medialis (0an4)	median margin of scapal base	along median margin of ata	along median margin of ata	on median extension of ata	on median extension of ata	on median extension of ata	on median extension of ata	along median margin of ata	on median extension of ata	medianmost antennal muscle
M. cranioandibularis internus (0md1)	with thick tendon at median edge of mandible	vertex, occiput, gena, and ocular diaphragm	vertex, occiput, gena, and ocular diaphragm	vertex, occiput, gena, and ocular diaphragm	vertex, occiput, gena, and ocular diaphragm	vertex, occiput, gena, and ocular diaphragm	occiput	vertex, occiput, gena, and ocular diaphragm	vertex, occiput, gena, and ocular diaphragm	
M. cranioandibularis externus posterior (0md3)	with a tendon on posteroproximal part of mandible	gena and small part of postgena	gena, between compound eye and occipital carina	gena and small part of postgena	gena and small part of postgena	gena, between compound eye and occipital carina	gena and postgena	gena and small part of postgena	gena and postgena	
M. tentorio-man-dibularis lateralis inferior (0md6)	ventrally on inner wall of mandible	absent	ata	ata, around mid-length	absent	absent	absent	ata, in indentation of anterior ata	ata, in indentation of anterior ata	
M. tentorio-man-dibularis medialis inferior (0md8)	dorsally, on inner wall of mandible	absent	ata	ata, around mid-length	ata	absent	absent	ata, in indentation of anterior ata	ata	
M. craniocardinalis externus (0mx1)	the very end of the proximal cardinal process	postgena	postgena	postgena	postgena	postgena	posterior tentorial pit	postgena	postgena	
M. craniolacinalis (0mx2)	next to 0mx6, or even with common tendon	absent	postgena, lateral of 0mx1	absent	absent	absent	absent	absent	absent	
M. tentoriocardinalis (0mx3) or M. tentorioscapalis posterior (0mx5)	around stiptocardinal hinge – see comments for each species	medioventrally on ata anterior to origin of dta; inserting at stiptocardinal suture	anteriorly on ata, anterior to 0mx5; inserting on proximal end of stipes next to stiptocardinal hinge	anteriorly on ata, anterior to anterior component of 0mx4; inserting at stiptocardinal suture	anteriorly on ata, near atp; inserting on stiptocardinal hinge	anteriorly on median flange of ata; inserting on stipes and cardo	ata and median extension of ata; inserting at stiptocardinal suture	anteriorly on ata; inserting proximolaterally on stipes, next to stiptocardinal hinge	anteriorly on ata; inserting at stiptocardinal hinge	
M. tentorioscapalis anterior (0mx4)	medial stiptal wall	ata, between 0mx3 and 0hy3	one component anteriorly on ata, just behind 0mx3, another posteriorly on ata at height of origin of dta	one component originating on ata posterior to 0mx3, the ventral bridge	medioventrally on median flange of ata and just posterior to origin of dta	median flange of ata	median flange of ata, medial of 0mx3	one component posteriorly on ata at level of dta, inserting on medial stiptal wall around mid-length; second component at atp, inserting further distally on stiptal wall	on component on the median flange of ata, second smaller component on premental-clypeal sclerite (Segelhalter sensu Osten 1982)	

Table 2 continued.

Name of muscle	Insertion	<i>Ibalia</i>	<i>Orthogonolys</i>	<i>Evaniella</i>	<i>Gasteruption</i>	<i>Pristaulacus</i>	<i>Doryctes</i>	<i>Pison</i>	<i>Sapyga</i>	Remarks
M. stiptolacinalis (0mx6)	basal edge of lacinia	lateral stiptal wall, lateral of 0mx8	lateral stiptal wall, lateral of 0mx8	lateral stiptal wall, lateral of 0mx8	absent	proximal stiptal wall, lateral of 0mx8	lateral stiptal wall, lateral of 0mx8	lateral stiptal wall and cardostiptal ridge	lateral half of stipes	
M. stiptogalealis (0mx7)	basal edge of galea	median stiptal wall, distally of 0mx8	median stiptal wall, distally of 0mx8	median stiptal wall, distally of 0mx8	stiptal wall, distally of 0mx8	two components, stiptal wall, distally and disto-ventrally of 0mx8	stiptal wall, distally of 0mx8	broadly along stiptal wall, distally of 0mx8	median stiptal wall, distally of 0mx8	
M. stiptopalpalis externus (0mx8)	basal edge of the first palpomere of maxillary palp	basally on stipes	basal median wall of stipes near cardostiptal ridge	basal median wall of stipes near cardostiptal ridge	basal median wall of stipes near cardostiptal ridge	basal median wall of stipes near cardostiptal ridge	basally on stipes	basal lateral wall of stipes near cardostiptal ridge	basal median wall of stipes	
M. stiptopalpalis internus (0mx10)	mesobasal margin of palpomere 1	absent	medial stiptal wall, distally of 0mx8	medial stiptal wall, distinctly thinner than 0mx8	absent	absent	absent	absent	absent	
M. frontooralis (0hy1)	distal end of oral arm	frons, between antennae	frons, dorsomedial of antennae, nearly half way to median ocellus	frons, ventromedial of antennal base, very close to it	frons, dorsomedial of antennae, approx. 1/3 the way to median ocellus	frons, between antennae	frons, ventromedial of antennae	frons, dorsomedial of antennae, closer to median ocellus than to antennae	frons, dorsomedial of antennae	
M. tentoriooralis (0hy2)	distal end of oral arm	invagination area of ata	anteriorly on ata	invagination area of ata	anteriorly on ata	anteriorly on ata	frons, mediadorsal of atp	clypeofrontal ridge, next to atp	anteriorly on ata	
M. tentoriohyopharyngalis (0hy3)	hypopharyngeal button	ventrally on ata posterior to origin of dta	median surface of pia and tb	lateroventrally on posterior end of ata/ventral bridge	head capsule at ptp	laterally on posterior tentorium at height of tb	posterior end of ata	occiput, at dorso-lateral margin of occipital foramen	dorsolaterally on occiput	
M. praemento-salivariis anterior (0hy7A)	ventral wall of salivarium	broadly on proximal part of prementum	broadly on proximal part of prementum	broadly on proximal part of prementum	broadly on proximal part of prementum	broadly on proximal part of prementum	proximal part of prementum	absent	absent	insertion area on salivaria wall sclerotized in <i>Ibalia</i>
M. praemento-salivariis anterior (sclerite; 0hy7B)	hypopharyngeal button	tiny bundle, proximal surface of prementum	proximal surface of prementum	proximal surface of prementum	merged with 0hy7A	proximal surface of prementum	merged with 0hy7A	absent	absent	
M. hypopharyngo-salivariis (0hy12A)	dorsolateral surface of salivarium	small process of hypopharyngeal rod	hypopharyngeal rod, median and anterior of 0hy12B	hypopharyngeal lobe (hypopharyngeal rod could not be identified)	hypopharyngeal rod, postero-median of 0hy12B	hypopharyngeal rod, median of 0hy12B	hypopharyngeal rod	spatulate process of prementum	spatulate process of prementum	
M. hypopharyngo-salivariis (sclerite; 0hy12B)	hypopharyngeal button	absent	spatulate process of prementum	spatulate process of prementum	hypopharyngeal rod	hypopharyngeal rod and spatulate process of prementum	absent	spatulate process of prementum	absent	
M. tentiopræmentalis (0la5)	median proximal margin of prementum	posterior end of ata	posterior end of ata, at height of origin of dta	posterior end of ata, at height of origin of dta	posteriorly on the ata, just posterior to origin of dta	posterior end of ata	median extension of ata, medial of 0mx3	thin bundle at ptp and cranium near 0hy3, second thicker bundle at ata and frons	posterior median extension of ata	bipartite in <i>Pison</i>
M. praementoparaglossalis (0la11)	posterior glossal plate	at mid-length of prementum	anteriorly on prementum	at mid-length of prementum, distal of 0la12	anteriorly on prementum	at mid-length of prementum, lateral of 0la12	at mid-length of prementum, distal of 0la12	posteriorly on prementum	on posterior wall of prementum	

