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Short communication

The insect head rewound: Clarifications to the groundplan of Hexapoda (Pancrustacea)

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ABSTRACT

The organization of the hexapod head remains a cornerstone problem in arthropod systematics, central to segmental homology, character definition, higher-level phylogeny, and functional and evolutionary morphology. Recently, Nel et al. (2025) proposed an alternative interpretation of insect head segmentation that departs markedly from established anatomical and comparative frameworks. We evaluate the internal consistency and external coherence of that hypothesis using their model groups, broader taxonomic samples, prior studies (including crustaceomorph Pancrustacea) and our own investigations. We identify multiple implausible anatomical interpretations and logical contradictions in their reconstruction. Our reanalysis, supported by microtomographic imaging (μ- and SR-μ-CT), shows that the proposed revision lacks empirical foundation (*e.g.* Psocodea), does not meet its own definitions (*e.g.* Neuropteroidea), misidentifies homologs (*e.g.* Coleoptera, Formicidae), and is unsupported by fossil or developmental evidence. Consequently, the new theory yields unreliable homology statements and obscures groundplan conditions and character polarities of the hexapod head. We therefore reject the hypothesis that "intercalate" and "promandible" sclerites existed in the groundplan of Hexapoda, and the assumed plesiomorphy of dicondyly. Our findings clarify relationships among major head sclerites, endoskeletal elements, and the head capsule's strengthening ridges, underscoring the need for comprehensive anatomy, broad sampling, and logical rigor in resolving arthropod head evolution.

1. Introduction

The head of insects *sensu lato* (Hexapoda) is one of the most functionally significant and character-rich regions of the body, as explicitly shown in Beutel et al. (2011) for Holometabola. The evolution of the ancestral segmental boundaries and their markers is a longstanding conundrum (*e.g.*, Savigny, 1816; Crampton, 1928; Snodgrass, 1935) and remains a hotspot of paleo-evo-devo debate (*e.g.*, Zrzavý and Štys, 1997; Scholtz and Edgecombe, 2006; Fusco and Minelli, 2013; Ortega-Hernández et al., 2017; Lev et al., 2022; Posnien et al., 2023; Chipman, 2025). The head is generally agreed to be composed of the anterior procephalon, a non-segmental region bearing the (clypeo-)labrum and the compound eyes, innervated by the protocerebrum, and the posterior gnathocephalon, bearing the antennal, intercalary, mandibular, maxillary, and labial segments, and innervated by the deuterocerebrum, tritocerebrum, and subesophageal ganglia (*e.g.*, Posnien et al., 2023). Whether the boundaries of these ancestral regions remain identifiable in the head capsule of living Hexapoda

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remains imperfectly understood.

In a recent study, Nel et al. (2025) propose a resolution to the problem of insect head regionalization by invoking two novel sclerites and new interpretations of the anterior tentorial arms and the secondary mandibular articulation. Specifically, the authors propose multiple new groundplan conditions: (1) the intercalary segment of the adult insect head is present and identifiable across insects as a sclerite with clearly defined boundaries, which they name the “intercalate”; (2) the anterior tentorial arm is not an invagination, but a fold marking the segmental boundary between the oculolabral region and the gnathal or appendage-bearing region; (3) an additional sclerite is present between the mandible and head capsule, which they name the “promandible”; and (4) mandibular dicondyly is a symplesiomorphy of Hexapoda, rather than a derived and defining feature of Zygentoma + Pterygota. The authors base their hypothesis on three main observations: the presence of a seemingly differentiated sclerite laterad the postclypeus in a fossil stem-group of Thysanoptera (†*Moundthrips beatificus*), the apparent occurrence of a similar region in crickets (Gryllidae), and external morphological comparison across a sample of insects plus some crustaceomorphs (Malacostraca: Peracarida). They further justify their interpretation by invoking the bend-and-zipper model of head development (Fig. 1b), which is based on experimental falsification of the traditional banded model of dorsal head segmentation as classically illustrated by Snodgrass (1935, figures 54–59 therein) (Fig. 1a).

