

Head anatomy of adult *Nevrorthus apatelios* and basal splitting events in Neuroptera (Neuroptera: Nevorthidae)

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Abstract

External and internal features of the head of adult *Nevrorthus apatelios* are described in detail. The results are compared with data from literature. The mouthpart muscle M. stipitalis transversalis and a hypopharyngeal transverse ligament are newly described for Neuroptera and herewith reported for the first time in Endopterygota. A submental gland with multiporous opening is described for Nevorthidae and Osmylidae and is apparently unique among insects. The parsimony analysis indicates that Sisyridae is the sister group to all remaining Neuroptera. This placement is supported by the development of 1) a transverse division of the galea in two parts in all Neuroptera excluding Sisyridae, 2) the above mentioned submental gland in Nevorthidae and Osmylidae, and 3) a poison system in all neuropteran larvae except Sisyridae. Implications for the phylogenetic relationships from the interpretation of larval character evolution, specifically the poison system, cryptonephry and formation of the head capsule are discussed.

Key words

Head anatomy, cladistic analysis, phylogeny, M. stipitalis transversalis (0mx11), submental gland, Partitioned Bremer Support, cryptonephry.

1. Introduction

The family Nevorthidae is an engrossing neuropteran lineage which presently contains 17 described species in four genera: *Nevrorthus* Costa, 1863, *Nipponeurorthus* Nakahara, 1958, *Austroneurorthus* Nakahara, 1958 and *Sinoneurorthus* Liu et al., 2012. Their distribution is highly disjunct, restricted to the Mediterranean region, the Japanese Islands, the Eastern parts of Australia and, only recently discovered, the mainland of Eastern Asia (ASPÖCK & ASPÖCK 2007; LIU et al. 2012; MONSERRAT & GAVIRA 2014).

In contrast to most other neuropteran families, the Nevorthidae have aquatic larvae, and they even pupate in an aquatic environment (MALICKY 1984). They live in

rivulets between stones and capture their prey with sucking tubes which are a peculiarity of neuropteran larvae. The adults are often found under overhanging twigs and leaves of the vegetation along such waters (ASPÖCK & ASPÖCK 2010).

According to ASPÖCK (1992, 1993, 1995, 2002), Neuroptera are divided into three suborders: Myrmeleontiiformia, Hemerobiiformia and Nevorthiiformia; the latter containing the single family Nevorthidae. In the last years Nevorthidae was retrieved as the sister group to all other Neuroptera in several phylogenetic analyses: a holomorphological analysis by ASPÖCK et al. (2001), a molecular analysis by HARING & ASPÖCK (2004) and

analyses based on larval characters (BEUTEL et al. 2010a) and larval + adult head anatomical characters (BEUTEL et al. 2010b). In these analyses the position of Sisyridae varied; it was either deeply nested within Hemerobiiformia (ASPÖCK et al. 2001; BEUTEL et al. 2010a,b) or was the second offshoot at the base of Neuroptera (HARING & ASPÖCK 2004). An alternative hypothesis is a sister group relationship between Sisyridae and all other Neuroptera. This was retrieved in two related analyses of larval and adult head characters (ZIMMERMANN et al. 2011; RANDOLF et al. 2013). Moreover, a sister group relationship of Nevrothidae and Sisyridae has been proposed recently by WINTERTON et al. (2010), which agrees with NAKAHARA's (1958) classification of Nevrothidae as the subfamily Neurorhinae within the family Sisyridae. Nineteen years later, in a study on the larvae of *Nevrorthus fallax*, the *Nevrorthus* lineage was raised to family level (ZWICK 1967).

The late recognition of the significance of the Nevrothidae is certainly one of the reasons why they are seldom studied. Since the taxon was not considered a separate family at that time, it was neither represented in MACLEOD's (1964) comprehensive treatise of the neuropteran larval head, nor in the only comprehensive study of the neuropteran head capsule by SHEPARD (1967). Meanwhile the larval head of *Nevrorthus* has been studied and analyzed by BEUTEL et al. (2010a).

By investigating the head anatomy of adult *Nevrorthus apatelios* Aspöck et al., 1977 (Fig. 1), we aim to shed light on the basal splitting events and early character evolution in Neuroptera. We explore whether the hypothesized position of Sisyridae as the sister group to the other neuropteran families can be retained when the data for Nevrothidae are added to a previously published matrix (RANDOLF et al. 2013) and whether new synapomorphies of either Neuroptera excluding Sisyridae or Neuroptera excluding Nevrothidae can be retrieved by adding new data. Finally, major implications of the phylogenetic results on the interpretation of the evolution of larval characters are discussed.



Fig. 1. *Nevrorthus apatelios*, habitus, length of forewing ca. 7 mm; photo: Dominique Zimmermann.

Osmylidae: *Osmylus fulvicephalus* (Scopoli, 1763) sex unknown: microCT stack from BEUTEL et al. 2010b, male; REM.

Polystoechotidae: *Polystoechotes punctata* (Fabricius, 1793): male: microCT, histological sections (2 µm).

2. Material and methods

2.1. List of taxa examined

Chrysopidae: *Chrysopa dorsalis* Burmeister, 1839 female: microCT, histological sections (1 µm), dissection; *Chrysopa perla* (Linnaeus, 1758) male: histological sections (2 µm).

Hemerobiidae: *Hemerobius humulinus* Linnaeus, 1758: female: microCT; male: histological sections (1 µm), dissection.

Nevrothidae: *Nevrorthus apatelios* Aspöck, Aspöck & Hölzel, 1977 female: histological sections (1 µm), dissection; male: microCT, histological sections (1 µm), dissection, REM.

2.2. Semithin-sections and dissections

The specimens were killed in 96% alcohol, fixed in alcoholic Bouin's fluid for three hours and embedded in Araldite. Semithin histological sections 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; sections are deposited at the Natural History Museum Vienna. For dissection, specimens stored in 75%

ethanol were macerated with KOH for two hours. Figs. 4 and 5 were drawn with Adobe Illustrator CS 11.0.0 from photographs of those specimens.

2.3. Scanning electron microscopy

The specimens were dehydrated in an ethanol series, 100% acetone. Subsequently they were chemically dried using HMDS (hexamethyldisilazane; after BROWN 1993), mounted on insect pins and sputter coated with gold. Scanning electron micrographs were taken with a JEOL JSM-6610 (Natural History Museum Vienna). For imaging Fig. 3A, a rotatable specimen holder designed by POHL (2010) was used.

2.4. Micro-computed tomography and 3D-reconstruction

The specimens were imaged with an Xradia MicroXCT x-ray microtomography system (University of Vienna, Department of Theoretical Biology) with a tungsten or rhodium source at 40–80 kVp and 4–8 W and 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. Reconstructions were made using the software Amira 5.1. The structures were labeled manually and reconstructed using the Arithmetics tool (KLEINTEICH et al. 2008). Isosurfaces of the segmented volumes were created, extracted and smoothed. Since the resolution of the microCT images was insufficient for reconstructions of the hypopharyngeal sclerites and adjacent structures, histological sections were photographed, imported and aligned in Amira 5.1. Based on these reconstructions the schematic drawings in Figures 6 and 7 were made with Adobe Illustrator CS 11.0.0. MicroCT image stacks are deposited in the Natural History Museum Vienna and the University of Vienna, Department of Theoretical Biology.

2.5. Character description and phylogenetic analyses

The analysis comprises 114 characters for 18 genera and 6 outgroup taxa. The character matrix from ZIMMERMANN et al. (2011) and RANDOLF et al. (2013), which included larval characters published by BEUTEL et al. (2010a; chars. 1–63), was amended and new head anatomical characters were defined. Moreover, characters of the

postabdominal sclerites from ASPÖCK et al. (2001) were added and updated (chars. 105–114). The genera *Croce* and *Pterocroce*, included in ZIMMERMANN et al. (2011) and RANDOLF et al. (2013), were excluded since for these genera data on adult characters are missing.

Only informative characters were included in the data matrix. The data set was analyzed in TNT 1.1. (GOLOBOFF et al. 2008). Space for 500000 trees was reserved in the memory. Analyses were performed under equal and implied weights. For implied weighting (GOLOBOFF 1993), the concavity constant K was set from 1–15. For each weighting scheme, traditional analyses with 10000 replications and TBR saving 20 trees per replication were conducted. All analyses were run with collapsing rule 1. The root was *Trachypachus* (Coleoptera; DRESSLER & BEUTEL 2010). To calculate the Bremer Support values (BREMER 1994) suboptimal trees up to 15 steps longer were used (hold + 10000; sub [1–15]; bb=fill;). Partitioned Bremer Support (BAKER & DESALLE 1997) values were calculated with the TNT script Pbsup.run (PEÑA et al. 2006). Bootstrap values (GOLOBOFF et al. 2003) were calculated with 10000 replications and are displayed as absolute frequencies.

2.6. Terminology

The classification of musculature follows WIPFLER et al. (2011). In addition, the hitherto more commonly used classification by VON KÉLER (1963) is provided in brackets in the results section. The terminology of the external head capsule follows SHEPARD (1967) if not otherwise mentioned. The classification of sensilla is based on SCHAFER (1971).

3. Results

3.1. Head capsule

The orthognathous head of *Nevrorthus apatelios* (Fig. 1) is widely exposed and the posterior region is not covered by the prothorax. A coronal sulcus (*sensu* SNODGRASS 1935; Figs. 2B; 3B: cs) is recognizable as a slight inflection lacking long setae. Its posterior third is underlaid by a coronal ridge. Anteriorly it bifurcates into two short branches, which represent vestiges of the frontal sulci (*sensu* SNODGRASS 1935; Figs. 2B; 3A: frs). The temporal sulcus runs between the dorsolateral angle of the occipital foramen and the dorsomesal rim of the compound eye (Fig. 2B: ts). It is internally represented by a prominent temporal ridge.

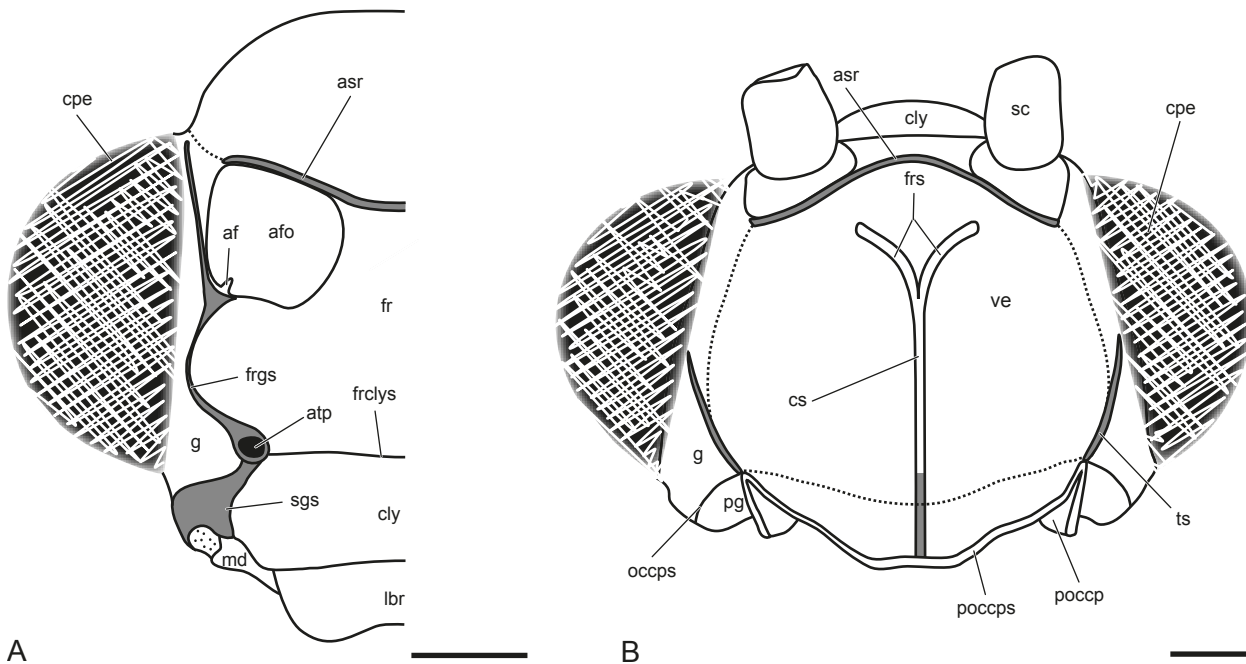


Fig. 2. *Nevrorthus apatelios*, head, habitus: **A:** frontal view; **B:** dorsal view. Dotted line: boundary of the dome-shaped elevation of the vertex. Internal ridges indicated in grey. **Abbreviations:** af – antennifer, afo – antennal foramen, asr – ridge of antennal socket, atp – anterior tentorial pit, cly – clypeus, cpe – compound eye, cs – coronal sulcus, fr – frons, frclys – frontoclypeal sulcus, frgs – frontogenal sulcus, frs – frontal sulcus, g – gena, lbr – labrum, md – mandible, occps – occipital sulcus, pg – postgena, poccp – postocciput, poccps – postoccipital sulcus, sc – scapus, sgs – subgenal sulcus, ts – temporal sulcus, ve – vertex. Scale bars: 100 µm.

The anterior vertex (Figs. 2B; 3A,B: ve) and the posterior frons are strongly domed and distinctly covered with numerous long setae. Additionally, the area anterior to the frontal sulcus is arched to a pulvinus (Fig. 3A: pulv). The posterior vertex is strongly sclerotized and lacks long setae. The occiput does not constitute a distinct region of the head separate from the vertex. The occipital sulcus (Figs. 2B; 3B: occps) runs from the posterior end of the temporal sulcus towards the rim of the eye and lacks an internal ridge; it delimits the genae (Fig. 2A,B: g) from the postgenae (Fig. 2B: pg). The postocciput (Fig. 2B: poccp) is separated from the area of the vertex by a distinct postoccipital sulcus (Figs. 2B; 3B: poccps) at which the cervical membrane (Fig. 3B: cvm) attaches. In the dorsolateral corners of the occipital foramen the postoccipital sulcus forms an angle on each side. The postocciput is deeply inflected and covered by the cervical membrane. The occipital condyles are positioned at half height of the occipital foramen.

The compound eyes (Figs. 2A,B; 3A,B: cpe) are sparsely covered with short inter-ommatidial setae (*sensu* KRISTENSEN & NIELSEN 1979). Ocelli are absent. The antennal sockets (Fig. 3A: as) and the antennal foramina (Fig. 2A: afo) are roundish; the distance between the foramina is about the width of their diameter. A small and narrow antennifer (Fig. 2A: af) is present at the ventrolateral margin of the antennal foramen. Dorsal ridges of the antennal sockets (Fig. 2A,B: asr) meet at the midline of the frons and are recognizable externally as dark line. The subantennal region is distinctly protruding and bears a few setae. A distinct frontogenal sulcus (Figs. 2A; 3A:

frgs) runs from the anterior margin of the antennal foramina to the anterior tentorial pits close to the eye margin and is strongly curved mesad towards the anterior tentorial pits (Figs. 2A; 3A; 6A,D: atp). It delimits the frons from the gena. The frontogenal ridge extends dorsolaterally beyond the rim of the antennal socket to the rim of the compound eye. Clypeus and gena are separated by the subgenal sulcus (Fig. 2A: sgs) with a broad internal subgenal ridge (Fig. 8F: sgr) that forms the articulatory process of the secondary mandibular joint (Fig. 8F: smj). The frontoclypeal sulcus (Figs. 2A; 3A: frclys) is discernible as distinct inflection and does not form an internal ridge. It transversely connects the anterior tentorial pits and delimits the frons (Figs. 2A; 3A: fr) from the clypeus (Figs. 2A,B; 3A: cly). The clypeus is rather short, broad and elevated in the middle. It is not divided in pre- and postclypeus and bears only a few setae. A gula, a hypostomal bridge and a postgenal bridge are absent.