Table 2 continued.

Name of muscle	Insertion	<i>Ibalia</i>	<i>Orthogonalyis</i>	<i>Evaniella</i>	<i>Gasteruption</i>	<i>Pristaulacus</i>	<i>Doryctes</i>	<i>Pison</i>	<i>Sapyga</i>	Remarks
M. praementoglossalis (0la12)	anterior glossal plate	at mid-length of prementum, proximal of 0la11	at mid-length of prementum	at mid-length of prementum, proximal of 0la11	at mid-length of prementum	at mid-length of prementum, median of 0la11	posteriorly on prementum	on posterior wall of prementum, dorsal of 0la11	on posterior wall of prementum, dorsal of 0la11	
M. praementopalpalis externus (0la14)	lateral basal margin of labial palp	absent	lateral wall of prementum	ventral wall of prementum at mid-length, one bundle laterally, another more medially	lateral wall of prementum	lateral wall of prementum	dorsal wall of prementum at mid-length	basally on ventral wall of prementum	anteriorly on ventral wall of prementum	
M. fronto-epipharyngalis (0lb2)	labral tormae	absent	absent	absent	absent	medial of antennae	absent	frons, dorsomedial of antennae, anterior to 0hy1	absent	
M. clypeopalatalis (0ci1)	roof of cibarium	absent	absent	absent	few bundles, median on clypeus ventral of 0bu1	few bundles, median on clypeus ventral of 0bu1	thin bundle, clypeus, ventral of 0bu1	median on clypeus ventral and medial of 0bu1	thin bundle, median on clypeus, dorsal of 0bu1	
M. clypeobuccalis (0bu1)	bucca, ventrally to the frontal ganglion, on buccal lobe or epipharyngeal wall dorsal of it – see comments for each species	proximally on clypeus, just below epistomal sulcus; inserting on buccal lobe	clypeus, just below epistomal sulcus until mid-length; inserting on buccal lobe	one bundle proximally on clypeus, another distally; one bundle inserting on buccal lobe, the other dorsally of it	clypeus, just below epistomal sulcus; inserting dorsal of buccal lobe	clypeus, at mid-length; inserting dorsal of buccal lobe	proximally on clypeus; inserting on epipharyngeal wall	clypeus, just below epistomal sulcus dorsal and lateral of 0ci1; intersecting with 0ci1; inserting on buccal lobe and (bigger part) dorsally of it	distally on clypeus; inserting on buccal lobe	
M. frontobuccalis anterior (0bu2)	dorsal buccal wall, posterior to frontal ganglion	frons, dorsally of antennal heart, ventral of the antennal foramina	frons, between antennal foramina	mid-line of frons, ventromedial of antennal foramina	mid-line of frons, ventromedial of antennal foramina	frons between antennal foramina	frons, ventromedial of antennal foramina	frons, dorsomedial of antennal foramina	frons, medial of antennae	
M. frontobuccalis posterior (0bu3)	dorsal buccal wall	tiny bundle, posterior to 0hy1	mid-line of frons, dorsal of antennal foramina	frons, just posterior to 0hy1, dorsal of antennal foramina	absent	frons, at level of antennal foramina	frons, medial of 0hy1	frons, about halfway between antennal foramina and ocelli	frons, medial of antennae	
M. tentoriobuccalis anterior (0bu5)	sitophore plate	with a long tendon on median process of tb	with a long tendon on median process of tb	with a long tendon on median process of tb	with a long tendon on median process of tb	with a long tendon on median process of tb	with a long tendon on median process of tb	with a long tendon on median process of tb	with a long tendon on median process of tb	antagonist of 0bu2
M. tentoriobuccalis posterior (0bu6)	ventral wall of bucca, anterior to or at level with supraesophagealganglion	median process of tb, inserting far anteriorly	absent	thin muscle, ventrally on tb	absent	absent	absent	tb; insertion far posteriorly, directly adjacent to 0ph2	insertion far posteriorly, directly adjacent to 0ph2	antagonist of 0bu3
M. verticopharyngalis (0ph1)	dorsal wall of posterior pharynx	just posterior to lateral ocellus	just posterior to lateral ocellus	just posterior to lateral ocellus	just posterior to lateral ocellus	just posterior to lateral ocellus	on occipital foramen	latero-posteriorly of the lateral ocellus	just posterior to lateral ocellus	
M. tentoriopharyngalis (0ph2)	ventral wall of posterior pharynx	absent, or adjacent to 0bu6?	tb, lateral to median process	tb and median process of tb	tb and median process of tb	laterally on tb	absent	median process of tb	absent	antagonist of 0ph1
M. pharyngo-epipharyngealis	proximal epipharyngeal wall	weakly developed, ventromedial of insertion of 0bu3	dorsal pharyngeal wall, dorsal of insertion of 0bu3	dorsal pharyngeal wall, near distal end of sitophore plate and insertion of 0bu3	dorsal pharyngeal wall, near distal end of sitophore plate and insertion of 0bu3	dorsal pharyngeal wall, just below distal end of sitophore plate	weakly developed, near insertion of 0bu3	dorsal pharyngeal wall, near insertion of 0bu3	dorsal pharyngeal wall, near insertion of 0bu3	

(0bu3) is absent in *Gasteruption*. In the species where *M. tentoriobuccalis* posterior is present (*Ibalia*, *Evaniella*, *Pison*), only in *Ibalia* it does insert at the same level as its supposed antagonist *M. frontobuccalis* posterior which, however, is reduced to a tiny bundle. In *Pison* and *Evaniella* *M. frontobuccalis* posterior is well-developed and *M. tentoriobuccalis* posterior inserts clearly further posteriorly than its antagonist, posterior to the supraoesophageal ganglion instead of anterior to it. Moreover, *M. tentoriobuccalis* posterior is reduced to a tiny bundle in *Evaniella*. *M. pharyngoepipharyngealis* is present in all studied Hymenoptera and developed most strongly in *Sapyga* and *Pison*.