We fully acknowledge and respect the ambition and integrative intent of Nel et al.’s (2025) proposal. However, as evolutionary morphologists working across extant and fossil lineages, we find that the proposed framework introduces substantial inconsistencies with experimental, comparative, and fossil data. While we support the ongoing re-examination of insect groundplans, the system presented in Nel et al. risks propagating confusion within the wider morphological, systematic, and paleontological communities. We therefore address the alternative hypotheses for the groundplan and evolution of the insect head below, dividing our responses among six sections: (2.1) the interpretation of experimental work on *Tribolium* and the authors' chosen fossil representative; (2.2) the authors' interpretations of the “intercalate” across their sampled extant taxa; (2.3) implications from developmental work overlooked by the authors; (2.4) phylogenetic evidence contradicting the authors' inference that the “promandible” is a groundplan sclerite; (2.5) the distinction between supportive ridges and segmental boundaries, with examples across the Arthropoda, including †Trilobita and Remipedia; and (2.6) the inferences drawn from the authors' comparison to non-insect Pancrustacea, emphasizing evidence from Remipedia and the apterygote orders. Comparisons to the Remipedia are especially important for understanding the groundplan of Hexapoda, given that they are the most closely related group that does not have a strongly reduced in metameric organization (*e.g.*, Regier et al., 2010; Misof et al., 2014; Schwentner et al., 2017; Bernot et al., 2023). We base our critique on our published experience with questions of head anatomy and homology (*e.g.*, Wipfler et al., 2011; Beutel et al., 2014; Richter et al., 2019), the broader literature (see the references included below), and a selection of SR-μ-CT data, which we use to illustrate anatomical details that are not available from prior publications (Figs. 2 and 3). Throughout the text, we marked terms that required our judgement (~) from those of direct evidence (*).

2. Evaluating the head theory of Nel et al

2.1. On the “intercalate” sclerite: the model

At the model level, the authors’ assumption about the location of the cuticle of the intercalary segment would require substantial reorganization of the head, for which there is neither experimental evidence (*) nor available anatomical justification (~) (Fig. 1c). Nel et al. (2025) provide two central cases representing distantly related and highly derived species for the presence of the intercalate: the developmental study and synthesis of Posnien and Bucher (2010a, b) on *Tribolium castaenum* (Tenebrionidae, Coleoptera) and the fossil †*M. beatificus* (Thysanoptera), for which they report this sclerite.

Given the results of the experimental developmental study

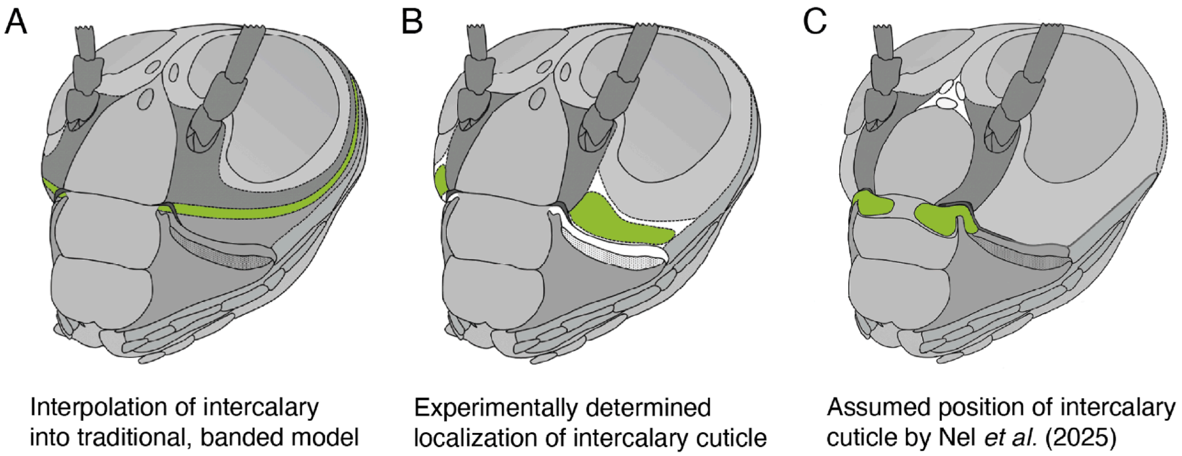

Fig. 1. The assumed location of the intercalary cuticle (green) does not match the experimental data and requires substantial head reorganization. **(A) The traditional, banded model.** This falsified model of head regionalization implies that the intercalary cuticle would form a narrow ring posteriorly around the head from the anterior tentorial pits, as indicated by Nel et al. (2025). **(B) The experimental RNA interference of the *HOX* gene *Tc-labial* on *Tribolium castaneum*** by Posnien and Bucher (2010). This model identified the genal region posterad the antenna and dorsad the mandible and anterior tentorial pit as the location of the intercalary cuticle. (C) The position of the intercalary cuticle as illustrated by Nel et al. (2025) (see figure S8 of Nel et al., 2025). This model that relies on the study of Posnien and Bucher (2010) requires that the intercalary region crosses over the anterior tentorial pit and invades the clypeal region, hence displacing the postclypeus medially. Under this assumption the intercalary no longer forms the “seam” region between the pregnathal and gnathal head regions, as required by the “bend and zipper” model of development. This hypothesis also directly contradicts the results of Posnien and Bucher (2010). Illustrations modified from Nel et al. (2025, their Fig. 1a–d, 4b).