3.2. Tentorium

The tentorium has well-developed anterior tentorial arms (Figs. 6A,D; 8A–C: ata) that are round in cross section and lack medially projecting laminatentoria. The slightly narrower dorsal arms (Figs. 6A,D; 8B,C: dta) diverge apically; they originate just in front of the tentorial bridge (Figs. 6D; 8E: tb) and attach to the head capsule immediately laterad of the antennal foramina and on the ocular ridges by fibrillae (Figs. 8B,F: fib). The posterior tento-

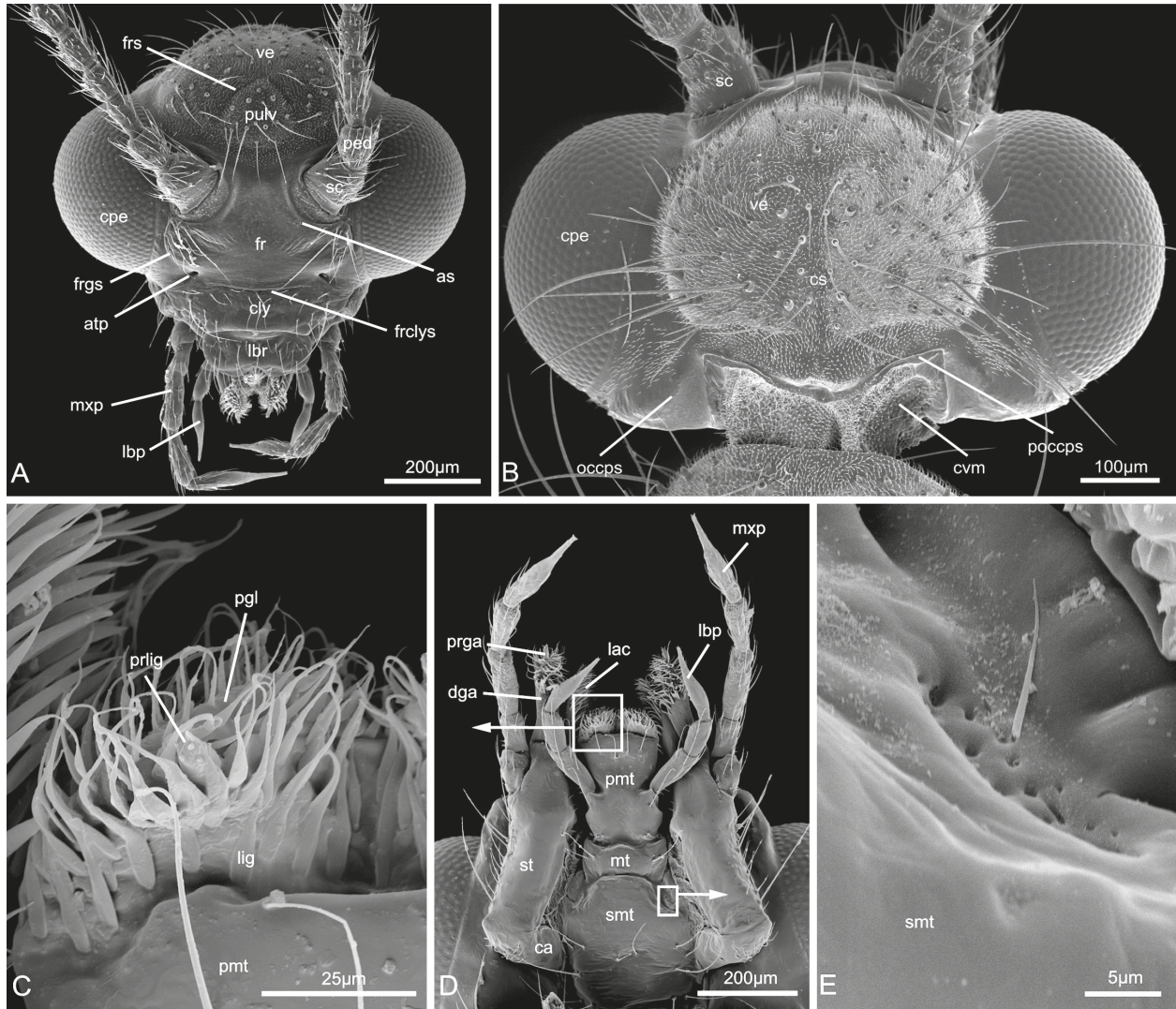


Fig. 3. *Nevrorthus apatelios*, head, SEM images: **A:** frontal view; **B:** dorsal view; **C:** tip of labium, detail of **D**; **D:** maxillae and labium; **E:** multiporous oval plate, detail of **D**. **Abbreviations:** as – antennal socket, atp – anterior tentorial pit, ca – cardo, cly – clypeus, cpe – compound eye, cs – coronal sulcus, cvm – cervical membrane, dga – distigalea, fr – frons, frclys – frontoclypeal sulcus, frgs – frontogenal sulcus, frs – frontal sulcus, lac – lacinia, lbp – labial palp, lbr – labrum, lig – ligula, mt – mentum, mxp – maxillary palp, occps – occipital sulcus, ped – pedicellus, pgl – paraglossae, pmt – prementum, poccps – postoccipital sulcus, prga – process of the galea, prlig – process of the ligula, pulv – pulvinus, sc – scapus, smt – submentum, st – stipes, ve – vertex.

rial arms (Fig. 6D: pta) are short and flattened. The tentorium is approximately X-shaped, with a rather broad tentorial bridge lacking a median process. It is hollow throughout. The anterior tentorial pits are roundish, the posterior tentorial pits are slit-like.

Musculature. The muscles of the tentorium 0te1–0te6 are absent.

3.3. Labrum

The labrum (Figs. 2A; 3A; 4A; 8E: lbr) is approximately transversely oval with a deep emargination medially on the apical margin. Numerous long setae are inserted along its apical margin (Fig. 4A: se), whereas on the dorsal surface long setae are sparse. The tormae (Fig. 4A: to)

are well-developed and converging. The dorsal sclerite of the labrum is well separated from the clypeus by a narrow transverse membrane.

Musculature (Fig. 8E). **0lb1:** *M. frontolabralis* (M8), O: below antennal foramina, I: medially on hind margin of dorsal labral wall; **0lb2:** *M. frontoepipharyngalis* (M9), O: slightly laterad of M8, I: on the tormae; **0lb3:** *M. epistoepipharyngalis* (M10), absent; **0lb4:** *M. labralis transversalis*, absent; **0lb5:** *M. labroepipharyngalis* (M7), absent; **0lb6:** *M. labrolabralis*, absent.

3.4. Antenna

The scapus (Figs. 2B; 3A,B: sc) articulates lateromedially with the antennifer of the antennal foramen and the

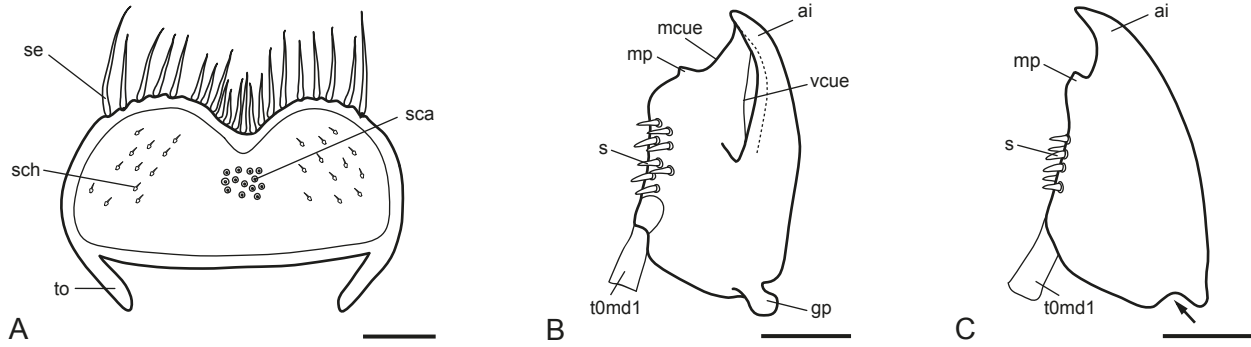


Fig. 4. *Nevrorthus apatelios*: **A**: labrum and anterior epipharynx, ventral view; **B**: left mandible, ventral view; **C**: right mandible, dorsal view. Arrow: articulatory cavity of the secondary mandibular joint. **Abbreviations:** ai – apical incisor, gp – globular protrusion, mcue – mesal cutting edge, mp – molar process, s – sensilla, sca – sensilla campaniformia, sch – sensilla chaetica, se – setae, t0md1 – tendon of *M. craniomandibularis internus*, to – tormae, vcue – ventral cutting edge. Scale bars: 50 µm.

pedicellus (Fig. 3A: ped) with a mesal condylus of the scapus. The pedicellus is approximately 2/3rds the length of scapus. The antenna has 29 flagellomeres; each is approximately 2/3rds the length of the pedicellus, and towards the antennal tip they are slightly shorter. Scapus and pedicellus are dark brown and bear irregularly distributed long sensilla chaetica B and at the basal articulations short sensilla chaetica A. The flagellomeres are cream white and bear long sensilla chaetica B and differently sized sensilla trichodea.

Musculature (Fig. 8B,C). **0an1**: *M. tentorioscapalis anterior* (M1), O: two components, anterior tentorial arm and dorsal tentorial arm beyond origin of 0an4, I: ventral base of scapus; **0an2**: *M. tentorioscapalis posterior* (M2), O: mesal side of anterior tentorial arm, I: dorsolateral base of the scapus; **0an3**: *M. tentorioscapalis lateralis*, absent; **0an4**: *M. tentorioscapalis medialis* (M4), O: lateral side of dorsal tentorial arm, I: dorsally on the base of scapus; **0an5**: *M. frontopedicellaris*, absent; **0an6**: *M. scapopedicellaris lateralis* (M5), O: lateral wall of scapus, I: lateral base of pedicellus, at process of pedicellus; **0an7**: *M. scapopedicellaris medialis* (M6), O: mesal base of scapus; I: mesal base of pedicellus, in front of condylus of scapus; **0an8**: *M. intraflagellaris*, absent; **0an9**: *M. scapopedicellaris posterior*, O: posteromesal lower wall of scapus, I: posterior base of pedicellus; **0an10**: *M. scapopedicellaris anterior*, O: anterior basal margin of scapus, I: anterior basal margin of pedicellus.

3.5. Mandible

The mandibles are strongly sclerotized and asymmetrical; only the left mandible has a ventral cutting edge (Fig. 4B: vcue). Both mandibles have an apical (Fig. 4B,C: ai), but no subapical incisivus. A molar process (Fig. 4B,C: mp) is present in both mandibles. Proximal of the molar process is a mandibular field of short sensilla (Fig. 4B,C: s). Mandibular rows of stiff bristles are absent. The primary mandibular joint (Fig. 8F: pmj) is formed by a globular protrusion (Figs. 4B; 6A: gp) of the man-

dible that articulates with a shallow emargination of the postgena. The secondary mandibular joint (Fig. 8F: smj) consists of a cavity in the mandible and a corresponding protrusion of the subgenal ridge (Fig. 8F: sgr). A lateral protrusion (Fig. 6A: lp) is formed on the rim of the mandible between the two joints.

Musculature (Figs. 6A; 8A–C,F). **0md1**: *M. craniomandibularis internus* (M11), O: strongly sclerotized area on the posterior vertex and on postgena, I: with a strongly developed tendon (Fig. 4B,C: t0md1) at mesal basal margin of mandible; **0md2**: *M. craniomandibularis externus anterior*, absent; **0md3**: *M. craniomandibularis externus posterior* (M12), O: lower part of gena and postgena, I: lateral protrusion of the mandibular base with a tendon; **0md4**: *M. hypopharyngomandibularis* (M13), absent; **0md5**: *M. tentoriomandibularis lateralis superior*, absent; **0md6**: *M. tentoriomandibularis lateralis inferior* (M14), O: anterior tentorial arm, I: medioventral margin of the mandibular cavity; **0md7**: *M. tentoriomandibularis medialis superior*, absent; **0md8**: *M. tentoriomandibularis medialis inferior*, O: anterior tentorial arm, I: medio-dorsal wall of the mandibular cavity.

3.6. Maxilla

The maxillae and the labium are connected with each other by a wide articulatory membrane. The cardo (Figs. 3D; 5; 6B; 8F: ca) is inserted anterior to the posterior tentorial pits and articulates with the postgena by a knob-like protrusion (Fig. 5: kp). It has a field with short setae and is reinforced by an internal cardinal ridge (Fig. 8C: car) that forms laterally a cardinal process (Fig. 8F: cap). The stipes (Figs. 3D; 5; 6B; 8A,B,D,F: st) is equipped with long setae along its lateral edge and reinforced by an internal stipital ridge (Fig. 8D: str). The stipes is not divided into basi- and mediostipes. The maxillary palp (Figs. 3D; 5; 6B; 8F: mxp) is five-segmented, the first, second and fourth segments are shorter than the third and the distinctly pointed fifth segment. The first two segments bear only a few long setae; the other segments

exhibit additionally an irregular pubescence. A palpifer is not developed. The galea is divided by a membrane into a small basigalea (subgalea *sensu* SNODGRASS 1935, FERRIS 1940, BEUTEL et al. 2010b) and a well-developed distigalea with a setose tip on which a small, sclerotized finger-like structure is inserted (process of the galea; Figs. 3D; 5: prga). The basigalea is fully sclerotized whereas the proximal third of the distigalea is membranous. The distigalea is densely covered with setae on its distal third. The laterally sclerotized lacinia (Figs. 3D; 5; 6B: lac) has mesally dense rows of setae forming a brush-like structure.

Musculature (Figs. 6B; 8A–C, F). **0mx1**: M. cranio-cardinalis (M15), O: postgena, I: basal cardinal process; **0mx2**: M. craniolacinialis (M19), bipartite origin on gena and postgena, I: basal edge of lacinia; **0mx3**: M. tentorio-cardinalis (M17), O: along posterior half of anterior tentorial arms until tentorial bridge, I: large parts of cardo; **0mx4**: M. tentoriostipitalis anterior (M18), fan-shaped muscle, O: along anterior tentorial arms, I: stipital ridge; **0mx5**: M. tentoriostipitalis posterior, absent; **0mx6**: M. stipitolacinialis (M20), O: basal margin of stipes, I: basal margin of lacinia; **0mx7**: M. stipitogalealis (M21), O: ventrally at mid-length of stipes anterad the stipital ridge, I: basal margin of distigalea; **0mx8**: M. stipitopalpalis externus (M22), O: stipital ridge, I: distal margin of basal palpomere; **0mx9**: M. stipitopalpalis medialis, absent; **0mx10**: M. stipitopalpalis internus (M23), thin muscle, O: stipital ridge anterad 0mx8, I: median margin of palpomere 1; **0mx11**: M. stipitalis transversalis, running between 0mx3 and 0mx4, and above 0mx6, thin muscle, thinnest in the middle, connecting a membranous fold at dorsolateral margin of stipes with a membranous fold between stipes and cardo; **0mx12**: M. palpopalpalis maxillae primus (M24), bipartite, O: lateral and mesal margin of palpomere 1, I: mesal margin of palpomere 2; **0mx13**: M. palpopalpalis maxillae secundus (M25), absent; **0mx14**: M. palpopalpalis maxillae tertius (M26), bipartite, O: lateral and mesal margin of palpomere 3, I: mesal margin of palpomere 4; **0mx15**: M. palpopalpalis maxillae quartus (M27), bipartite, O: lateral and mesal wall of palpomere 4, about one third of the length away from the margin, I: mesal margin of palpomere 5.