4. Cladistic analysis

4.1. Annotated character list

1. **Dorsal tentorial arm extent: (0) reaches and connects with head capsule (Figs. 5A–C, 8C); (1) does not connect with head capsule (Fig. 5D).** — The dorsal tentorial arms are well developed, consistently hollow until their tip and firmly fused with the frons in all the studied non-aculeate Hymenoptera. Well-developed dorsal tentorial arms were observed in all previously studied non-aculeate Hymenoptera (e.g. MATSUDA 1957: *Filacus*; ALAM 1951: *Stenobraccon*; BEUTEL & VILHELMSSEN 2007: *Xyela*; VILHELMSSEN 2000: figs. 8–14: basal Hymenoptera) except *Orussus* (VILHELMSSEN 2000: fig. 15), which is lacking dorsal arms; however, in the fossil orussid †*Baltorussus*, the dorsal tentorial arms are fully developed (VILHELMSSEN & ZIMMERMANN 2014). In Aculeata the dorsal tentorial arms are consistently reduced to different degrees and never connect with the head capsule (e.g. PRENTICE 1998; PORTO et al. 2016).
2. **Dorsal tentorial arm origin: (0) on posterior half of anterior tentorial arm (Fig. 2A,B,F); (1) at mid-length or on anterior half of anterior tentorial arm (Fig. 2C,D).** — The dorsal tentorial arms originate around mid-length in *Doryctes* (see also KARLSSON & RONQUIST 2012: *Opius*, *Biosteres*) and *Pristaulacus*, on the anterior half of the anterior arms in *Gasteruption* (see also CROSSKEY 1951), and on the posterior half in the other studied species.
3. **Ventral tentorial bridge: (0) absent (Fig. 2A,B); (1) present (Fig. 2C–F).** — The tentoria of all studied evanioid and aculeate wasps have posteriorly fused anterior tentorial arms forming a secondary tentorial bridge; a secondary tentorial bridge is also documented for apoid wasps (PRENTICE 1998: secondary tentorial bridge in figs. 12–14) and bees (MICHENER 1944). In *Doryctes*, *Apis* (BERRY & IBBOTSON 2010) and *Vespula* (DUNCAN 1939) no discrete secondary tentorial bridge is present. However, in these species the subforaminal bridge is bent inwards, and it cannot be determined whether the bridge is primarily absent or fused with the subforaminal region as described by PRENTICE (1998) for several apoid taxa. Thus in these three taxa the character was scored with a question mark. There is no ventral connection between the anterior arms in *Orthogonalys* and *Ibalia*, Platygastriidae (MIKÓ et al. 2007) and Xyelidae (BEUTEL & VILHELMSSEN 2007).
4. **Origin of antennal muscles and anterior component of *M. tentoriostipitalis* (0mx4): (0) on dorsal and ventral side of the same part of the anterior tentorial arms; (1) displaced from each other.** — In Evanioidea, *Ibalia* and *Doryctes* and *Orthogonalys* a more or less developed median extension is present at mid-length on the anterior tentorial arms which serves as an apodeme for the antennal muscles on its dorsal surface and for *M. tentoriostipitalis* (if divided for its anterior component) and *M. tentoriocardinalis* on its ventral surface (Fig. 5A–C). In Aculeata, the tentorium appears twisted, with a ventrolateral extension anteriorly on the anterior tentorial arms, and a secondary tentorial bridge posteriorly (see DUNCAN 1939: figs. 10, 23; PRENTICE 1998: paroculoclypeal brace). This structural change is accompanied by a shift of the musculature that has already been noticed by MATSUDA (1957): the origins of the antennal muscles shift posterior to the secondary tentorial bridge, and *M. tentoriocardinalis* and the anterior component of *M. tentoriostipitalis* shift anterior to the lateral extension of the anterior arms (Fig. 5D) or even to the clypeal region as in *Vespula* (DUNCAN 1939). The shift of the muscle groups relative to each other has also been observed in the honeybee (YOUSSEF 1971) and in Scoliidae, Mutillidae and Tiphidae (OSTEN 1982). In *Sapyga* only the origin of *M. tentoriocardinalis* is shifted anteriorly while a well-developed simple *M. tentoriostipitalis* originates from the same area as the antennal muscles. However, *Sapyga* has highly modified mouthparts which might explain its aberrant configuration. The shift of the muscle origins was chosen as a character as it is very distinct while the accompanying structural changes are less clear.
5. **Origin of antennal muscles and *M. tentoriocardinalis* (0mx3): (0) on dorsal and ventral side of the same area or extension (Fig. 5A–C); (1) displaced from each other (Fig. 5D).** — For discussion see previous character.
6. **Posterior processes: (0) originating on the anterior tentorial arm (Fig. 1A); (1) originating externally, just inside posterior tentorial pit or on the cranial wall (Fig. 2E,F).** — In all studied species a more or less distinct tubular posterior process of the tentorium is present. It corresponds to the postocipital apodeme in VILHELMSSEN (1999). It originates on the inner surface of the anterior tentorial arms in *Ibalia* and Evanioidea, and just inside the posterior tentorial pit or even slightly outside the posterior tentorial pit on the cranial wall in Aculeata, *Orthogon-*

- alys*, *Doryctes* and *Macroxyela*. When they originate on the posterior tentorial pit or the cranial wall they can be recognized as additional external pits.
7. **Posterior processes: (0) separated from each other by at least the diameter of the internal tube (Fig. 2E,F); (1) in contact at posterior end (Figs. 1A,B, 2A,B); (2) in contact for at least 1/3 of their length.** — Even if embedded in another part of the head capsule or tentorium the posterior processes can clearly be recognized by their tubular structure. In all cases known to us the posterior processes converge towards their posterior ends, but the degree of convergence differs. In *Gasteruption* and *Pristaulacus* the posterior processes converge anteriorly and run parallel for the posterior third of their length. In *Ibalia*, *Doryctes*, *Orthogonalys* and *Evaniella* they converge along their whole length and are in contact only at their posterior ends. In basal Hymenoptera and in the studied Aculeata the posterior ends of the tubes are separated from each other by more than their own diameter.
 8. **Attachment site of ventral profurcopostoccipital muscles (0) inconspicuous (Fig. 3B,E); (1) developed as subforaminal cup (Figs. 3H,K, 4B,E,H).** — A subforaminal cup is developed in Evanioidea, *Pison*, *Sapyga* and *Apis* (BERRY & IBBOTSON 2010: fig. 2C–F: subforaminal cup) while the attachment site of the profurcopostoccipital muscle is inconspicuously developed in the other taxa studied.
 9. **Secondary tentorial bridge and posterior processes: (0) fused (Fig. 4C,F,I); (1) not fused (Fig. 3I,L).** — In the taxa with a secondary tentorial bridge, the posterior processes form the posterolateral margin of the bridge by being fused to it along their median margin in Evanioidea. In *Pison* and *Sapyga* the secondary tentorial bridge extends to the posterior tentorial arms and pits.
 10. **Dorsolateral corners of occipital foramen (0) inconspicuous; (1) distinctly extended forming lateral flanges (Figs. 1B, 4A,D: elf).** — The dorsolateral corners of the occipital foramen are distinctly extended in *Doryctes*, *Gasteruption* and *Pristaulacus*. A similar formation can be found in Torymidae (VILHELMSSEN 2011: fig. 6C; BURKS & HERATY 2015: fig. 5G–I) and Orussidae (VILHELMSSEN 1999: fig. 4), where it obviously developed convergently.
 11. **Cibarium: (0) bent posteriorly (Fig. 8A,D); (1) not bent (Fig. 8E).** — The cibarium is bent posteriorly between the distal end of the sitophore and the infrabuccal pouch, which corresponds to the area of the buccal lobe sensu BEUTEL & VILHELMSSEN (2007; Fig. 8A,D: bl), in *Orthogonalys*, *Pristaulacus*, *Gasteruption*, *Evania* (POPOVICI et al. 2014: fig. 10), *Evaniella*, *Pison*, *Sapyga*, *Myrmica* (Formicidae; JANET 1900: pl. 10–11), *Priscomasarina* (Vespidae; KRENN et al. 2002: Fig. 6) and *Vespula* (DUNCAN 1939). A slightly bent cibarium is also documented for *Orussus* (VILHELMSSEN 1996: fig. 13). The cibarium is straight distally of the sitophore in *Ibalia*, *Doryctes* and most basal Hymenoptera (VILHELMSSEN 1996).
 12. **M. tentoriomandibularis lateralis inferior (0md6): (0) present; (1) absent.** — Present in *Orthogonalys*, *Evaniella*, *Gasteruption*, *Pison* and *Sapyga*, and in *Apis* and *Vespula* (DUNCAN 1939; YOUSSEF 1971); absent in *Ibalia*, *Pristaulacus*, *Doryctes*, and *Macroxyela* (BEUTEL & VILHELMSSEN 2007), *Filacus* (MATSUDA 1957), Scoliidæ, Mutillidæ and Tiphidæ (OSTEN 1982).
 13. **M. tentoriomandibularis medialis inferior (0md8): (0) present (Fig. 8B: 0md8); (1) absent.** — Present in *Orthogonalys*, *Evaniella*, *Pison* and *Sapyga*, *Macroxyela* (BEUTEL & VILHELMSSEN 2007), *Apis* and *Vespula* (DUNCAN 1939; YOUSSEF 1971) absent in *Filacus* (MATSUDA 1957), Scoliidæ, Mutillidæ and Tiphidæ (OSTEN 1982).
 14. **M. praementosalivarialis anterior (0hy7A): (0) present (Fig. 8D); (1) absent.** — M. praementosalivarialis anterior is absent in *Pison*, *Sapyga*, *Apis* (YOUSSEF 1971) and *Vespula* (DUNCAN 1939). The M. dorsoprementsalivariis sensu YOUSSEF (1971) represents the dorsal salivary muscle which is M. hypopharyngosalivariis sensu WIPFLER et al. (2011).
 15. **M. praementosalivarialis anterior, component attaching to hypopharyngeal button (0hy7B): (0) present (Fig. 8D); (1) absent.** — This muscle which inserts on the hypopharyngeal button close to M. tentoriohypopharyngalis can be clearly distinguished from the salivary component of M. praementosalivarialis anterior in some species (*Evaniella*, *Filacus* [MATSUDA 1957: pl. 3B], *Pristaulacus*), and is confluent with the salivary component of M. praementosalivarialis anterior in others (*Doryctes*, *Gasteruption*, *Orthogonalys*). As the salivary component of M. praementosalivarialis anterior, it is absent in *Pison*, *Sapyga*, *Apis* (YOUSSEF 1971) and *Vespula* (DUNCAN 1939).
 16. **M. hypopharyngosalivariis, component attaching to hypopharyngeal button (0hy12B): (0) present (Fig. 8D); (1) absent.** — An additional dorsal salivary muscle inserting at the hypopharyngeal button is present in *Orthogonalys*, *Evanioidea*, *Pison*, as well as in *Filacus* (MATSUDA 1957: pl. 3B: M.41), *Apis* (YOUSSEF 1971: M. basiprementsalivariis) and *Vespula* (DUNCAN 1939: pmslv). Typically M. tentoriohypopharyngalis runs between M. hypopharyngosalivariis and M. hypopharyngosalivariis B.
 17. **M. craniolacinalis (0mx2): (0) present; (1) absent.** — A craniolacinal muscle is developed in *Orthogonalys* and *Macroxyela* (BEUTEL & VILHELMSSEN 2007) while it is absent in all other studied species.
 18. **Origin of M. tentoriostipitalis anterior (0mx4): (0) single origin midway or on anterior half of ata (Fig. 5A,B); (1) two separate origins distanced from each other by at least the width of one bundle; anterior component (0mx4a) midway or on anterior half of ata, posterior component (0mx4b) on posterior half of ata (Figs. 5C,D, 8D).** — M. tentoriostipitalis anterior has a bipartite origin in