3.7. Labium

Submentum (Figs. 3D,E; 5; 6C; 8D, E: smt) and mentum (Figs. 3D; 5; 6C; 8E: mt) are nearly rectangular with median projections on their distal margins; the submentum is as large as the mentum and prementum (Figs. 3C,D; 5; 6C: pmt) together. The three sclerites are almost coplanar. The submentum articulates with the postgenae without a specialized formation; its proximal edge delimits ventromedially the occipital foramen. The prementum is inconspicuous and lacking posteriorly extended arcuate processes. The ligula (Figs. 3C; 5; 8E: lig) (*sensu* MATSUDA 1965: fused glossae) is membranous and entirely

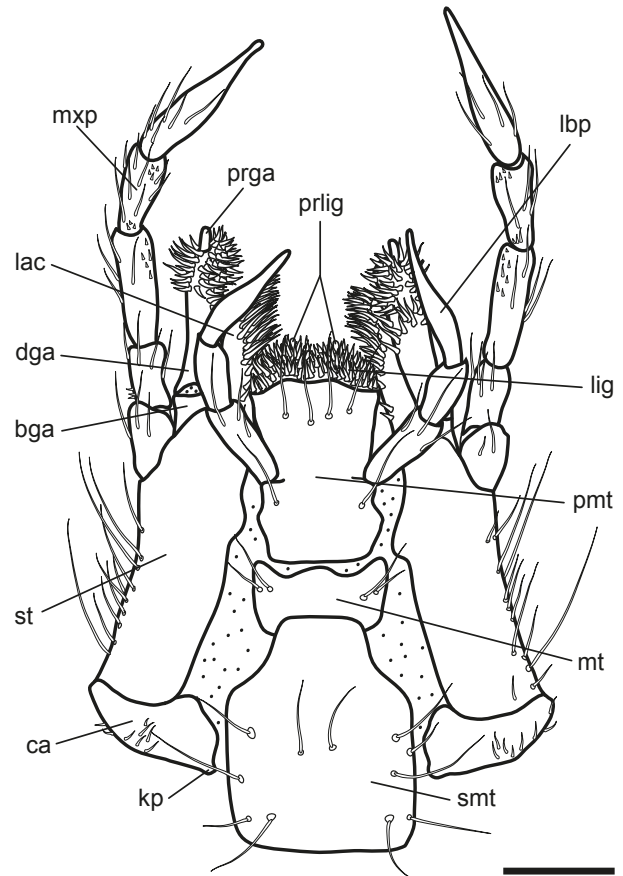


Fig. 5. *Nevrorthus apatelios*, labium and maxillae, ventral view. **Abbreviations:** bga – basigalea, ca – cardo, dga – distigalea, kp – knob-like protrusion, lac – lacinia, lbp – labial palp, lig – ligula, mt – mentum, mxp – maxillary palp, pmt – prementum, prga – process of galea, prlig – process of ligula, smt – submentum, st – stipes. Scale bar: 100 μ m.

covered with setae. Two small finger-like processes are present at the ventrodistal margin of the ligula (process of the ligula; Figs. 3C; 5: prlig). They are sclerotized and resemble the processes of the galeae. The equally membranous and setose paraglossae (Figs. 3C; 7A,B; 8E: pgl) are laterally fused with the ligula and fold onto the dorsal side of the ligula. They are covered with setae in a similar way as the ligula. The labial palps (Figs. 5; 6C: lbp) are three-segmented, with the first and the third palpomere being longer than the second. The third palpomere is pointed and has no sensory field (palpimacula).

Musculature (Figs. 6C; 8A–E). **0la1**: M. postoccipitoglossalis medialis, absent; **0la2**: M. postoccipitoglossalis lateralis, absent; **0la3**: M. postoccipitoparaglossalis, absent; **0la4**: M. postoccipitopraementalis, absent; **0la5**: M. tentoriopraementalis (M29), O: near posterior tentorial pits, I: posterior margin of prementum; **0la6**: M. tentorioparaglossalis (M30): absent; **0la7**: M. tentorioglandularis, absent; **0la8**: M. submentopraementalis (M28), absent; **0la9**: M. postmentomembranus, absent; **0la10**: M. submentomentalis, O: medially at midlength of the submentum, I: posterior margin of mentum; **0la11**: M. praementoparaglossalis (M31): absent; **0la12**:

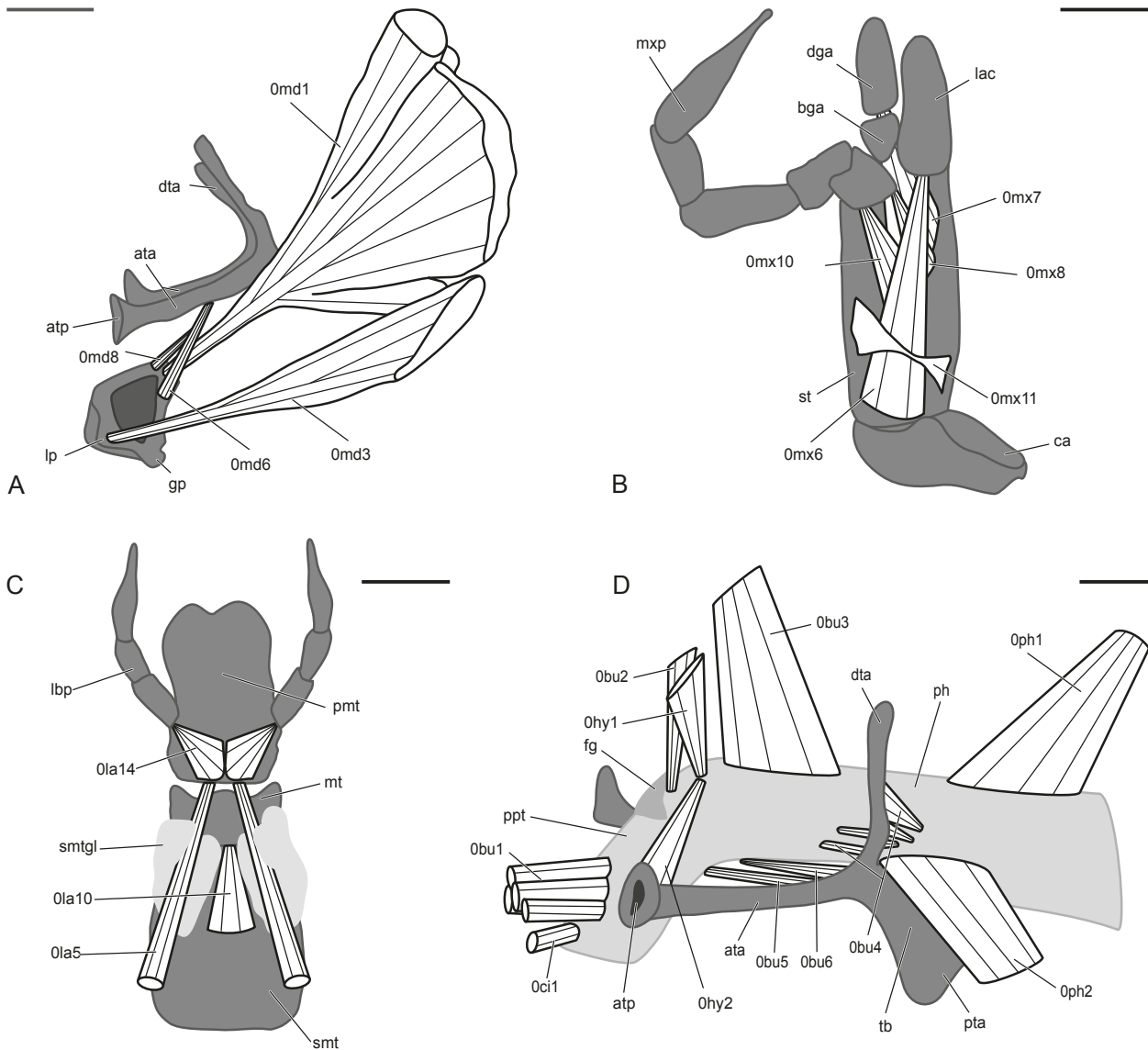


Fig. 6. *Nevrorthus apatelios*: **A**: musculature of the left mandible; **B**: intrinsic musculature of the left maxilla; **C**: musculature and gland of the labium; **D**: musculature of prepharyngeal tube and pharynx. **Abbreviations:** ata – anterior tentorial arm, atp – anterior tentorial pit, bga – basigalea, ca – cardo, dga – distigalea, dta – dorsal tentorial arm, fg – frontal ganglion, gp – globular protrusion, lac – lacinia, lbp – labial palp, lp – lateral protrusion, mt – mentum, mxp – maxillary palp, ph – pharynx, pmt – prementum, ppt – prepharyngeal tube, pta – posterior tentorial arm, smt – submentum, smtgl – submental gland, st – stipes, tb – tentorial bridge, Obu1 – *M. clypeobuccalis*, Obu2 – *M. frontobuccalis anterior*, Obu3 – *M. frontobuccalis posterior*, Obu4 – *M. tentoriobuccalis lateralis*, Obu5 – *M. tentoriobuccalis anterior*, Obu6 – *M. tentoriobuccalis posterior*, Oci1 – *M. clypeopalatalis*, Ohy1 – *M. frontooralis*, Ohy2 – *M. tentoriooralis*, Ola5 – *M. tentoriopraementalis*, Ola10 – *M. submentomentalis*, Ola14 – *M. praementopalpalis externus*, Omd1 – *M. craniomandibularis internus*, Omd3 – *M. craniomandibularis externus posterior*, Omd6 – *M. tentoriomandibularis lateralis inferior*, Omd8 – *M. tentoriomandibularis medialis inferior*, Omx6 – *M. stipitolacinalis*, Omx7 – *M. stipitogalealis*, Omx8 – *M. stipitopalpalis externus*, Omx10 – *M. stipitopalpalis internus*, Omx11 – *M. stipitalis transversalis*, Oph1 – *M. verticopharyngalis*, Oph2 – *M. tentoriopharyngalis*. Scale bars: 100 μ m.

M. praementoglossalis (M32): absent; **Ola13**: *M. praementopalpalis internus* (M33): absent; **Ola14**: *M. praementopalpalis externus* (M34), well developed, O: on proximal margin and median ridge of prementum, I: posterobasal margin of palpomere 1; **Ola15**: *M. praementomembranus*, absent; **Ola16**: *M. palpopalpalis labii primus* (M35), O: mesal wall of palpomere 1, I: mesobasal margin of palpomere 2; **Ola17**: *M. palpopalpalis labii secundus* (M36), O: on lateral wall of palpomere 2, close to its base; I: mesobasal margin of palpomere 3.

3.8. Hypopharynx and salivary system

The hypopharynx and labium form together a structural and functional unit. The anterior hypopharynx (Figs. 7A,B; 8E: hyph) is tongue-shaped; it has a thickened but unsclerotized cuticula with a thick layer of endocuticula. Dorsally it is densely covered with posterad directed microtrichia. The hypopharyngeal suspensorial sclerites are represented by a pair of undifferentiated lateral plates

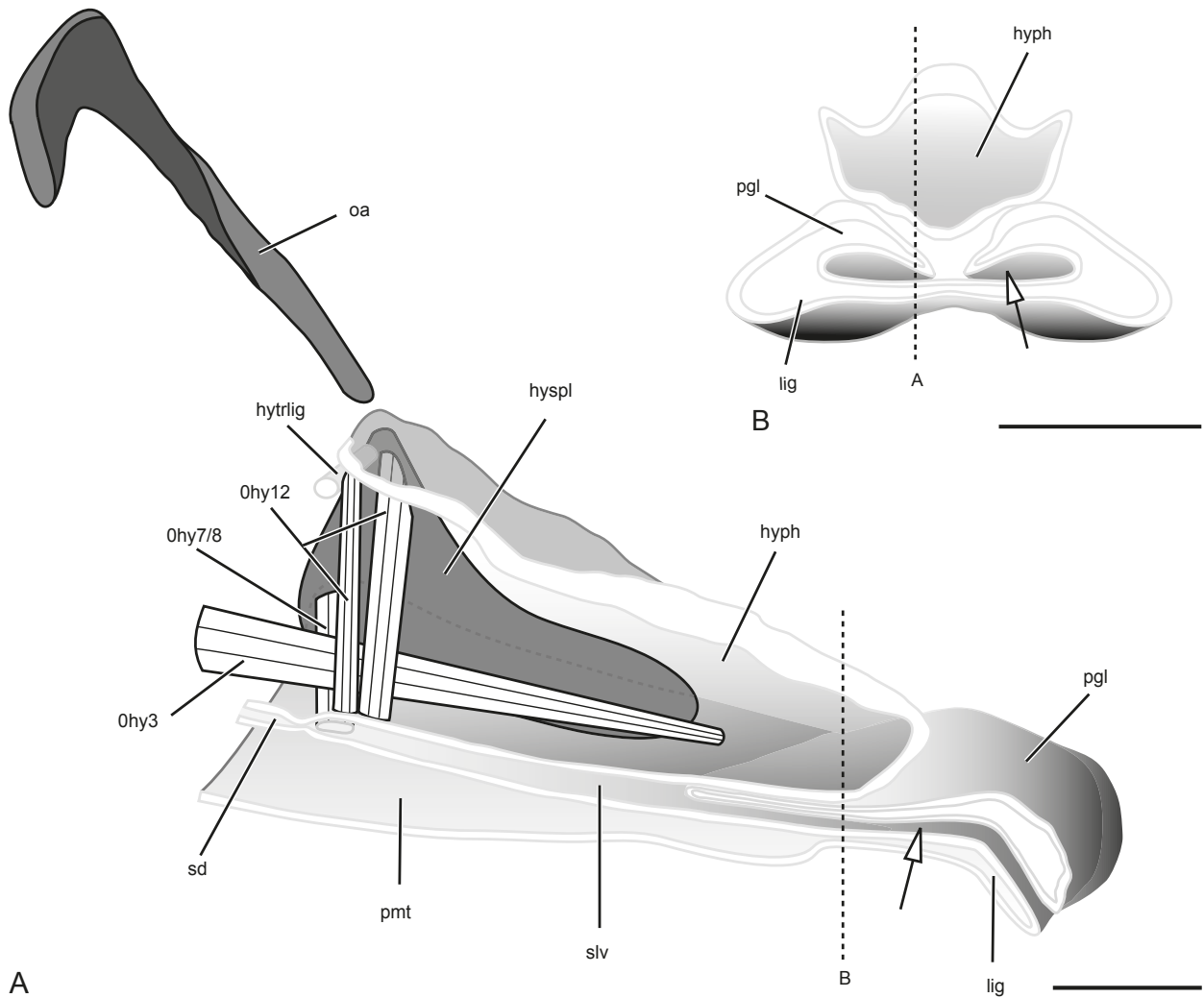


Fig. 7. *Nevrorthus apatelios*, hypopharynx and salivary system: **A**: lateral view. Black dotted line: cutting plane of Fig. 7B; arrow: secondary prolongation of the salivary system. **B**: posterior view. Black dotted line: cutting plane of Fig. 7A; arrow: secondary prolongation of the salivary system. **Abbreviations:** hyph – hypopharynx, hyspl – hypopharyngeal suspensorial plate, hytrlig – hypopharyngeal transverse ligament, lig – ligula, oa – oral arm, pgl – paraglossae, pmt – prementum, sd – salivary duct, slv – salivarium, 0hy3 – M. craniohypopharyngalis, 0hy7/8 – M. praementosalivaris anterior/posterior, 0hy12 – M. hypopharyngosalivaris. Scale bars: 50 µm.

(hypopharyngeal suspensorial plates; Fig. 7A: hyspl), reinforcing the anterior hypopharynx posteriorly. Sclerites framing the anterior most part of the hypopharynx are not discernible. A transverse ligament connecting the hypopharyngeal suspensorial plates is present (hypopharyngeal transverse ligament; Figs. 7A; 8A,E: hytrlig). The collateral oral arms (Figs. 7A; 8A: oa) are separated from the suspensorial plates by a membranous area; they are twisted at mid-length and flattened apically. The paired salivary ducts (Figs. 7A; 8B–E: sd) unite at the level of the hind margin of the mentum and open into the salivarium (Figs. 7A; 8A,E: slv) at the level of the hind margin of the prementum.