- Orthogonalys*, *Evaniella*, *Sapyga* and *Pison*. In *Orthogonalys*, *Evaniella* and *Sapyga* the posterior component originates adjacent to *M. tentoriopremental*; in *Pison* *M. tentoriostipitalis* anterior is not directly adjacent to *M. tentoriopremental* which is bipartite in this species. In *Sapyga* the anterior component has shifted from the tentorium to the premental-clypeal sclerite (“Segelhalter” sensu OSTEN 1982) which is a structure correlated with the modification of the mouthparts to a proboscis in Sapygidae (OSTEN 1982). A bipartition of *M. tentoriostipitalis* anterior is also described for *Scolia* (OSTEN 1982), *Apis* (YOUSSEF 1971), and *Macroxyela* (BEUTEL & VILHELMSSEN 2007); in the latter four bundles with independent origin and common insertion are listed. A bipartition is absent in *Doryctes*, *Ibalia*, *Pristaulacus* and *Gasteruption*, as well as in *Filacus* (MATSUDA 1957) and *Vespula* (DUNCAN 1939).
19. **Insertion of posterior component of *M. tentoriostipitalis* anterior (0mx4b): (0) together with anterior component of *M. tentoriostipitalis* anterior (0mx4a) (Fig. 5C); (1) separate from anterior component of *M. tentoriostipitalis* anterior (0mx4a) (Fig. 5D).** — The two components of *M. tentoriostipitalis* anterior (0mx4) have independent insertions in *Pison* and *Apis* (YOUSSEF 1971).
 20. ***M. stipitopalpalis internus* (0mx10): (0) present; (1) absent.** — An inner stipitopalpal muscle is developed in *Orthogonalys*, *Evaniella*, *Filacus* (MATSUDA 1957), *Macroxyela* (BEUTEL & VILHELMSSEN 2007), *Apis* (YOUSSEF 1971) and *Vespula* (DUNCAN 1939). It is absent in *Ibalia*, *Doryctes*, *Pristaulacus*, *Gasteruption*, *Pison* and *Sapyga*.
 21. ***M. frontoepipharyngalis* (0lb2): (0) present; (1) absent.** — A frontoepipharyngeal muscle is present in *Pristaulacus*, *Pison*, as well as in *Macroxyela* (BEUTEL & VILHELMSSEN 2007), *Filacus* (MATSUDA 1957) and *Apis* (YOUSSEF 1971). It is absent in *Ibalia*, *Doryctes*, *Orthogonalys*, *Evaniella*, *Gasteruption* and *Sapyga*.
 22. ***M. clypeopalatalis* (0ci1): (0) present (Fig. 8A,E); (1) absent.** — A clypeopalatal muscle is present in *Doryctes*, *Pristaulacus*, *Gasteruption* as well as in the investigated aculeate taxa and *Macroxyela* (BEUTEL & VILHELMSSEN 2007); it is absent in *Ibalia*, *Orthogonalys* and *Evaniella*.
 23. ***M. tentoriobuccalis posterior* (0bu6): (0) present; (1) absent.** — Present in *Ibalia*, *Evaniella*, *Pison*, *Sapyga*, as well as in *Filacus* (MATSUDA 1957), *Apis* (YOUSSEF 1971) and *Vespula* (DUNCAN 1939); absent in *Macroxyela* (BEUTEL & VILHELMSSEN 2007), *Doryctes*, *Orthogonalys*, *Pristaulacus* and *Gasteruption*.
 24. **Hypopharyngeal gland: (0) absent; (1) present (Figs. 6D, 7A).** — Present in *Pison*, *Sapyga*, *Vespula* (LANDOLT & AKRE 1979), *Apis* and in other aculeate wasps (CRUZ-LANDIM & COSTA 1998); absent in the other studied Hymenoptera as well as in *Macroxyela* (BEUTEL & VILHELMSSEN 2007).
 25. **Hypopharyngeal salivary gland: (0) absent; (1) present (Figs. 6D, 7B).** — Present in *Pison* and *Sapyga*; absent in the other studied Hymenoptera as well as in *Vespula* (LANDOLT & AKRE 1979), *Apis* (KRATKY 1931) and *Macroxyela* (BEUTEL & VILHELMSSEN 2007).
 26. **Glossal gland: (0) absent; (1) present (Figs. 6B,C, 7G).** — Present in *Gasteruption*, *Evaniella*, *Orthogonalys* and *Doryctes*, as well as in *Vespula* (LANDOLT & AKRE 1979: sublingual gland); absent in *Pison*, *Ibalia*, *Pristaulacus*, as well as in *Macroxyela* (BEUTEL & VILHELMSSEN 2007) and *Apis* (KRATKY 1931).
 27. **Galeal gland: (0) absent; (1) present (Fig. 7H).** — Present in *Gasteruption* and *Orthogonalys*; absent in the other studied Hymenoptera, as well as in *Macroxyela* (BEUTEL & VILHELMSSEN 2007), *Vespula* (LANDOLT & AKRE 1979) and *Apis* (KRATKY 1931).
 28. **Notch on the inner margin of the eye: (0) absent; (1) present.** — Present in *Pison*, *Sapyga*, *Vespula*, absent in all others. From VILHELMSSEN (2011).
 29. **Distance from antennal foramen to clypeus: (0) equal to or less than foramen diameter; (1) more than foramen diameter.** — The antennal foramina are further from clypeus than their own diameter in *Ibalia*, *Doryctes*, *Evaniella* and *Gasteruption*. From VILHELMSSEN (2011).
 30. **Ventral sclerotisation between occipital and oral foramina: (0) absent; (1) present.** — A sclerotisation between occipital and oral foramina is absent in *Macroxyela* and *Filacus*. From VILHELMSSEN (2011).
 31. **Longitudinal sulci on ventral head sclerotisation (ordered): (0) none; (1) one median sulcus or hair line present, at least ventrally; (2) two sublateral sulci present, not merging ventrally.** — One medial sulcus is developed in *Evaniella*, *Gasteruption*, *Pison*, *Sapyga*, *Vespula*, while two sublateral sulci are present in *Ibalia*, *Doryctes*, *Orthogonalys* and *Apis*. The character status of *Pristaulacus* was changed from 2 to 1 based on the current data, as the sulci merge ventrally. The character is inapplicable for taxa lacking a subforaminal bridge. From VILHELMSSEN (2011).
 32. **Occipital carina: (0) absent; (1) present.** — The occipital carina is absent in *Macroxyela* and *Sapyga*. From VILHELMSSEN (2011).
 33. **Occipital carina configuration: (0) reaching ventral margin of head capsule; (1) not reaching ventral margin and not continuous medially; (2) continuous ventrally of occipital foramen.** — The occipital carina is continuous ventrally of the occipital foramen in *Gasteruption*, and is reaches the ventral margin of the head capsule in *Ibalia*, *Evaniella* and *Vespula*. From VILHELMSSEN (2011).

For character state matrix see Table 3.

4.2. Results of cladistic analyses

The tree topology of SHARKEY et al. (2012) is most compatible with our dataset and results in a tree length of

Table 3. Character state matrix.

taxon/character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
<i>Macroxylela</i>	0	0	0	0	0	1	0	0	–	1	0	0	1	1	?	?	1	1	0	1	1	0	0	0	0	0	0	0	0	0	–	0	–
<i>Filacus</i>	0	0	0	0	0	?	0	0	–	0	0	0	0	1	1	1	0	0	–	1	1	1	1	?	?	?	?	0	0	0	–	?	?
<i>Ibalia</i>	0	0	0	0	0	0	1	0	–	0	0	0	0	1	1	0	0	0	–	0	0	0	1	0	0	0	0	0	1	1	2	1	0
<i>Doryctes</i>	0	1	?	0	0	1	1	0	–	1	0	0	0	1	1	0	0	0	–	0	0	1	0	0	0	1	0	0	1	1	2	1	1
<i>Orthogonalys</i>	0	0	0	0	0	1	1	0	–	0	1	1	1	1	1	1	1	1	0	1	0	0	0	0	0	1	1	0	0	1	2	1	1
<i>Evaniella</i>	0	0	1	0	0	0	1	1	1	0	1	1	1	1	1	1	0	1	0	1	0	0	1	0	0	1	0	0	1	1	1	1	0
<i>Pristaulacus</i>	0	1	1	0	0	0	2	1	1	1	1	0	0	1	1	1	0	0	–	0	1	1	0	0	0	0	0	0	0	1	1	1	1
<i>Gasteruption</i>	0	1	1	0	0	0	2	1	1	1	1	0	1	1	1	1	0	0	–	0	0	1	0	0	0	1	1	0	1	1	1	1	2
<i>Pison</i>	1	0	1	1	1	1	0	1	0	0	1	1	1	0	0	1	0	1	1	0	1	1	1	1	1	0	0	1	0	1	1	1	1
<i>Sapyga</i>	1	0	1	0	1	1	0	1	0	0	1	1	1	0	0	0	0	1	0	0	0	1	1	1	1	?	0	1	0	1	1	0	–
<i>Apis</i>	1	0	?	1	1	1	0	1	–	0	?	0	1	0	0	1	0	1	1	1	1	1	1	1	0	0	0	0	0	1	2	0	–
<i>Vespula</i>	1	0	?	1	1	1	0	0	–	0	1	0	1	0	0	1	0	0	–	1	0	1	1	1	0	1	0	1	0	1	1	1	0

75 steps (CI 0.46; RI 0.55; Fig. 9C). The sister group relationship of Aculeata and Evanioidea is supported by three non-homoplasious synapomorphies: the presence of a secondary tentorial bridge (char. 3), the presence of subforaminal cup (char. 8) and the presence of one medial sulcus instead of two sublateral ones (char. 31). Mapping the characters on the topology from KLOPFSTEIN et al. (2013) increases tree length to 78 steps (CI 0.44; RI 0.52; Fig. 9B). No synapomorphy supporting Trigonaloidea + Aculeata is retrieved.

Mapping the head anatomical characters on the topology of RASNITSYN (1988) increases tree length to 84 steps (CI 0.41; RI 0.45; Fig. 9A). No synapomorphy supporting Ichneumonoidea + Aculeata is retrieved. The bent cibarium (char. 11) supports the monophyly of Trigonaloidea, Evanioidea and Aculeata, a clade present in both SHARKEY et al. (2012) and KLOPFSTEIN et al. (2013).

5. Discussion

5.1. Morphology

5.1.1. Dorsal tentorial arms. It is highly likely that the dorsal tentorial arms were well developed in the hymenopter ground pattern. The firm connection with the head capsule in non-aculeate Hymenoptera is conspicuous and might be an autapomorphy of the order. The nature of the connection between the dorsal arms and the head capsule is described only for few insect orders: In Neuroptera and Coleoptera the dorsal arms are connected with the head capsule by fibrillae (BEUTEL et al. 2008; ZIMMERMANN et al. 2011). In Dictyoptera the dorsal arms are reported to be attached to the head capsule but their ends are detached after maceration (KLASS & EULITZ 2007). The firm connection in Hymenoptera is even more remarkable as the dorsal arms serve only to a minor degree for muscle attachment (i.e., for an antennal muscle, or part of one).

In contrast to other Hymenoptera, the dorsal tentorial arms are generally weakly developed in Aculeata (present study; DUNCAN 1939; ERICKSON & SHENG 1984; PRENTICE 1998). However, they are consistently present, even if their function is unclear. PRENTICE (1998) rules out that the dorsal arms might counter compression of the head capsule but suggests they may brace the frons from bending outwards when the mandibular adductors contract. ERICKSON & SHENG (1984) found the tips of the dorsal tentorial arms of the honeybee to be highly modified, porous and sandwiched between the ocular lobe and the antennal nerve, and suggest they might have a sensory function. However, we did not observe a similar configuration in the dorsal arms of *Pison* and *Sapyga*.

In non-aculeates a reduction of the dorsal tentorial arms is inferred within Orussidae, where in the extinct genus †*Baltorussus* well developed dorsal arms are present (VILHELMSEN & ZIMMERMANN 2014), whereas in the extant genus *Orussus* they are reduced (VILHELMSEN 2000).

5.1.2. Secondary tentorial bridge and tentorial lamellae.

All evanioid and aculeate wasps that were examined have a secondary tentorial bridge. It corresponds with posteriorly fused ventral lamellae sensu the HYMENOPTERA ANATOMY CONSORTIUM (2015) and a discrete secondary tentorial bridge sensu PRENTICE (1998). Hitherto a discrete secondary tentorial bridge has been only known from apoid wasps and bees (MICHENER 1944; PRENTICE 1998). PRENTICE (1998) differentiates a discrete shelf-like secondary tentorial bridge from one that is smoothly continuous with the subforaminal bridge, and assumes the latter to be the plesiomorphic condition in apoid wasps. The presence of a secondary tentorial bridge in the three evanioid families and in Sapygidae is highly interesting in the context of the present study as it is a likely synapomorphy of Evanioidea and Aculeata. Further investigations in Ichneumonoidea are desirable as the situation in *Doryctes* and *Stenobracon* (ALAM 1951) indicates that a secondary tentorial bridge might also be present in the ichneumonoid ground pattern.