Musculature (Figs. 6D; 7A; 8A,E). **0hy1**: M. frontooralis (M41), O: on frons, close to origin of 0lb2, I: internal apex of oral arm; **0hy2**: M. tentoriooralis (M47), O: at invagination area of anterior tentorial arms, I: internal apex of oral arm ventral to the insertion of 0hy1; **0hy3**:

M. craniohypopharyngalis (M42), O: posterior tentorial arms, adjacent to 0la5, I: lateral at the base of the hypopharynx; **0hy4**: M. postoccipitalohypopharyngalis, absent; **0hy5**: M. tentoriosuspensorialis, absent; **0hy6**: M. postmentoloralis, absent; **0hy7/0hy8**: M. praementosalivaris anterior/posterior (M38/M39), O: hind margin of prementum, I: lateral wall of salivarium; **0hy9**: M. oralis transversalis dorsalis (M67), well developed, connecting the anterior edges of the oral arms; **0hy10**: M. loroloralis, absent; **0hy11**: M. lorosalivariialis, absent; **0hy12**: M. hypopharyngosalivaris (M37), well-developed, O: five bundles on posterior hypopharyngeal suspensorial sclerites, and four bundles on hypopharyngeal transverse ligament, I: anterodorsal wall of salivarium; **0hy13**: M. annularis salivarii (M40), absent. **0hy14**: M. submentosuspensorialis, absent; **0hy15**: M. ducti salivarii, absent; **0hy16**: M. oralis transversalis ventralis, well developed, connecting the posterior edges of the oral arms.

3.9. Epipharynx

The anterior epipharynx (Fig. 4A) is membranous and equipped with a median field of sensilla campaniformia (Fig. 4A: sca) and lateral fields of anterad directed sensilla chaetica (Fig. 4A: sch). The posterior epipharynx and the posterior hypopharynx form a prepharyngeal tube (Figs. 6D; 8E: ppt), which is reinforced by the hypopharyngeal oral arms. The wall of the prepharyngeal tube is strongly folded at the attachment area of 0bu1.

Musculature (Figs. 6D; 8E). **0ci1**: M. clypeopalatalis (M43), O: anterior margin of clypeus, on both sides of the median elevation, I: hind margin of anterior epipharynx between the tormae; **0bu1**: M. clypeobuccalis (M44), O: clypeus, posterior to 0ci1, I: anterior wall of the prepharyngeal tube between the bundles of 0hy9.

3.10. Pharynx

The anatomical opening of the mouth, defined as the insertion site of M. frontobuccalis anterior by BEUTEL et al. (2014), is not precisely discernable since M. frontobuccalis anterior (0bu2) inserts anterior to the hypopharyngeal muscles (0hy1, 0hy2) (Fig. 6D). The lumen of the precerebral pharynx is crescent-shaped in cross section due to the longitudinal dorsal fold for M. longitudinalis stomodaei. The lumen of the postcerebral pharynx is oval in cross section, the folds for M. longitudinalis stomodaei and dilator muscles are indistinct. The wall of the precerebral and postcerebral pharynx (Figs. 6D; 8A–C,E: ph) is very thick as the intima (Fig. 8E: int) expands up to 10 µm.

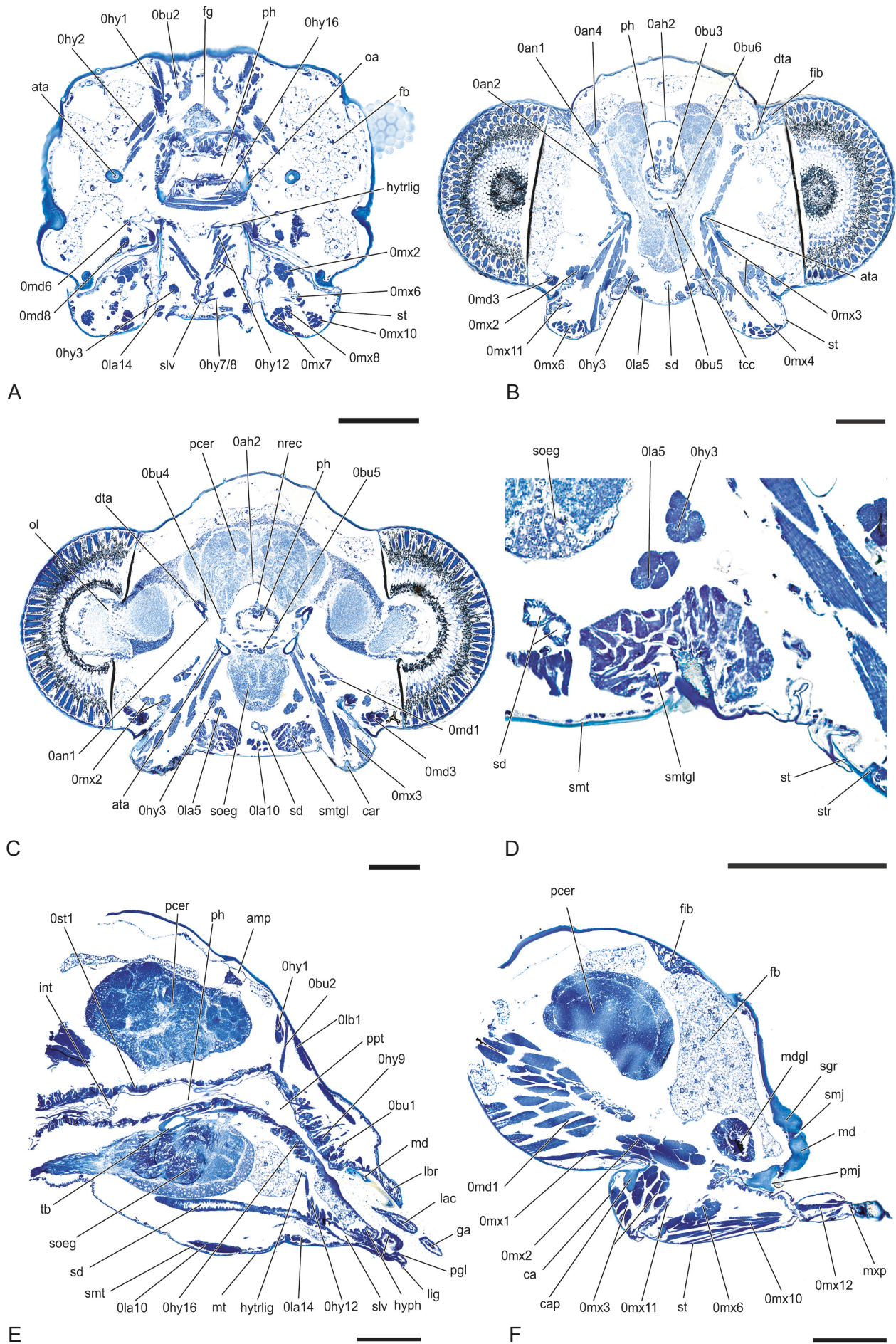
Musculature (Figs. 6D; 8A–C, E). **0bu2**: M. frontobuccalis anterior (M45), O: frons, medially to 0hy1, I:

precerebral pharyngeal wall, posterolaterally to the ganglion frontale; **0bu3**: M. frontobuccalis posterior (M46), O: frons, I: dorsal precerebral pharyngeal wall; **0bu4**: M. tentoriobuccalis lateralis (M49), several bundles, O: dorsal tentorial arm, I: lateral precerebral pharyngeal wall; **0bu5**: M. tentoriobuccalis anterior (M48), O: tentorial bridge, I: ventral wall of food tract attributed to the pre-oral domain; **0bu6**: M. tentoriobuccalis posterior (M50), O: tentorial bridge, I: ventral precerebral pharyngeal wall posterior to 0bu5 at level of attachment of 0bu3; **0ph1**: M. verticopharyngalis (M51), O: vertex, near the median line, I: dorsally on posterior pharyngeal wall, right behind the brain; **0ph2**: M. tentoriopharyngalis (M52), O: posterior tentorial arm and head capsule, I: broadly along ventral posterior pharyngeal wall; **0ph3**: M. postoccipitopharyngalis, absent; **0st1**: M. annularis stomodaei (M68), pharyngeal ring musculature, posterior to insertion of 0hy1 and 0hy2; **0st2**: M. longitudinalis stomodaei (M69), longitudinal muscles beneath 0st1 and 0hy9.

3.11. Nervous system

The brain and suboesophageal ganglion (Fig. 8C–E: soeg) occupy about one quarter of the head volume. The protocerebrum (Fig. 8C, E, F: pcer) has large lateral optical lobes (Fig. 8C: ol), giving it the form of a dumb-bell. The frontal ganglion (Figs. 6D; 8A: fg) is triangular; the nervus procurrens originates ventrally and innervates the labral muscles (0lb1 and 0lb2). The nervus recurrens (Fig. 8C: nrec) originates dorsally on the frontal ganglion and passes backwards along the pharynx to the hypocerebral ganglion. A pair of frontal connectives link the frontal ganglion with the tritocerebrum. The antennal nerve originates far laterally from the deutocer-

→ **Fig. 8.** *Nevrorthus apatelios*, head: **A–D**: cross sections, **E–F**: longitudinal sections. **A**: level of frontal ganglion; **B**: level of tritocerebral commissure; **C**: level of 0bu4; **D**: level of submental gland opening; **E**: level of salivarium; **F**: level of mandibular gland. **Abbreviations:** amp – ampulla, ata – anterior tentorial arm, ca – cardo, cap – cardinal process, car – cardinal ridge, dta – dorsal tentorial arm, fb – fat body, fg – frontal ganglion, fib – fibrillae, ga – galea, hyph – hypopharynx, hytrlig – hypopharyngeal transverse ligament, int – intima, lac – lacinia, lbr – labrum, lig – ligula, md – mandible, mdgl – mandibular gland, mt – mentum, mxp – maxillary palp, nrec – nervus recurrens, oa – oral arm, ol – optical lobe, pcer – protocerebrum, pgl – paraglossae, ph – pharynx, pmj – primary mandibular joint, ppt – prepharyngeal tube, sd – salivary duct, sgr – subgenal ridge, slv – salivarium, smj – secondary mandibular joint, smt – submentum, smtgl – submental gland, soeg – suboesophageal ganglion, st – stipes, str – stipital ridge, tb – tentorial bridge, tcc – tritocerebral commissure; 0ah2 – M. ampulloaortica, 0an1 – M. tentorioscapalis anterior, 0an2 – M. tentorioscapalis posterior, 0an4 – M. tentorioscapalis medialis, 0bu1 – M. clypeobuccalis, 0bu2 – M. frontobuccalis anterior, 0bu3 – M. frontobuccalis posterior, 0bu4 – M. tentoriobuccalis lateralis, 0bu5 – M. tentoriobuccalis anterior, 0bu6 – M. tentoriobuccalis posterior, 0hy1 – M. frontooralis, 0hy2 – M. tentiiooralis, 0hy3 – M. craniohypopharyngalis, 0hy7/8 – M. praementosalivaris anterior/posterior, 0hy9 – M. oralis transversalis dorsalis, 0hy12 – M. hypopharyngosalivaris, 0hy16 – M. oralis transversalis ventralis, 0la5 – M. tentoriopraementalis, 0la10 – M. submentomentalis, 0la14 – M. praementopalpalis externus, 0lb1 – M. frontolabralis, 0md1 – M. craniomandibularis internus, 0md3 – M. craniomandibularis externus posterior, 0md6 – M. tentoriomandibularis lateralis inferior, 0md8 – M. tentoriomandibularis medialis inferior, 0mx1 – M. craniocardinalis, 0mx2 – M. craniolacinalis, 0mx3 – M. tentoriocardinalis, 0mx4 – M. tentiostipitalis anterior, 0mx6 – M. stipitolacinalis, 0mx7 – M. stipitogalealis, 0mx8 – M. stipitopalpalis externus, 0mx10 – M. stipitopalpalis internus, 0mx11 – M. stipitalis transversalis, 0mx12 – M. palpopalpalis maxillae primus, 0st1 – M. anularis stomodaei. Scale bars: 100 µm.



ebrum; at the base of the scapus it furcates into a motorical branch that innervates the antennal and scapopedicellar muscles and a sensorial branch that enters the antenna. The sensorial branch furcates before entering the pedicellus. The circumoesophageal connectives (tritocerebrum) are connected by the tritocerebral commissure (Fig. 8B: tcc), which runs dorsally of M. tentoriobuccalis anterior. Ocellar nerves and a nervus connectivus are absent.

3.12. Circulatory system

The cephalic aorta is distinctly developed and encloses the nervus recurrens. Approximately quadrangular in cross-section in the posterior region of the head it becomes roundish below the brain. The paired and completely separated antennal ampullae (Fig. 8E: amp) are located between the antennal foramina and the origin of 0bu3. They are attached to the median rim of the antennal sockets by tissue.

Musculature (Fig. 8B,C). **0ah1**: M. interampullaris, absent; **0ah2**: M. ampulloaortica, O: antennal ampulla, I: dorsal wall of cephalic aorta; **0ah3**: M. ampulloparyngalis, absent; **0ah4**: M. ampullofrontalis, absent; **0ah5**: M. frontoparyngalis, absent; **0ah6**: M. frontofrontalis, absent.

3.13. Glands

There are two exocrine glands in both sexes: paired compact mandibular glands (Fig. 8F: mdgl) and less compact paired submental glands (Figs. 6C; 8C, D: smtgl). The mandibular glands (*sensu* BUDER & KLASS 2013) extend from the mandible to the optical lobes. They consist of a thick outer layer of secretory cells surrounding the globular cavity and open into the preoral cavity. The orifice lies lateral to the hypopharyngeal transverse ligament in the membrane connecting mandible and hypopharynx. The smaller submental glands extend from the tentorial bridge to the middle of the mentum and are situated between the adductors of the maxillae and the labial and hypopharyngeal retractors. They open by an oval multiporous plate (Fig. 3E) in a thickened membrane on both sides of the median projection of the submentum.

3.14. Fat body

A compact fat body (Fig. 8A,F: fb) is mainly located in the lateral parts of the head, below the pharynx and over the brain.

4. Character description and cladistic analyses

4.1. Phylogenetically relevant characters

Characters 1–63 refer to larval morphology; they are described in BEUTEL et al. (2010a). Modifications to some of these characters are discussed below. Characters 64–104 pertain to adult head morphology and were largely taken from ZIMMERMANN et al. (2011) and RANDOLF et al. (2013), and additionally new characters were defined. Characters 105–114 concern the postabdominal sclerites of both sexes and were assembled from ASPÖCK et al. (2001) and ASPÖCK & ASPÖCK (2008). The complete data matrix can be found online (El. Suppl. file).

Characters 37 (presence of a poison channel of maxillary stylet) and 53 (presence of a mesal gland of maxillary stylet) of BEUTEL et al. (2010a) are merged to “Poison system: (0) absent; (1) present” (character 37 in our matrix) for the following reason: In all investigated specimens (WUNDT 1961; ROUSSET 1966; GAUMONT 1976; BEUTEL et al. 2010a) a poison gland occurs together with a poison channel and there is strong evidence that these structures are correlated to each other. Thus, as long as no species have one structure but not the other, we suggest treating it as one character. A poison system is absent in the outgroup taxa (BEUTEL et al. 2010a) and Sisyridae (GAUMONT 1976). Due to this fusion, characters 53–64 from BEUTEL et al. (2010a) are characters 52–63 in our matrix.

Regarding *Osmylus*, the state of character 43 (subdivision of the postmentum) is changed from “(1) undivided” to “(0) subdivided into mentum and submentum” (see WUNDT 1961: small unpaired sclerite distal of the postmentum).

Character 61 of BEUTEL et al. (2010a) (cryptonephry) is changed from “(0) absent; (1) five or six Malpighian tubules attached; (2) one Malpighian tubule attached” to “Cryptonephric Malpighian tubules: (0) absent; (1) present, attachment site embedded in a pear-shaped organ, (2) present, attachment site not embedded in a pear-shaped organ” (char. 60 in our matrix), since the number of cryptonephric Malpighian tubules is variable within genera and even species of Neuroptera: In the specimen of *S. vicaria* investigated by ANTHONY (1902) (given as *S. umbrata*) there were five tubules, of which three were cryptonephric, while in the same species, PUPEDIS (1985) found eight tubules of which five were cryptonephric. In *S. nigra*, GAUMONT (1976) (given as *S. fuscata*) found eight tubules one of which was cryptonephric. Considerable variability is also documented for the larvae of *Osmylus fulvicephalus*: HAGEN (1852) (given as *O. chrysops*) found seven Malpighian tubules, four of which were cryptonephric, WITHYCOMBE (1922) eight Malpighian tubules, six of which were cryptonephric and GAUMONT (1976) seven Malpighian tubules, five of which were

cryptonephric. The character definition now accounts for the attachment of cryptonephric Malpighian tubules to the pear-shaped organ, which has been well documented by MC DUNNOUGH (1909: “Rectalring”), ŁOZIŃSKI (1911: “birnenförmiges Organ”) and GAUMONT (1976: “organe pyriforme”).

64. *Dorsal tentorial arms: absent (0), present (1)* see ZIMMERMANN et al. (2011; char. 65). — *Chauliodes* and *Lomamyia* were scored as “present” (MAKI 1936; SHEPARD 1967).
65. *Dorsal tentorial arms: well developed (0), weakly developed (1)* see ZIMMERMANN et al. (2011; char. 66). — We scored *Chauliodes* as “well developed” and *Lomamyia* as “weakly developed” (MAKI 1936; SHEPARD 1967). Character 65 is not applicable to taxa with state (0) in character 64.
66. *Laminatentorium: absent (0), present (1)* see ZIMMERMANN et al. (2011; char. 67). — We scored *Chauliodes* as “absent” and *Lomamyia* as “present” (MAKI 1936; SHEPARD 1967).
67. *Anteriorly projecting median process on the tentorial bridge: absent (0), present (1)* see ZIMMERMANN et al. (2011; char. 68). — We scored *Chauliodes* and *Lomamyia* as “absent” (MAKI 1936; SHEPARD 1967).
68. *Anterior tentorial pits: open (0), slit-like constricted (1), trumpet-like (2), closed (3)* see ZIMMERMANN et al. (2011; char. 69). — *Chauliodes* was scored with state (1): “slit-like constricted” (MAKI 1936).
69. *Anterior tentorial arms: cylindrical tubes (0), flat tubes (1)* see ZIMMERMANN et al. (2011; char. 70). — *Chauliodes* was scored as possessing “cylindrical tubes” (MAKI 1936; fig. 10).
70. *Origin of M. tentorioscapalis anterior (0an1): ata (0), ata-dta (1)* see ZIMMERMANN et al. (2011; char. 71). — We scored *Chauliodes* with state (0): “ata” (MAKI 1936).
71. *Origin of M. tentorioscapalis lateralis (0an2): ata-dta (0), ata (1)* see ZIMMERMANN et al. (2011; char. 72). — *Chauliodes* was scored with state (1): “ata” (MAKI 1936).
72. *Origin of M. tentorioscapalis medialis (0an4): dta (0), ata (1)* see ZIMMERMANN et al. (2011; char. 73). — *Chauliodes* was scored with state (0): “dta” (MAKI 1936).
73. *M. tentoriomandibularis medialis inferior (0md8): absent (0), present (1)*. — In the present study, the “M. zygomaticus mandibulae, component a” of ZIMMERMANN et al. (2011; char. 74) is interpreted as *M. tentoriomandibularis medialis inferior* (0md8).
74. *M. tentoriomandibularis lateralis inferior (0md6): absent (0), present (1)* see ZIMMERMANN et al. (2011; char. 75). — We follow the homologization of WIPFLER et al. (2011) that *M. zygomaticus mandibulae* of VON KÉLER (1963) is *M. tentoriomandibularis lateralis inferior* (0md6).
75. *M. tentoriomandibularis medialis superior (0md7): absent (0), present (1)*. — In the present study the “M. zygomaticus mandibulae, component c” of ZIMMERMANN et al. (2011; char. 76) is interpreted as *M. tentoriomandibularis medialis superior* (0md7) of WIPFLER et al. (2011).
76. *Origin of M. tentoriocardinalis (0mx3): gular ridge (0), pta (1), tb (2), ata (3)* see ZIMMERMANN et al. (2011; char. 77). — *Chauliodes* was scored with state (2): “tb” (MAKI 1936).
77. *Anterior component of M. tentoriostipitalis (0mx4): absent (0), present (1)* see ZIMMERMANN et al. (2011; char. 78). — We scored *Chauliodes* as “absent” (MAKI 1936).
78. *Posterior component of M. tentoriostipitalis (0mx5): absent (0), present (1)* see ZIMMERMANN et al. (2011; char. 79). — We scored *Chauliodes* as “present” (MAKI 1936).
79. *Origin of the posterior component of M. tentoriostipitalis (0mx5): postgular ridge (0), pta (1), tb-ata (2)*, see ZIMMERMANN et al. (2011; char. 80). — *Chauliodes* was scored with state (2): “tb-ata” (MAKI 1936). Character 79 is not applicable to taxa with state (0) in character 78.
80. *M. tentoriobuccalis lateralis (0bu4): absent (0), present (1)* see ZIMMERMANN et al. (2011; char. 81). — We scored *Euroleon* (KORN 1943) and *Libelloides* as “present”.
81. *Origin of M. tentoriobuccalis lateralis (0bu4): dta (0), ata (1)* see ZIMMERMANN et al. (2011; char. 82). — In *Chauliodes* (MAKI 1936), *Nevrorthus*, *Osmylus* and *Sisyra* (ZIMMERMANN et al. 2011), the *M. tentoriobuccalis lateralis* originates on the dorsal tentorial arms, in *Euroleon* (KORN 1943) and *Libelloides* on the anterior tentorial arms. Character 81 is not applicable to taxa with state (0) in character 80.
82. *Ocelli: absent (0), present (1)* see RANDOLF et al. (2013; char. 83). — Ocelli are present in the raphidiopteran family Raphidiidae and the megalopter family Corydalidae, as well as in the neuropteran family Osmylidae (ASPÖCK & ASPÖCK 2005a,b,c). They are absent in Sialidae (RÖBER 1941) and all remaining neuropteran families (SHEPARD 1967).
83. *Gula: absent (0), present (1)* see RANDOLF et al. (2013; char. 84). — A gula *sensu* SNODGRASS (1935) is present in Coleoptera, Raphidioptera (ACHTELIG 1967) and Megaloptera (MAKI 1936; RÖBER 1941) and absent in all Neuroptera.
84. *Temporal sulcus: absent (0), present (1)*. — A temporal sulcus is present in *Nevrorthus*, *Polystoechotes* (SHEPARD 1967), *Ithone* (SHEPARD 1967: fig. 12), *Hemerobius* (SHEPARD 1967: fig. 23), *Nallachius* (SHEPARD 1967: fig. 48), *Lomamyia* (SHEPARD 1967: fig. 50), *Coniopteryx* (MEINANDER 1972), *Helicconis* (TJEDER 1957), *Chrysopa* (MORSE 1931) and *Sisyra* (TJEDER 1957). It is absent in *Euroleon* (SUNDERMEIER 1940 as *Myrmeleon*), *Osmylus* (BEUTEL et al. 2010b), *Psychopsis* (SHEPARD 1967), *Nemoptera* (SHEPARD 1967), *Dichrostigma* (ACHTELIG 1967 as *Raphidia*), *Chauliodes* (MAKI 1936), *Sialis* (RÖBER 1941) and Coleoptera (BEUTEL et al. 2003; DRESSLER & BEUTEL 2010).

85. *Molar process of mesal mandibular edge: absent (0), present (1).* — As described for *Osmylus* (BEUTEL et al. 2010b) and *Sisyra* (RANDOLF et al. 2013), a characteristic molar process is present on the mesal mandibular edge in *Nevrorthus* (Fig. 4B,C: mp). Molar processes are present in *Polystoechotes* (SHEPARD 1967: mandibular tooth), *Hemerobius* (STELZL 1992: fig. 5), *Chrysopa* (MORSE 1931), *Helicoconis* (TJEDER 1960: fig. 4), *Mantispa* (STITZ 1931: “zahnartiger Höcker”), *Lomamyia* (SHEPARD 1967: fig. 51), *Psychopsis* (SHEPARD 1967: fig. 63), *Nymphes* (SHEPARD 1967: fig. 65), *Libelloides* (STELZL 1992: fig. 2) and *Euroleon* (SUNDERMEIER 1940: “abgesetzter Zahn”). They are absent in *Ithone* (TILLYARD 1919), *Nemoptera* (STITZ 1931) and the outgroup taxa (MAKI 1936; RÖBER 1941; KELSEY 1954; ACHTELIG 1967; BEUTEL et al. 2003; DRESSLER & BEUTEL 2010).
86. *Mandibular row of stiff bristles: absent (0), present (1).* — Regular rows of narrow fields of stiff bristles on the posterior mandibular surface, as described for *Osmylus* (BEUTEL et al. 2010b), are present in *Hemerobius* (STELZL 1992: fig. 5), *Chrysopa* (STELZL 1992: fig. 6), *Mantispa* (STITZ 1931: “Reihe von Ringborsten”), *Psychopsis* (SHEPARD 1967: fig. 63: MdBr), *Nymphes* (SHEPARD 1967: fig. 66: MdBr), *Libelloides* (STELZL 1992: fig. 2) and *Euroleon* (SUNDERMEIER 1940: fig. 6), as well as the outgroup taxa *Trachypachus* (DRESSLER & BEUTEL 2010: ventral fringe of hairs) and *Ochthebius* (BEUTEL et al. 2003: longitudinal brush of trichia present close to ventromesal edge). They are absent in *Nevrorthus* and *Sisyra* (RANDOLF et al. 2013), as well as in Raphidioptera and Megaloptera (MAKI 1936; RÖBER 1941; ACHTELIG 1967).
87. *Mandibular field of short sensilla: absent (0), present (1).* — A field of very short sensilla between the molar process and the insertion of Omd1 is present in *Nevrorthus* (Fig. 4B,C) and *Sisyra* (RANDOLF et al. 2013: fig. 4b,c). This mandibular field of short sensilla is also present in females of *Sialis* (RÖBER 1941). They are absent in *Osmylus* (BEUTEL et al. 2010b: fig. 5), *Hemerobius* (STELZL 1992: fig. 5), *Chrysopa* (STELZL 1992: fig. 6), *Mantispa* (STITZ 1931), *Psychopsis* (SHEPARD 1967: fig. 63), *Nymphes* (SHEPARD 1967: fig. 66), *Libelloides* (STELZL 1992: fig. 2) and *Euroleon* (SUNDERMEIER 1940: fig. 6), as well as Raphidioptera, Megaloptera (MAKI 1936; RÖBER 1941; ACHTELIG 1967) and Coleoptera (BEUTEL et al. 2003; DRESSLER & BEUTEL 2010).
88. *Galea: not transversely divided in 2 parts (0), distinctly transversely divided in 2 parts (basi- and distigalea) by membrane [character 89] see RANDOLF et al. (2013; char. 85).* — The galea is divided in 2 parts in Nevorthidae and most neuropteran families (FERRIS 1940; KORN 1943; TJEDER 1957, 1959, 1960, 1961, 1966, 1967, 1992). An undivided galea is reported only for Sisyridae (RANDOLF et al. 2013) and the coniopterygid subfamily Coniopteryginae (TJEDER 1957). Data are missing for Dilaridae, Ithonidae, Polystoechotidae and Nymphidae. In the outgroup taxa Raphidioptera and Megaloptera the galea is undivided (MAKI 1936; RÖBER 1941; ACHTELIG 1967). The division in *Trachypachus* (DRESSLER & BEUTEL 2010) is not assumed to be homologous as in Neuroptera the *M. stipitogalealis* (0mx7) inserts on the distal sclerite (“true galea” *sensu* SNODGRASS 1935) while in *Trachypachus* it inserts on the proximal one.
89. *Finger-like process on galea: absent (0), present (1) [character 90] see RANDOLF et al. (2013; char. 86).* — An apical finger-like process on the galea as in *Nevrorthus* is present in all neuropteran families (SHEPARD 1967; TJEDER 1957, 1959, 1960, 1961, 1966, 1967). In the families Sisyridae, Coniopterygidae and Hemerobiidae, this character is variable [MEINANDER 1972: Aleuropteryginae present, Coniopteryginae absent; SHEPARD 1967: *Climacia* (Sisyridae) and some Hemerobiidae present]. The process is not reported for any member of the outgroup (CRAMPTON 1923; ACHTELIG 1967; MAKI 1936; DRESSLER & BEUTEL 2010). — The character was deactivated for the present analysis. Its inclusion led to misleading results regarding the crucial question of the basal splitting events in Neuroptera, since it supported a clade containing all Neuroptera with the exclusion of Sisyridae, although the character is present in the other genus of Sisyridae which, however, was not included in the matrix.
90. *Stipes divided into basi- and mediostipes sensu BEUTEL & LESCHEN (2005): absent (0), present (1).* — A division of the stipes into a lateral basistipes and a ventral mediostipes is present in *Trachypachus* and *Ochthebius* (BEUTEL et al. 2003; DRESSLER & BEUTEL 2010). In all studied Neuropterida the stipes is undivided, as in *Nevrorthus*, *Dichrostigma* (ACHTELIG 1967), *Chauliodes* (MAKI 1936), *Sialis* (RÖBER 1941), *Sisyra* (TJEDER 1957), *Osmylus* (BEUTEL et al. 2010b), *Hemerobius* (TJEDER 1961), *Chrysopa* (MORSE 1931), *Coniopteryx* (MEINANDER 1972), *Helicoconis* (TJEDER 1960), *Mantispa* (POIVRE 1982), *Ithone* (TILLYARD 1919), *Nemoptera* (CRAMPTON 1923), *Euroleon* (KORN 1943), *Libelloides* (STITZ 1931), *Lomamyia*, *Psychopsis* and *Nymphes* (SHEPARD 1967).
91. *Paraglossae: absent (0), present (1) [character 92] see RANDOLF et al. (2013; char. 87).* — Paraglossae are present in *Nevrorthus*, *Sisyra*, *Osmylus*, *Chrysopa*, *Hemerobius* and *Polystoechotes* (SULC 1914; RANDOLF et al. 2013). Data are missing for most other Neuroptera. Paraglossae are lacking in *Euroleon* (KORN 1943), *Nemoptera* (KRENN et al. 2008), Raphidioptera (ACHTELIG 1967), Megaloptera (MAKI 1936; RÖBER 1941) and Coleoptera (BEUTEL et al. 2003; DRESSLER & BEUTEL 2010).
92. *Palpiger: without process (0), with process (1) see RANDOLF et al. (2013; char. 88).* — *Nevrorthus*, *Chrysopa* (MORSE 1931) and *Euroleon* (SUNDERMEIER 1940) have palpiger without a process. The pal-