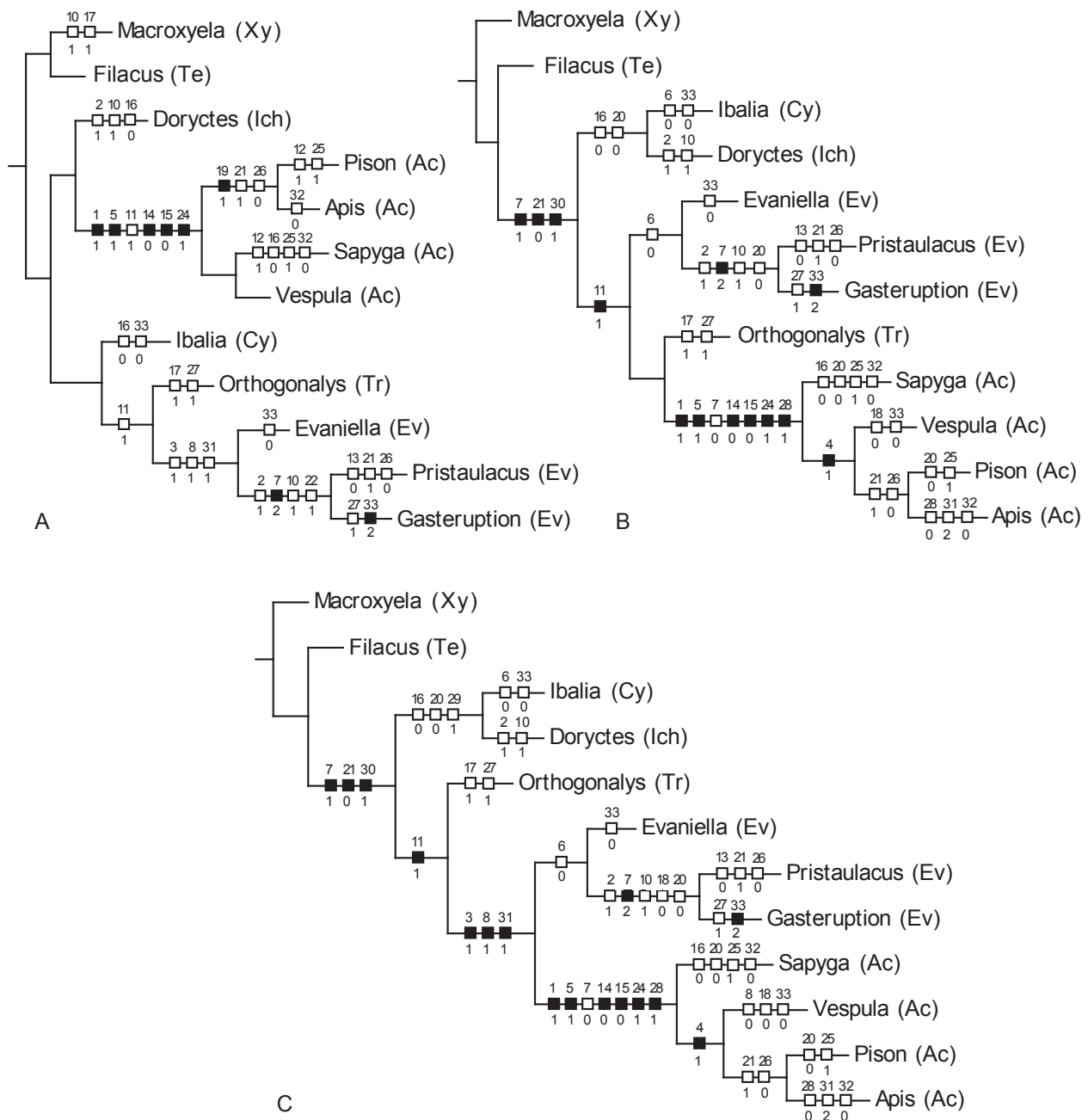


Fig. 9. Characters described in the present study (4.1) mapped on the phylogenetic hypotheses from **A:** RASNITSYN (1988; 84 steps), **B:** KLOPFSTEIN et al. (2013; 78 steps) and **C:** SHARKEY et al. (2012; 75 steps). Black boxes indicate non-homoplasious synapomorphies, white boxes homoplasious ones. Only unambiguous changes are mapped on the tree. — **Abbreviations:** Ac – Aculeata, Cy – Cynipoidea, Ev – Evanioidae, Ich – Ichneumonoidea, Te – Tenthredinoidea, Tr – Trigonoidea, Xy – Xyeloidea.

In contrast to the secondary tentorial bridge, the tentorial lamellae appear to have limited value in resolving higher level relationships as also noticed by PRENTICE (1998) for apoid wasps. The backwards shift of the antennal muscles relative to the tentoriostipital and tentoriocardinal muscles in Aculeata (chars. 4 and 5) seems to be accompanied by a structural change of the tentorium which is, however, much less distinctly developed than the muscular shift. The usage of the antennae and the maxilla in the respective taxa influences the size of the correlated muscles and thus also the shape and size of the lamellae on which they attach.

5.1.3. Posterior processes and subforaminal cup. Tubular posterior processes of the tentorium are present in all studied species and are described for many other Hymenoptera in detailed treatments of the tentorium or the postoccipital region: They are documented for vespids as posterior tentorial roots (DUNCAN 1939), for the honeybee as ventral cervical bars (ERICKSON & SHENG 1984) and for basal Hymenoptera as postoccipital apodemes (VILHELMSSEN 1999: poa). When they originate on the posterior tentorial arms or the postocciput they are recognizable as additional pits besides the posterior tentorial pits as described by ERICKSON & SHENG (1984: vt in fig. 2D)

for the honeybee and BURKS & HERATY (2015) for Ichneumonidae, *Megischus* (Stephanidae) and *Ceraphron* (Ceraphronidae). However, it may require methods such as histological sections or microCT to identify them by their internal tube if they are merged with surrounding structures as it is the case in Evaniidae. The posterior processes are integrated with the subforaminal cup to different degrees in Aculeata and Evaniidae. Specifically, they end in and constitute a small part of the subforaminal cup in Aculeata (the rest seems to be formed by the ventral collar-like prolongation of the postocciput) while they form the entire subforaminal cup in Evaniidae.

The attachment site of the ventral profurcatopostoccipital muscle (*M. profurcatentorialis* sensu VON KÉLER 1963; *M. profurca-tentorialis* sensu FRIEDRICH & BEUTEL 2008), which is the depressor of the head, is consistently located on the external surface of the head capsule in Hymenoptera. In most other holometabolous insects the depressor of the head inserts on the tentorium (FRIEDRICH & BEUTEL 2010: char. 75). The external attachment site in Hymenoptera might be correlated with the comparatively narrow occipital foramen in Hymenoptera that might not permit the muscle to insert inside the head capsule.

5.1.4. Glands. Most of the glands observed are simple glands consisting only of glandular units which yield the secretion directly to the surface through pores. Only the mandibular, the hypopharyngeal and the hypopharyngeal salivary gland are more complex gland organs with a common excretory duct.

The hypopharyngeal gland is most likely a synapomorphy of aculeate wasps. It is present in *Pison* and *Sapyga* representing the families Crabronidae and Sapygidae, and has previously been reported for Apidae (CRUZ-LANDIM 1967; CRUZ-LANDIM & COSTA 1998; GALVANI & SETTEMBRINI 2013), other Sphecidae (SAENZ & CRUZ-LANDIM 1972), Formicidae (GAMA & CRUZ-LANDIM 1982) and Vespidae (e.g. LANDOLT & AKRE 1979; PENAGOS-AREVALO et al. 2015). It is noteworthy that the hypopharyngeal cell group of the hypopharyngeal-maxillary gland in *Evanioidea* is located in the same region as the hypopharyngeal gland. However, as the ducts do not open into the hypopharyngeal wall but lead into the maxillary region we do not consider it to be a homologous structure.

The hypopharyngeal salivary gland is only found in *Pison* and *Sapyga*. A cephalic salivary gland is also described for Apidae (CRUZ-LANDIM 1967; POIANI & CRUZ-LANDIM 2010b). However, the gland in Apidae is a paired structure that opens into the salivary duct posterior to the labium and just anterior to the point where the paired salivary ducts merge to a single one (CRUZ-LANDIM 1967). This is different to the hypopharyngeal salivary gland which is unpaired and opens into the salivarium anterior of the insertion of the salivary muscles. Thus we do not consider these two glands to be homologous which implies that the hypopharyngeal salivary gland is a new, hitherto undescribed gland. It is puzzling that the hypopharyngeal salivary gland is found in *Pison* and *Sapyga* which are representatives of two only distantly

related families, the Crabronidae and the Sapygidae (e.g. DEBEVEC et al. 2012), while no such gland was found in other aculeate families (Apidae: CRUZ-LANDIM 1967; Vespidae: LANDOLT & AKRE 1979, PENAGOS-AREVALO et al. 2015; Formicidae: NICULITA et al. 2007). Possibly the fact that most of the previously studied taxa are eusocial species plays a role in this unexpected distribution, as they have different needs and life histories than solitary species. However, this is highly speculative and it would be worthwhile to screen a broader variety of aculeate taxa for the presence of this gland.