- pigera with a process are present in *Sisyra* (TJEDER 1957; RANDOLF et al. 2013) and some Coleoptera (DRESSLER & BEUTEL 2010).
93. *Palpimaculae*: *absent (0), present (1)* see RANDOLF et al. (2013; char. 89). — Palpimaculae are absent in Nevrothidae, Sisyridae (RANDOLF et al. 2013) and Coniopterygidae (SHEPARD 1967; ZIMMERMANN et al. 2009). They are reported for representatives of the families Osmylidae, Hemerobiidae, Chrysopidae, Mantispidae, Polystoechotidae, Nymphidae, Psychopsidae, Ascalaphidae and Myrmeleontidae (SHEPARD 1967). They are absent in the outgroup taxa (MAKI 1936; RÖBER 1941; ACHTELIG 1967; DRESSLER & BEUTEL 2010).
 94. *Hypopharyngeal suspensorial sclerites represented by a pair of undifferentiated lateral plates*: *absent (0), present (1)*. — The broadening of the posterior part of the hypopharyngeal suspensorial sclerites to hypopharyngeal suspensorial plates as in *Nevrothus* (Fig. 7A) is reported for *Chrysopa*, *Polystoechotes* (SHEPARD 1967), *Sisyra* (RANDOLF et al. 2013), *Hemerobius* (TOWNSEND 1935: fig. 74) and *Sialis* (RÖBER 1941; TOWNSEND 1935: fig. 78). It is absent in *Dichrostigma* (ACHTELIG 1967), *Chauliodes* (MAKI 1936), *Trachypachus* (DRESSLER & BEUTEL 2010: fig. 3C: su-va) and *Ochthebius* (BEUTEL et al. 2003).
 95. *M. scapopedicellaris posterior (0an9)* and *M. scapopedicellaris anterior (0an10)*: *absent (0), present (1)* see RANDOLF et al. (2013; char. 90). — As in all other studied Neuroptera four scapopedicellar muscles (0an7–0an10) with four distinctly different insertions are present in Nevrothidae, while in Megaloptera and Raphidioptera there are only two scapopedicellar muscles (MAKI 1936; RÖBER 1941; KELSEY 1954; MATSUDA 1956; ACHTELIG 1967). In *Trachypachus* two are present, one of which is bipartite (DRESSLER & BEUTEL 2010). The presence of four muscles is the ancestral condition in insects (MATSUDA 1965), which can be observed in *Machilis* (BITSCH 1963) and Embioptera (RÄHLE 1970), but also within some Endopterygota, e.g. Lepidoptera (HANNEMANN 1956: *Micropterix calthella*).
 96. *M. ampulloaortica (0ah2)*: *absent (0), present (1)*. — In *Nevrothus* and other examined neuropteran species (*Chrysopa dorsalis*, *Polystoechotes punctata*, *Sisyra terminalis*), *M. ampulloaortica* (0ah2) could be identified to be the dilator of the antennal ampulla. In Megaloptera, as in *Nevrothus*, *M. ampulloaortica* (0ah2) is present (SELMAN 1965). The treatments of MATSUDA (1956) and ACHTELIG (1967) do not cover the muscles of the antennal ampullae, so the condition in Raphidioptera is unclear. In Coleoptera dilator muscles of the antennal ampullae are absent (PASS et al. 2006).
 97. *M. labroepipharyngalis (0lb5)*: *absent (0), present (1)* see RANDOLF et al. (2013; char. 91). — The *M. labroepipharyngalis* is absent in *Nevrothus*, *Sisyra*, *Polystoechotes*, *Hemerobius*, *Osmylus*, *Euroleon* and *Nemoptera* (KORN 1943; BEUTEL et al. 2010b; RANDOLF et al. 2013). The *M. labroepipharyngalis* is present in the outgroup taxa Raphidioptera and Megaloptera (MAKI 1936; RÖBER 1941; ACHTELIG 1967) and absent in Coleoptera (BEUTEL et al. 2003; DRESSLER & BEUTEL 2010).
 98. *M. palpopalpalis maxillae secundus (0mx13)*: *absent (0), present (1)*. — The *M. palpopalpalis maxillae secundus* is present in *Chauliodes* (MAKI 1936) and *Osmylus* (BEUTEL et al. 2010b). It is absent in *Nevrothus*, *Sisyra* (RANDOLF et al. 2013), *Chrysopa*, *Hemerobius*, *Polystoechotes*, *Nemoptera* (KRENN et al. 2008), *Euroleon* (KORN 1943), *Dichrostigma* (ACHTELIG 1967), and Coleoptera (BEUTEL et al. 2003; DRESSLER & BEUTEL 2010).
 99. *M. submentopraementalis (0la8)*: *absent (0), present (1)* see RANDOLF et al. (2013; char. 92). — The *M. submentopraementalis* is absent in Nevrothidae as in other Neuroptera (KORN 1943; BEUTEL et al. 2010b), Megaloptera (MAKI 1936; RÖBER 1941; KELSEY 1954) and Raphidioptera (ACHTELIG 1967). It is present in Coleoptera (BEUTEL et al. 2003; DRESSLER & BEUTEL 2010).
 100. *M. submentomentalis (0la10)*: *absent (0), present (1)* see RANDOLF et al. (2013; char. 93). — The *M. submentomentalis* is present in Nevrothidae as in all hitherto studied Neuroptera (KORN 1943; BEUTEL et al. 2010b), Megaloptera (MAKI 1936; RÖBER 1941; KELSEY 1954) and Raphidioptera (MATSUDA 1956; ACHTELIG 1967; see char. 92). It is absent in Coleoptera (BEUTEL et al. 2003; DRESSLER & BEUTEL 2010).
 101. *M. praementopalpalis internus (0la13)*: *absent (0), present (1)*. — *M. praementopalpalis internus* is absent in *Dichrostigma* (ACHTELIG 1967), *Chauliodes* (MAKI 1936), *Sialis* (RÖBER 1941), *Nevrothus*, *Hemerobius*, *Nemoptera* (KRENN et al. 2008) and Coleoptera (BEUTEL et al. 2003; DRESSLER & BEUTEL 2010). It is present in *Sisyra* (RANDOLF et al. 2013), *Osmylus* (BEUTEL et al. 2010b), *Chrysopa*, *Polystoechotes* and *Euroleon* (KORN 1943).
 102. *M. oralis transversalis ventralis (0hy16)*: *absent (0), present (1)* see RANDOLF et al. (2013; char. 94). — The *M. oralis transversalis ventralis* is present in *Nevrothus* and other neuropteran families (KRENN et al. 2008; RANDOLF et al. 2013), as well as in Raphidioptera (ACHTELIG 1967: *M. transversalis buccae ventralis*), *Sialis* (RANDOLF et al. 2013) and *Corydalus* (KELSEY 1954). MAKI (1936) did not describe the constrictors of the pharynx. In Coleoptera this muscle is absent (BEUTEL et al. 2003; DRESSLER & BEUTEL 2010). In Hymenoptera a homologous muscle seems to be present (DUNCAN 1939: *Vespa pensylvanica*: posterior intrinsic pharyngeal muscle).
 103. *Mandibular gland*: *absent (0), present (1)* see RANDOLF et al. (2013; char. 95). — A mandibular gland is present in *Nevrothus* as in other studied Neuroptera (BEUTEL et al. 2010b; RANDOLF et al. 2013) and *Sialis* (RÖBER 1941). It is absent in *Dichrostigma*

- ma*, *Corydalus*, *Chauliodes* (MAKI 1936; KELSEY 1957; ACHTELIG 1967) and Coleoptera (BEUTEL et al. 2003; DRESSLER & BEUTEL 2010).
104. *Submental gland with multiporous plate opening: absent (0), present (1).* — A submental gland with a multiporous plate opening is present in *Nevrorthus*. The presence of glandular tissue in *Osmylus* at the same position was previously reported by BEUTEL et al. (2010b); however, the distinctive opening, which is an oval multiporous plate and which is identical in both genera, was not described there.
 105. *Trichobothria on ectoproct in males: absent (0), loosely forming a band (1), organized in a rosette (2) see ASPÖCK et al. (2001).* — We replaced character state “reduced” (3) with “absent” (0) and added data for *Dichrostigma* (ASPÖCK et al. 1991: fig. 625), *Ithone* (ACKER 1960: fig. 59), *Hemerobius* (ASPÖCK et al. 1980: fig. 561), *Lomamyia* (MACLEOD & ADAMS 1967: fig. 13) and *Psychopsis* (ACKER 1960: fig. 74).
 106. *Ectoproct in males: unpaired (0), paired (1) see ASPÖCK et al. (2001).* — *Dichrostigma* was scored as “unpaired” (ASPÖCK et al. 1991: fig. 625).
 107. *Tergite and sternite of segment 9 in males: not forming a ring (0), forming a ring (1) see ASPÖCK et al. (2001).* — *Dichrostigma* was scored with state (1): “forming a ring” (ASPÖCK et al. 1991: fig. 625).
 108. *Gonapophyses of the ninth gonocoxites in males: absent (0), present (1) see ASPÖCK et al. (2001).* Gonapophyses are present in *Dichrostigma* (ASPÖCK et al. 1991: figs. 624, 625), *Polystoechotes* (ASPÖCK & ASPÖCK 2008: fig. 64), *Osmylus* (ASPÖCK & ASPÖCK 2008: fig. 23), *Coniopteryx* (ASPÖCK & ASPÖCK 2008: figs. 26, 27) and *Psychopsis* (ASPÖCK & ASPÖCK 2008: fig. 77). They are absent in *Chauliodes*, *Sialis* (ASPÖCK & ASPÖCK 2008), *Ithone* (ASPÖCK & ASPÖCK 2008: figs. 65, 66), *Sisyra* (ASPÖCK & ASPÖCK 2008: fig. 21), *Nallachius* (ASPÖCK & ASPÖCK 2008: figs. 31, 32), *Lomamyia* (MACLEOD & ADAMS 1967: fig. 11), *Mucroberotha* (ASPÖCK & ASPÖCK 2008: fig. 39), *Mantispa* (ASPÖCK & ASPÖCK 2008: figs. 40, 41), *Hemerobius* (ASPÖCK et al. 1980: fig. 562), *Chrysopa* (ASPÖCK et al. 1980: figs. 696, 697), *Nymphes* (ASPÖCK & ASPÖCK 2008: figs. 88, 89), *Libelloides* (ASPÖCK & ASPÖCK 2008: figs. 97–99), *Euroleon* (ASPÖCK et al. 1980: figs. 829–831) and *Nemoptera* (ASPÖCK & ASPÖCK 2008: figs. 86, 87).
 109. *Gonocoxite 10 complex in males: absent (0), present (1).* — The gonocoxite 10 complex is present in *Dichrochrysa* (ASPÖCK et al. 1991: figs. 624, 625 as “p”), *Chauliodes* (ACKER 1960: figs. 27, 28 as “paramere”), *Sialis* (ASPÖCK & ASPÖCK 2008: figs. 7, 8), *Nevrorthus* (ASPÖCK et al. 1980: fig. 347, apical part of sclerite labeled as S9), *Polystoechotes* (ASPÖCK & ASPÖCK 2008: fig. 64), *Hemerobius* (ASPÖCK et al. 1980: fig. 564 as “paramere”), *Chrysopa* (ASPÖCK et al. 1980: figs. 696, 697 as “psp”), *Osmylus* (ASPÖCK & ASPÖCK 2008: figs. 23, 24), *Nallachius* (ASPÖCK & ASPÖCK 2008: figs. 31, 32), *Lo-*
mamyia (MACLEOD & ADAMS 1967: figs. 11, 12 as “mu”), *Mucroberotha* (ASPÖCK & ASPÖCK 2008: fig. 39), *Mantispa* (ASPÖCK & ASPÖCK 2008: figs. 40, 41), *Helicoconis* (ASPÖCK et al. 1980: figs. 256, 257 as “pa” and “p”), *Coniopteryx* (ASPÖCK & ASPÖCK 2008: fig. 28), *Psychopsis* (ASPÖCK & ASPÖCK 2008: fig. 78), *Nymphes* (ASPÖCK & ASPÖCK 2008: fig. 89), and *Euroleon* (ASPÖCK et al. 1980: figs. 828–831 as “pa”). It is absent in *Ithone* (ASPÖCK & ASPÖCK 2008: figs. 65, 66), *Sisyra* (ASPÖCK & ASPÖCK 2008: fig. 22) and *Libelloides* (ASPÖCK & ASPÖCK 2008: figs. 98, 99).
 110. *Gonocoxite 11 in males: absent (0), present (1).* — Gonocoxite 11 is present in *Sialis* (ASPÖCK & ASPÖCK 2008: figs. 7, 8), *Nevrorthus* (ASPÖCK et al. 1980: figs. 346, 349 as “gs”), *Polystoechotes* (ASPÖCK & ASPÖCK 2008: figs. 63, 64), *Ithone* (ASPÖCK & ASPÖCK 2008: figs. 65, 66), *Osmylus* (ASPÖCK & ASPÖCK 2008: fig. 24), *Sisyra* (ASPÖCK & ASPÖCK 2008: figs. 21, 22), *Nallachius* (ASPÖCK & ASPÖCK 2008: figs. 31, 32), *Lomamyia* (MACLEOD & ADAMS 1967: figs. 10, 11 as “gs”), *Mucroberotha* (ASPÖCK & ASPÖCK 2008: fig. 39), *Mantispa* (ASPÖCK & ASPÖCK 2008: figs. 40, 41), *Psychopsis* (ASPÖCK & ASPÖCK 2008: fig. 75), *Nymphes* (ASPÖCK & ASPÖCK 2008: figs. 88, 89), *Libelloides* (ASPÖCK & ASPÖCK 2008: figs. 97, 98, 99), *Euroleon* (ASPÖCK et al. 1980: figs. 828–831 as “gs”) and *Nemoptera* (ASPÖCK & ASPÖCK 2008: fig. 87). It is absent in *Dichrostigma* (ASPÖCK et al. 1991: fig. 625), *Chauliodes* (ACKER, 1960, fig. 27), *Hemerobius* (ASPÖCK et al. 1980: fig. 561) and *Chrysopa* (ASPÖCK et al. 1980: figs. 695, 696).
 111. *Gonostylus 11 in males: absent (0), present (1).* — Gonostylus 11 is present in *Sialis* (ASPÖCK & ASPÖCK 2008: figs. 7, 8), *Nevrorthus* (ASPÖCK et al. 1980: figs. 346–349), *Polystoechotes* (ASPÖCK & ASPÖCK 2008: figs. 63, 64), *Sisyra* (ASPÖCK & ASPÖCK 2008: fig. 22), *Mantispa* (ASPÖCK & ASPÖCK 2008: fig. 41), *Psychopsis* (ASPÖCK & ASPÖCK 2008: figs. 75, 76), *Nymphes* (ASPÖCK & ASPÖCK 2008: figs. 88, 89), *Nemoptera* (ASPÖCK & ASPÖCK 2008: fig. 87) and *Euroleon* (ASPÖCK et al. 1980: figs. 828–831 as “med”). It is absent in *Dichrostigma* (ASPÖCK et al. 1991: fig. 625), *Chauliodes* (ACKER 1960: figs. 27, 28), *Ithone* (ASPÖCK & ASPÖCK 2008: figs. 65, 66), *Hemerobius* (ASPÖCK et al. 1980: figs. 561–563), *Chrysopa* (ASPÖCK et al. 1980: figs. 695–697), *Osmylus* (ASPÖCK & ASPÖCK 2008: figs. 23, 24), *Nallachius* (ASPÖCK & ASPÖCK 2008: figs. 31, 32), *Lomamyia* (MACLEOD & ADAMS 1967: figs. 10, 11), *Mucroberotha* (ASPÖCK & ASPÖCK 2008: fig. 39) and *Libelloides* (ASPÖCK & ASPÖCK 2008: figs. 97–99).
 112. *Attachment of ninth gonocoxites to tergite 9 in females: by a narrow articulation (0), broad connection (1) see ASPÖCK et al. (2001).* — We scored *Dichrostigma* with having “a narrow articulation” (ASPÖCK et al. 1991: fig. 2052).

113. *Length and shape of ninth gonocoxites in females: club-shaped (0), elongate, tube-shaped (1), shortened, broadly oval (2) see ASPÖCK et al. (2001). — We scored *Dichrostigma* as “elongate, tube-shaped” (ASPÖCK et al. 1991: fig. 2052).*
114. *Ninth gonocoxites in males, position: along the caudal margins of tergite 9 and sternite 9 (0), at or near the base of tergite 9 (1), associated with the gonarcus (= gonocoxites 11) (2), associated with the ectoproct (3) see ASPÖCK et al. (2001). — We scored *Dichrostigma* with state (1): “at or near the base of tergite 9” (ASPÖCK et al. 1991: fig. 625).*

4.2. Results of phylogenetic analyses

The analysis using equal weights yielded seven most parsimonious trees (MPTs) with a length of 259 steps, a consistency index (CI) of 0.525, and a retention index (RI) of 0.683. In five MPTs and the trees retrieved by implied weighting with K1 to K15, the Sisyridae were retrieved as sister to a clade comprising all other neuropteran families. In two of the MPTs, Nevrothidae was sister group to the rest of Neuroptera. In all MPTs and in K2 to K15 trees, *Osmylus* was retrieved as sister to the rest of Neuroptera excluding Sisyridae and Nevrothidae. Only in K1 was *Osmylus* sister to the clade (*Hemero-bius* + *Chrysopa*).

Bremer Support values are indicated in Fig. 9; Bootstrap and Partitioned Bremer Support values in Fig. 10. Apomorphies are listed in the following with homoplasious characters in italics.

Sialidae + Neuroptera: 61.1. *Habitat: aquatic larvae* (DELTRAN); 87.1. Mandibular field of short sensilla present; 94.1. Hypopharyngeal suspensorial sclerites represented by a pair of undifferentiated lateral plates present; 96.1. *M. ampullosa* present (DELTRAN); 103.1. Mandibular gland present; 110.1. Gonocoxite 11 present (ACCTRAN and DELTRAN); 111.1. Gonostylus 11 present (DELTRAN); 111.1. *Gonostylus 11 present* (ACCTRAN).

Neuroptera [Bremer Support (BS) = 14]: 1.1. Cervix present; 18.1. *Labrum fused with clypeus*; 22.1. Specialized terminal seta of flagellum present (ACCTRAN optimization); 26.1. Mandibulomaxillary stylets present; 27.1. Stylets slender, longer than head capsule; 38.1. Galea absent; 39.1. Maxillary palp absent; 40.1. *M. craniocardinalis* absent; 42.1. Intrinsic muscle of stylet present; 52.1. Mandibulomaxillary cephalic gland present; 53.1. Lateral gland of maxillary stylet present; 70.1. *Origin of M. tentorioscapalis anterior (0an1) on ata and dta*; 73.1. *M. tentoriomandibularis medialis inferior (0md8) present* (DELTRAN); 74.1. *M. tentoriomandibu-*

laris lateralis inferior (0md6) present (DELTRAN); 77.1. *Anterior component of M. tentoriostipitalis (0mx4) present* (ACCTRAN); 80.1. *M. tentoriobuccalis lateralis (0bu4) present*; 83.0. Galea absent; 84.1. Temporal sulcus present; 85.1. Molar process of mesal mandibular edge present; 91.1. Paraglossae present; 95.1. *M. scapopedicellaris posterior (0an9) and M. scapopedicellaris anterior (0an10) present*; 97.0. *M. labroepipharyngalis (0lb5) absent* (ACCTRAN); 101.1. *M. praementopalpalis internus (0la13) present* (ACCTRAN); 114.2. Ninth gonocoxites associated with the gonarcus.

Neuroptera excluding Sisyridae: 37.1. Poison system present; 88.1. Galea: distinctly transversely divided in 2 parts (basi- and distigalea) by membrane; 104.1. Submental gland with multiporous plate opening present (ACCTRAN).

Neuroptera excluding Sisyridae and Nevrothidae [BS = 3]: 60.1. Attachment site of cryptonephric Malpighian tubules embedded in a pear-shaped organ; 61.0. *Habitat terrestrial*; 65.1. Dorsal tentorial arms weakly developed; 66.1. *Laminatentorium present*; 75.1. *M. tentoriomandibularis medialis superior (0md7) present*; 76.3. Origin of *M. tentoriocardinalis (0mx3)* on ata; 86.1. *Mandibular row of stiff bristles present*; 87.0. *Mandibular field of short sensilla absent*; 93.1. *Palpimaculae present* (ACCTRAN); 101.1. *M. praementopalpalis internus (0la13) present* (DELTRAN); 111.0. *Gonostylus absent* (ACCTRAN).

Neuroptera excluding Sisyridae, Nevrothidae and Osmylidae [BS = 1]: 43.1. *Postmentum undivided*; 80.0. *M. tentoriobuccalis lateralis (0bu4) absent*; 81.1. Origin of *M. tentoriobuccalis lateralis (0bu4)* on ata (ACCTRAN); 104.0. *Submental gland with multiporous plate opening absent* (ACCTRAN); 113.2. *Ninth gonocoxites shortened and broadly oval*.

Polystoechotes + Ithone [BS = 5]: 2.1. *Dorsoventral depth of head capsule approximately equal to head length*; 4.1. Frontoclypeal region with abrupt change in the slope; 12.1. *Tentorium X-shaped, with distinctly constricted central part*; 20.1. Fixed curvature of antenna; 22.0. *Specialized terminal seta of flagellum absent* (ACCTRAN); 27.0. *Mandibulo-maxillary stylet short and compact*; 29.1. Distal thickness of mandibular stylet increased; 58.1. *Trumpet-shaped, elongate empodium of first instar larvae present* (ACCTRAN); 68.2. Anterior tentorial pits trumpet-like.

Neuroptera excluding Sisyridae, Nevrothidae, Osmylidae and Polystoechotes + Ithone [BS = 1]: 57.1. Tibia and tarsus of the hind legs fused (ACCTRAN); 70.0. *Origin of M. tentorioscapalis anterior (0an1) on ata* (ACCTRAN); 79.1. *Origin of the posterior component of M. tentoriostipitalis (0mx4) on pta*; 112.1. *Attachment of ninth gonocoxites to tergite 9 by broad connection*.

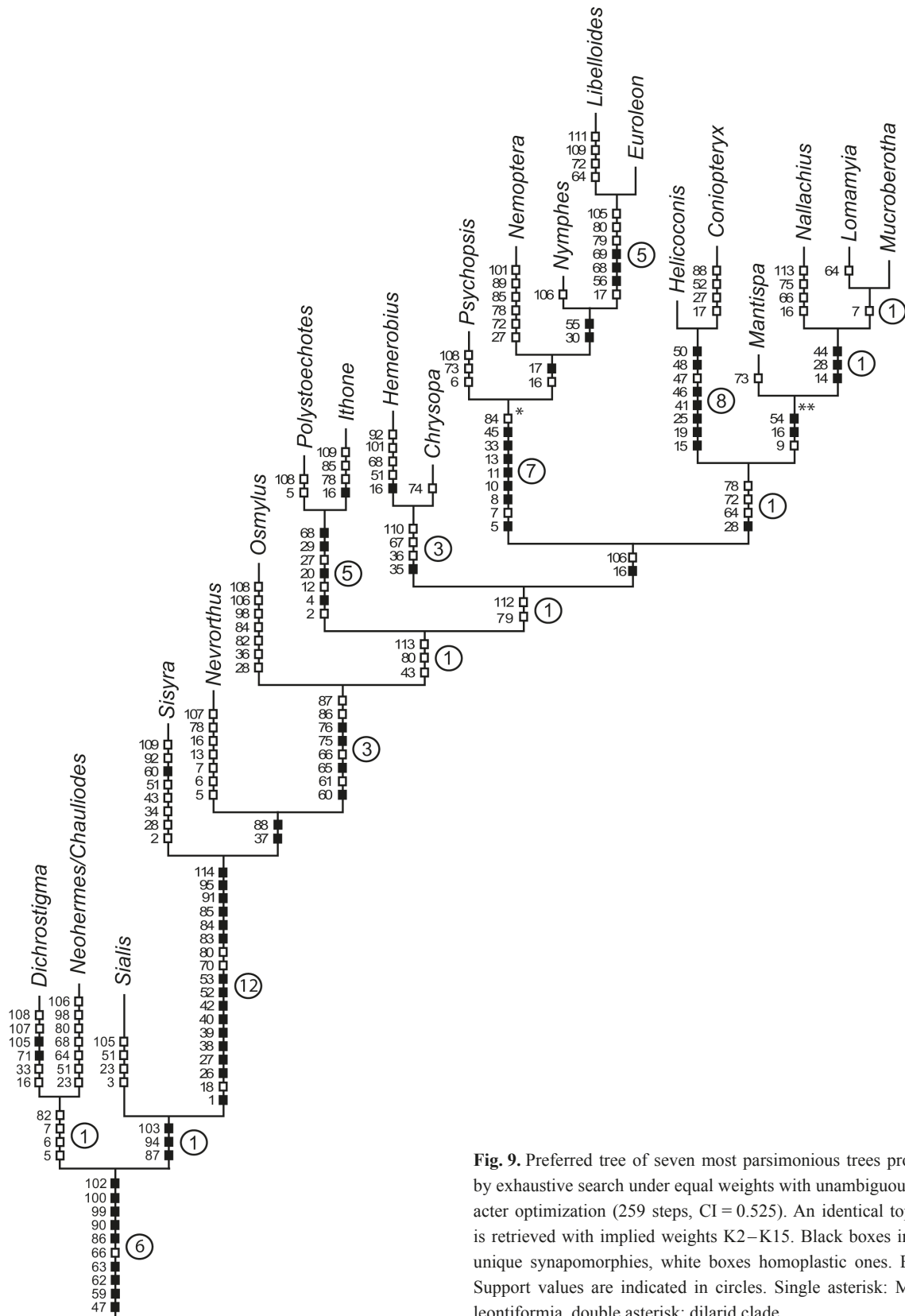


Fig. 9. Preferred tree of seven most parsimonious trees produced by exhaustive search under equal weights with unambiguous character optimization (259 steps, CI = 0.525). An identical topology is retrieved with implied weights K2–K15. Black boxes indicate unique synapomorphies, white boxes homoplastic ones. Bremer Support values are indicated in circles. Single asterisk: Myrmeleontiformia, double asterisk: dilariid clade.

***Hemerobius* + *Chrysopa* [BS = 3]:** 22.1. Specialized terminal seta of antenna (only in DELTRAN); 35.1. Longitudinal sulcus of basal maxillary element present; 36.1. Longitudinal apodemal ridge of intermediate maxillary element present; 57.1. Trumpet shaped empodium present, at least in first instar larvae (DELTRAN);

67.1. Median process on tentorial bridge present; 110.0. Gonocoxite 11 absent; 111.0. Gonostylus 11 absent (DELTRAN).

Myrmeleontiformia, Coniopterygidae and Dilarid clade: 16.2. Five corneae; 70.0. *Origin of M. tentorioscapalis anterior (0an1) on ata* (DELTRAN); 91.0. *Paraglossae absent* (ACCTTRAN); 106.1. *Paired ectoproct*; 111.1. *Gonostylus present* (ACCTTRAN).

Myrmeleontiformia [BS = 7]: 5.2. Gula small, triangular; 7.1. *Temples of late instar larvae absent*; 8.1. Hypostomal bridge present; 10.1. Mid-dorsal cervical apodeme present; 11.1. Dolichasterine setae present; 13.2. Posterior tentorial grooves located in the anterior third of the head capsule; 22.0. *Specialized terminal seta of flagellum absent* (ACCTTRAN); 33.1. Maxillary groove reduced; 45.1. Premental elements widely separated; 84.0. *Temporal sulcus absent*.

Myrmeleontiformia excluding Psychopsidae: 16.0. *Seven corneae*; 17.1. Ocular region forms a moderately raised, well-defined elevation; 21.1. Flagellum very slender and small (ACCTTRAN); 49.1. Sensory pit of distal labial palpomere present (ACCTTRAN); 57.0. *Tibia and tarsus of the hind legs not fused* (ACCTTRAN); 91.0. *Paraglossae absent* (DELTRAN).

Myrmeleontiformia excluding Psychopsidae and Neomopteridae: 21.1. Slender, small flagellum (DELTRAN); 30.1. Slender teeth of mandibular element of stylet; 55.1. Regular series of scoli on abdomen; 93.1. *Palpimaculae present* (DELTRAN).

Libelloides + Euroleon [BS = 5]: 17.2. *Ocular region forms a strongly convex elevation*; 32.1. Two or more mandibular teeth (DELTRAN); 49.1. *Sensory pit of distal labial palpomere* (DELTRAN); 56.1. Fusion of tibia and tarsus in the hind leg; 68.3. Anterior tentorial pits closed; 69.1. Anterior tentorial arms as flat tubes; 79.2. *Origin of the posterior component of M. tentoriostipitalis (0mx4) on tb-ata*; 80.1. *M. tentoriobuccalis lateralis (0bu4)*; 81.1 *Origin of M. tentoriobuccalis lateralis (0bu4) on ata* (DELTRAN); 105.0. *Trichobothria on ectoproct absent*.

Coniopterygidae + Dilarid clade [BS = 1]: 2.1. *Dorsoventral depth of head capsule approximately equal to head length* (ACCTTRAN); 28.2. Mandibulomaxillary stylet with straight distal inner margin, external margin concave; 34.1. *Proximal elements of maxilla strongly narrowed* (ACCTTRAN); 64.0. *Dorsal tentorial arms absent*; 72.1. *Origin of M. tentorioscapalis medialis (0an4) on ata*; 78.0. *Posterior component of M. tentoriostipitalis (0mx5) absent*; 93.0. *Palpimaculae absent* (ACCTTRAN); 105.0. *Trichobothria on ectoproct absent* (ACCTTRAN).

Helicoconis + Coniopteryx [BS = 8]: 2.1. *Dorsoventral depth of head capsule approximately equal to head length* (DELTRAN); 15.1. Posterior shift of the anterior tentorial arm; 19.1. Antennomeres 2 and 3 fused; 25.1. Tricondylic articulation of mandible; 34.1. *Proximal elements of maxilla strongly narrowed* (DELTRAN); 41.1. Teeth on lateral surface of the maxillary blade present; 46.1.

Large anterior process of the prementum present; 47.1. *Reduced number of labial palpomeres*; 48.1. Increased size of labial palpomeres; 50.1. Elongate sensory area on distal labial palpomere present; 57.0. *Fusion of tibia and tarsus in the hind leg absent* (ACCTTRAN); 75.0. *M. tentoriomandibularis medialis superior (0md7) absent* (ACCTTRAN); 105.0. *Trichobothria on ectoproct absent* (DELTRAN); 107.1. *Tergite and sternite of segment 9 form a ring* (ACCTTRAN); 108.1. *Gonapophyses of the ninth gonocoxites present* (ACCTTRAN); 114.3. Ninth gonocoxites associated with the ectoproct (ACCTTRAN).

Mantispidae + Dilaridae + Berothidae + Rhachiberothidae: 9.1. *Frontoclypeal sulcus absent*; 16.5. Two corneae (one in Dilaridae); 24.1. Overlapping scales on antennae and maxillae (ACCTTRAN); 54.1. Head of secondary larvae distinctly reduced in size; 57.1. *Trumpet shaped empodium present, at least in first instar larvae* (DELTRAN); 58.1. *Trumpet-shaped, elongate empodium of first instar larvae present* (ACCTTRAN); 112.0. *Attachment of ninth gonocoxites to tergite 9 by a narrow articulation* (ACCTTRAN).

Dilaridae + Berothidae + Rhachiberothidae [BS = 1]: 2.0. *Head of later instar larvae dorsoventrally compressed* (ACCTTRAN); 14.1. Tentorial bridge vestigial or absent; 28.1. Mandibulomaxillary stylet straight and nearly subparallel; 34.0. *Proximal elements of maxilla about as broad as base of maxillary stylet* (ACCTTRAN); 44.1. Postmentum at least two times longer than wide; 105.2. *Trichobothria on ectoproct organized in a rosette* (ACCTTRAN); 111.0. *Gonostylus II absent* (ACCTTRAN).

Berothidae + Rhachiberothidae [BS = 1]: 7.1. *Temples of later instar larvae present*; 24.1. Overlapping scales on antennae and maxillae present (DELTRAN); 74.0. *M. tentoriomandibularis lateralis inferior (0md6) absent* (ACCTTRAN); 112.1. *Attachment of ninth gonocoxites to tergite 9 by broad connection* (ACCTTRAN).