The mandibular gland is one of the most widespread exocrine glands among insects (BOONEN et al. 2013). In the taxa studied they are variable in their morphology, especially with respect to the amount and arrangement of the secretory cells around the reservoir. Changes in gland activity and correlated changes of the size and the shape of the secretory cells, the nuclei and the gland reservoir during the lifetime of an insect have been observed in ants (BOONEN et al. 2013: *Monomorium pharaonis*, mandibular gland), social bees (POIANI & CRUZ-LANDIM 2010a,b: *Apis mellifera* and *Scaptotrigona postica*, cephalic salivary gland) and polistine wasps (BRITTO & CAETANO 2006: *Polistes versicolor*, hypopharyngeal gland). Though all these treatments again cover only social species where different tasks of the workers can require different gland products in the course of the insect's life, it is possible that changes in the activity and histology of glands also occur in solitary species. CRUZ-LANDIM (1967) showed that the position and the differentiation of glands can vary between bees clades and thus be of phylogenetic importance. Among the studied taxa the mandibular gland fundamentally differs in structure in *Sapyga* where it is bifid with a second lobe in the postgenal region. This is not informative to answer the question of the sister group of aculeates, but might constitute a phylogenetically relevant character within Sapygidae.

5.1.5. Musculature. The absence of ventral salivary dilators is likely a synapomorphy of aculeates. The labial muscles originating on the prementum in *Lasius niger* (JANET 1905), as well as the anterior and the posterior flexor of the ligula in *Vespa* (DUNCAN 1939) represent the prementoglossal and the prementoparaglossal muscle. The dorsoprementosalivary and the basiprementosalivary muscle listed by YOUSSEF (1971) for *Apis* are understood as the two components of *M. hypopharyngosalivaris*; they are listed as “prementosalivary muscles” because in *Apis* the dorsal salivary muscles do not originate on the hypopharynx but on the spatulate process of the prementum as in many other Hymenoptera. Besides aculeates the ventral salivary muscles are also absent in *Cephalcia* (Pamphilidae) and *Sirex* (Siricidae; VILHELMSEN 1996), a loss that certainly occurred independently.

The presence of an additional dorsal salivary muscle inserting on the hypopharyngeal button in *Orthogonalys*, Evaniidae and the aculeates might represent a synapomorphy of this clade. The absence of this muscle in *Sapyga* is most likely correlated with its highly modified

mouthparts. However, this muscle is also illustrated and described for the tenthredinid *Filacus* (MATSUDA 1957). As it is not described for any other basal hymenopteran (VILHELSEN 1996) or for Platygastriidae (POPOVICI et al. 2014), we assume an independent development in Tenthredinidae. However, the investigation of a broader taxon sample in this context would be interesting. The division of the muscle into two subcomponents is easily recognizable as the tentoriohypopharyngeal muscle characteristically runs between the two components of the dorsal salivarial muscle. A corresponding second component of the ventral salivarial musculature inserting on the hypopharyngeal button is present in all studied species except in the aculeates where the ventral salivarial muscles are missing as mentioned above. In *Sparasion* it can also be noticed that the ventral salivarial muscle has an insertion reaching from a broad region on the salivarium to the hypopharyngeal button (POPOVICI et al. 2014: fig. 4A,B “pmnv-slv”).

The bipartition of the M. tentoriopremental in *Pison* into an anterior part originating near the anterior tentorial pit and a posterior part originating near the posterior tentorial pit is unusual. A bipartition of this muscle is not described for any other hymenopteran (DUNCAN 1939: posterior labial adductor muscles; MATSUDA 1957: M.36; YOUSSEF 1971: M. tentoriopremental; VILHELSEN 1996: ventral premental adductors), not even for other sphecoid wasps (PRENTICE 1998: protractor of labium). For *Stenobracon* a third extrinsic muscle of the labium is described (ALAM 1951: levator of the labium). It arises on the ventral surface of the anterior tentorial arm and attaches at the middle of the spatial process of the prementum. It has, however, a different insertion point than the M. tentoriopremental while in *Pison* it is clearly a second component of this muscle with exactly the same insertion. PRENTICE (1998) suggests that the muscle in *Stenobracon* represents a displaced postmental-premental muscle which might be also considered for the second component in *Pison*, although this seems highly unlikely given that in Hymenoptera this muscle has otherwise been found only in the tenthredinid *Filacus* (MATSUDA 1957: M.38).

5.2. Phylogeny

As beautifully explicated by GIBSON (1993), morphology and systematics are inextricably interrelated in a cyclical feedback system of studies and discoveries. New phylogenetic hypotheses on the sister group of aculeates have stimulated the present investigation, which in turn yields new morphological insights. The presence of a secondary tentorial bridge and a subforaminal cup in Evanioidea and Aculeata, and a bent cibarium in Trigonalidae, Evanioidea and Aculeata add morphological evidence to the molecularly supported hypothesis of a sister group relationship of Trigonalidae + (Aculeata + Evanioidea) presented by SHARKEY et al. (2012). Though the presence of an additional dorsal salivarial muscle is optimized as a hymenopteran ground pattern trait when mapped on the

phylogenetic tree, the absence of this muscle in other hymenopteran clades (see 5.1.5.) suggests that it evolved independently in Tenthredinidae and Trigonalidae + (Aculeata + Evanioidea) and thus additionally supports the latter clade. In addition, the presence of a hypopharyngeal gland, the backwards shift of the origin of the antennal muscles, the loss of the connection of the dorsal tentorial arms with the head capsule and the loss of ventral salivarial dilators were found to be synapomorphies of the aculeates, and the independent insertion of the two components of the tentoriostipital muscle in *Pison* and *Apis* a putative synapomorphy of Apoidea.

Studies using microCT and histological sectioning are distinctly more costly and time-consuming than studies of the external morphology or skeletal features only, but they can be crucial to scrutinize supposed homologies as well as reveal new ones. An example of the latter are the posterior processes of the tentorium: Since a tubular extension of the tentorium is described from various hymenopteran families and no other insect orders are known to have this structure we assume it to be an autapomorphy of the order. Based on this hypothesis structures such as the postoccipital bridge sensu VILHELSEN (1999) and (at least one pair of the) additional tentorial pits in Ichneumonoidea described and analyzed by BURKS & HERATY (2015) can be easier understood in context.

Though our present study is based on a small taxon sampling and the homology hypotheses discussed remain to be tested in a broader scale, we hope that they will be integrated in the next generation of phylogenetic analyses, helping to refine our picture of the evolution of Hymenoptera.

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Electronic Supplement Files

at <http://www.senckenberg.de/arthropod-systematics> (“Contents”)

File 1: zimmermann&vilhelmsen-aculeatasistergroup-asp2016-electronicsupplement-1.winc. – Character state matrix.

File 2: zimmermann&vilhelmsen-aculeatasistergroup-asp2016-electronicsupplement-2.xls. – List of used terms with definitions and references, extracted from the Hymenoptera Anatomy Ontology (SELTMAN et al. 2016).

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