5. Discussion

5.1. Morphology

The cephalic features of *Nevrorthus* are very similar to the condition described for other neuropteran taxa (MILLER 1933; TOWNSEND 1935; SHEPARD 1967). The temporal sulcus has the course specific for Neuroptera: it runs between the dorsolateral angle of the occipital foramen and the rim of the eye (SHEPARD 1967) while in other insects it is convergent between the eyes (SNODGRASS 1960). The clypeus is undivided and the postocciput is deeply in-

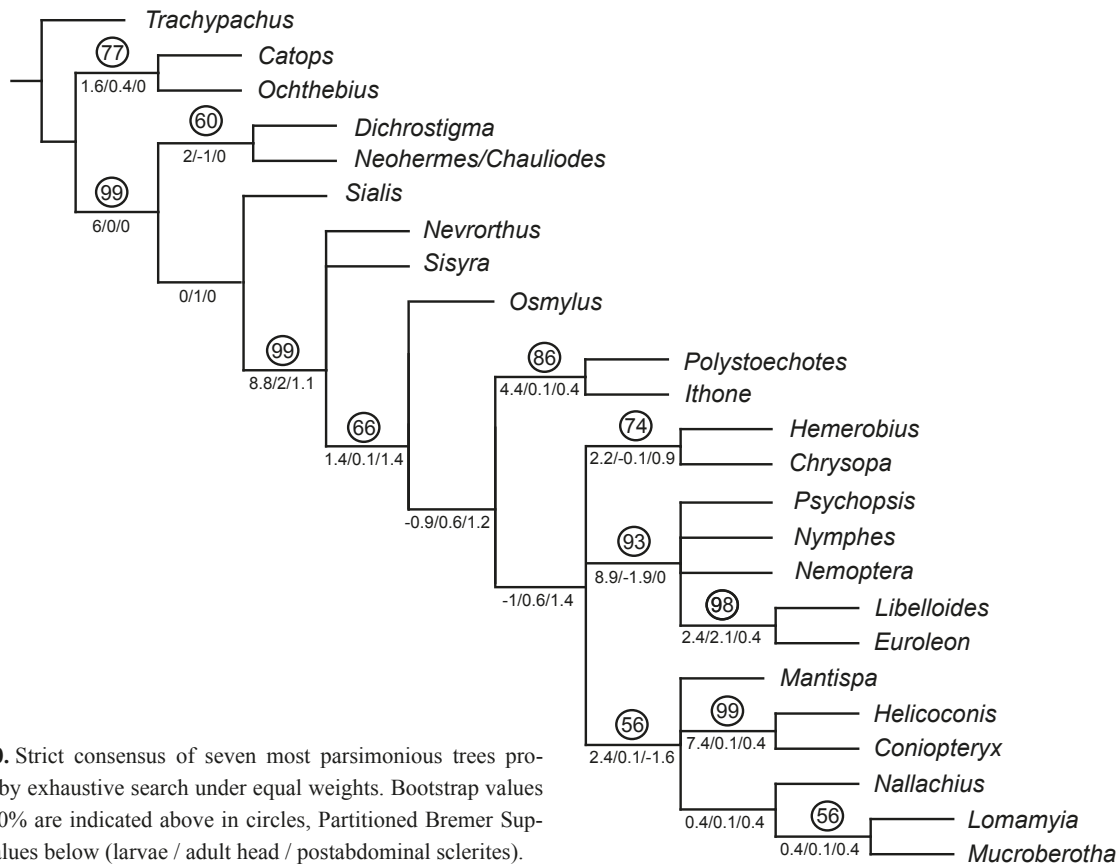


Fig. 10. Strict consensus of seven most parsimonious trees produced by exhaustive search under equal weights. Bootstrap values over 50% are indicated above in circles, Partitioned Bremer Support values below (larvae / adult head / postabdominal sclerites).

flected and enveloped by folds of the cervical membrane (SHEPARD 1967).

A conspicuous external feature of *N. apatlios* is the dome-shaped elevation of the frontodorsal head region, covered with long setae. Up to three setose elevated patches are present in some neuropteran families, called ocellar or cranial pulvini, and likely to be homologous with the ocelli-bearing prominences in Osmylidae (OSWALD 1993; BEUTEL et al. 2010b). The homology of the dome-shaped elevation in *Nevorthus* with the pulvini is assumed due to the similarity in structure, i.e., the covering with conspicuous long setae, and the same position. If three pulvini are present they occur at the same position as the ocelli, a median one in front of the frontal sulci and two dorsolateral ones on both sides of the coronal sulcus. In *Nevorthus* the median pulvinus is distinct and discernable, and an area bearing similar setae is described for Polystoechotidae and Ithonidae and was interpreted to be a vestige of the median ocellus by SHEPARD (1967). The posterior part of the dome in *Nevorthus* is interpreted to be the enlarged confluent dorsolateral cranial pulvini. The homologization is most plausible, particularly when considering the family Rhachiberothidae, where both states occur, i.e., three distinct pulvini and a single setose dome-shaped elevation, each in one of two closely related genera (ASPÖCK & MANSSELL 1994).

Paraglossae that are folded onto the ligula as observed in *Nevorthus* have previously been identified in several neuropteran families (SULC 1914; RANDOLF et al. 2013) and might be a common phenomenon in Neu-

roptera. They form, together with the ligula, a secondary prolongation of the salivary opening to the tip of the ligula. There are no observations on the feeding habits of *Nevorthus*, but MALICKY (1984) often found the adults on sticky leaves and assumes that they feed on honeydew. The secondary prolongation is most likely an adaptation to feeding not only on liquid but also on desiccated honeydew by applying the saliva to the leaf surface to liquidize it (RANDOLF et al. 2013).

PASS et al. (2006) assume *M. ampulloparyngalis* (0ah3) to be the dilator muscle of the antennal ampulla in Neuroptera. This does not correspond with our finding that in Nevorthidae and the other studied neuropteran families *M. ampulloaortica* (0ah2) is the dilator muscle of the antennal ampullae.

A submental gland with a multiporous plate opening, as found in *Nevorthus* and *Osmylus*, is absent in other studied Neuroptera and is not reported for any of the outgroup taxa (MAKI 1936; KELSEY 1954; ACHELIG 1967; BEUTEL et al. 2003; DRESSLER & BEUTEL 2010). A gland with an identical internal structure and multiporous opening is also reported for *Forficula auricularia* (Dermaptera) at the same position (LHOSTE 1957: glandes labiales, plaque criblée; MOULINS 1969: glandes labiales, plaque criblée) and was interpreted to be homologous with the salivary gland which is absent (MOULINS 1969). However, this interpretation is not plausible for Nevorthidae and Osmylidae, since they both possess a submental gland and an independent salivary system. A gland of identical internal structure and identical type of opening

but positioned on the first abdominal segment is present in the myrmecophilous beetle *Claviger testaceus*, where it secretes allomones to suppress aggressive behavior of ants (CAMMAERTS 1974: glande de Wasmann). The function of the submental gland in *Nevrorthus* and *Osmylus* remains open.

Unique characters of *Nevrorthus* within Endopterygota are the presence of *M. stipitalis transversalis* (0mx11) and a hypopharyngeal transverse ligament. *M. stipitalis transversalis* (0mx11) was hitherto only documented for *Thermobia* (CHAUDONNERET 1950: Muscle dépresseur stipital postérieur), *Machilis* (BITSCH 1963: ligament maxillaire 3), Grylloblattodea and Mantophasmatodea (WIPFLER et al. 2011). The transverse stipital muscle reported by ZWICK (1981) and KRISTENSEN (1991) for Plecoptera is probably homologous with 0mx9; for discussion see WIPFLER et al. (2011). A hypopharyngeal transverse ligament connecting the lateral sides of the hypopharynx is otherwise only described for *Zygentoma* (CHAUDONNERET 1950: *Thermobia*: muscle hypopharyngien transverse), Dermaptera (MOULINS 1969: *Forficula*: formation interfulcræle), Embioptera (RÄHLE 1970: *Embia*: LHYP) and Blattodea (MOULINS 1971: *Blaberus* [as *Blabera*]: FHT). MOULINS (1971) interprets this ligament as a stabilizing structure to prevent the deformation of the hypopharynx during food uptake and that it represents a relic of the ligamentous endoskeleton of apterygote insects. In *N. apateltios* it takes the function of an endoskeleton by serving as an attachment site for a part of the dorsal salivary muscles. In *Forficula auricularia* it is connected with the *M. craniomandibularis internus* so that the opening of the mandibles causes a forward movement of the hypopharynx (MOULINS 1969).

5.2. Phylogeny

In contrast to previous analyses based on a combination of larval and head anatomical characters (ZIMMERMANN et al. 2011; RANDOLF et al. 2013), we now retrieve also *Nevrorthidae* as the first offshoot in the most parsimonious trees. This result is due to deactivation of character 89 (see 4.1.), the presence of a finger-like process on galea, which previously emerged as an additional synapomorphy of Neuroptera excluding Sisyridae in RANDOLF et al. (2013). Still, the results retrieved under implied weighting strongly corroborate the divergence of Sisyridae in the first bifurcation (K1–15), which is thus our favored hypothesis. This relationship was hitherto supported only by larval characters (ZIMMERMANN et al. 2011; RANDOLF et al. 2013) and is now corroborated by two additional anatomical head characters: the division of the galea into basi- and distigalea (char. 88.1) in all Neuroptera excluding Sisyridae and the development of a submental gland in *Nevrorthidae* and *Osmylidae* (char. 104.1, ACCTRAN).

A clade of Neuroptera excluding Sisyridae and *Nevrorthidae* is supported by all three partitions (Fig. 10):

larvae (PBS: 1.4), adult head (PBS: 0.1) and postabdominal sclerites (PBS: 1.4). Crucial synapomorphies are the development of cryptonephric Malpighian tubules with a pyriform organ in larvae (char. 60.1), the transition of the larval habitat from aquatic to terrestrial (char. 61.0), as well as the development of a laminatentorium in the tentorium of the adult head (char. 66.1). This relationship was also retrieved in HARING & ASPÖCK (2004), ASPÖCK & ASPÖCK (2008), ZIMMERMANN et al. (2011) and RANDOLF et al. (2013).

The position of *Osmylidae* as third offshoot is supported by head anatomical characters (PBS: 0.6) and characters of the genital sclerites (PBS: 1.3), but contradicted by larval characters (PBS: –0.9). However, *Osmylidae* constituting a clade together with Hemerobiidae and Chrysopidae as retrieved in BEUTEL et al. (2010a,b), ZIMMERMANN et al. (2011) and RANDOLF et al. (2013), implies an independent evolution of the highly complex submental gland in *Nevrorthidae* and *Osmylidae* or multiple losses in the other neuropteran families. The relationship *Sisyridae* + (*Nevrorthidae* + (*Osmylidae* + (rest))) with a unique appearance and loss of this character as obtained under implied weighting with K2–15 (char. 104.1; Fig. 9; see 4.2.) is more plausible. *Osmylidae* as third offshoot was first retrieved in a molecular analysis (HARING & ASPÖCK 2004) and is supported by a study of the genital sclerites (ASPÖCK & ASPÖCK 2008).

The addition of data for adult *Chauliodes* did not resolve the conflict of paraphyletic Megaloptera (ZIMMERMANN et al. 2011; RANDOLF et al. 2013). On the contrary, it corroborates a sistergroup relationship of Sialidae and Neuroptera in the strict consensus tree (Fig. 10) as retrieved in the recent analysis by RANDOLF et al. (2013). The support for this sistergroup relationship is found predominantly in the adult head (Fig. 10: PBS 1) with the following unique character transformations resulting as synapomorphies: the development of a mandibular gland (char. 103.1), hypopharyngeal suspensorial sclerites represented by a pair of undifferentiated lateral plates (char. 94.1) and a mandibular field of short sensilla (char. 87.1). Furthermore, the possession of a gonostylus 11 (char. 111.1; DELTRAN) is a synapomorphy of Sialidae and Neuroptera. However, traces of gonostyli 11 are found in some raphidiopteran species (ASPÖCK & ASPÖCK 2008) and thus apparently belong to the ground pattern being secondarily reduced in Raphidioptera and Corydalidae. It needs to be clarified if *M. ampulloaortica* is a synapomorphy of Sialidae + Neuroptera (char. 96.1; DELTRAN) or Neuropterida (char. 96.1; ACCTRAN) since data for Raphidioptera and Corydalidae are missing. However, a paraphyletic Megaloptera conflicts with most recent independent analyses, e.g. HARING & ASPÖCK (2004), ASPÖCK & ASPÖCK (2008), BEUTEL & FRIEDRICH (2008), WANG et al. (2012), PETERS et al. (2014).

In general, the percentage of nodes supported by all three partitions, larvae, adult head and genital sclerites, is high (66.7%; 10 of 16 nodes; Fig. 10). In contrast to the findings of MEIER & LIM (2009), the Partitioned Bremer Support is higher for larval characters than for adult

characters in the present study (Fig. 10). This can be explained by the greater number of larval characters (63 vs. 49 in adult) and by the completeness of the matrix (see S1; 95% of all characters were scored for larvae vs. 71% for adults; datasets for 12 of 24 investigated taxa were complete for larval characters vs. two of 24 for adult characters).

The retrieved phylogenetic relationships have implications on the interpretation of the evolution of the following larval characters that have long been in the center of interest:

Poison system. In our results a poison system consisting of a poison gland with a poison channel is retrieved as a synapomorphy of all Neuroptera except Sisyridae (Fig. 9: char. 37.1). This stands in contrast to the traditional interpretation that the system is a synapomorphy of all Neuroptera with secondary loss in Sisyridae (ASPÖCK et al. 2012; BEUTEL et al. 2010a). One conflict that arises is whether the evolution of larval sucking tubes, the most prominent autapomorphy of Neuroptera, is plausible without simultaneous evolution of a poison gland and a poison channel to disable prey. The highly specialized feeding of sisyrid larvae on sessile sponges and bryozoans might explain a secondary loss of the poison system (BEUTEL et al. 2010a).

Cryptonephry. One alleged conflict with the hypothesis that the Sisyridae is the sister group to the remaining Neuroptera is that their larvae, in contrast to those of the Nevrothidae, have cryptonephric Malpighian tubules (char. 60.2). These are, among the taxa included in this analysis, otherwise only present in the terrestrial larvae of Neuroptera (char. 60.1), where they reabsorb water and in doing so prevent water deficiency. Cryptonephric Malpighian tubules were interpreted as a synapomorphy of all Neuroptera excluding Nevrothidae with reversal in the secondarily aquatic larvae of Sisyridae (ASPÖCK et al. 2001) or as a synapomorphy of Neuroptera with terrestrial larvae and an independent origin in Sisyridae (ASPÖCK et al. 2012). An independent evolution in Sisyridae is suggested by the different anatomy of the cryptonephric complex which lacks a pyriform organ in Sisyridae, a fact that has been not considered in previous analyses (BEUTEL et al. 2010a,b; ZIMMERMANN et al. 2011; RANDOLF et al. 2013). The necessity of larval Sisyridae to reabsorb water should be apparent by the fact that they pupate in a dry environment under barks of dead standing trees, moving up to 15 meter from the water edge and 6 meter high (WEISSMAIR 1993). In contrast to this, the aquatic larvae of Nevrothidae and Megaloptera which pupate in water (Nevrothidae; MALICKY 1984) or moist soil (Megaloptera; EVANS 1972) lack cryptonephric Malpighian tubules (NEW & THEISCHINGER 1993; LEIDY 1849). Finally, a scenario with cryptonephry as groundplan feature of Neuroptera, the development of a pyriform organ as a subsequent step in the transformation series and secondary loss of cryptonephry in Nevrothidae remains an optional hypothesis.

Maxillary head. A ventrally open head capsule constructed mainly from elements of the maxillae and absence of a gula (referred to as “maxillary head” by ASPÖCK 1992) has been interpreted as apomorphic for Hemerobiiformia (including Sisyridae) and Sialidae (ASPÖCK et al. 2001), whereas the ventrally closed compact head capsule of Nevrothiformia and Myrmeleontiformia has been understood to be the plesiomorphic condition (ASPÖCK 1992; ASPÖCK et al. 2001). Multiple independent evolution of the gula as retrieved in our analysis (char. 5) is certainly not plausible. As pointed out by ASPÖCK et al. (2001) the compact head capsule is likely to be the ground pattern for Neuropterida. However, BEUTEL et al. (2010a) emphasized that the ventral head closure in Myrmeleontiformia is established by a hypostomal bridge (char. 8.1) and not by a gula and thus is likely to have evolved independently as adaptation to capture a variety of large, active prey (MACLEOD 1964).

6. Concluding remarks

More data are highly desirable to achieve a solid phylogenetic reconstruction of Neuropterida. In the light of recent trends in the analysis of transcriptomic data, it can be hoped that a well-supported phylogeny is achieved soon. In any case, as BEUTEL & KRISTENSEN (2012) pointed out, morphological investigations are indispensable for tracing underlying evolutionary pathways and understanding transformations on the phenotypic level. In this context the newly discovered traits in *Nevrothus apatelios*, such as the submental gland, the hypopharyngeal transverse ligament and the *M. stipitalis transversalis*, are very exciting.

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Electronic Supplement Files

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

Files: randolf&al-nevrorthushead-asp2014-electronicsupplement.nex and –.winc. – Character matrix used in the present study.