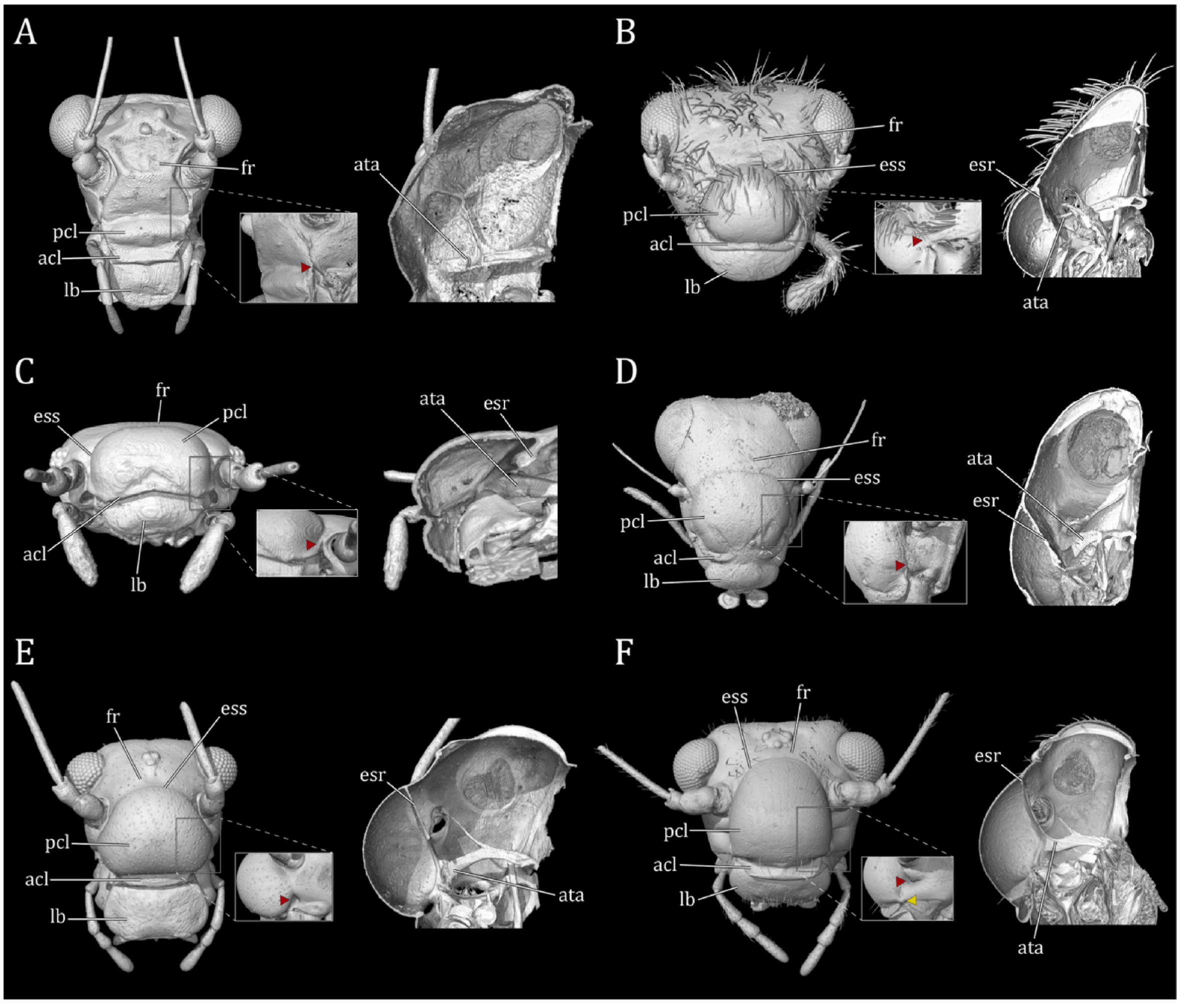

Fig. 2. There is no external or internal demarcation of the supposed "intercalate" sclerite in Psocodea. Comparison of external and internal head skeleton of "Psocoptera" (Psocodea), in anterior overview (left), the details of anterior pits and anterior mandibular articulation in anterolateral view (center), and sagittally cut with internal view of anterior arm and epistomal ridge (right). **(A)** *Prionoglaris* cf. *stygia* (Trogiomorpha: Prionoglaridetae), **(B)** Lepidopsocidae gen. et sp. indet. (Trogiomorpha: Atropetae), **(C)** *Liposcelis* sp. (Troctomorpha: Liposcelidetae), **(D)** †*Amphientomum knorrei* (Troctomorpha: Amphientometae), **(E)** *Valenzuela flavidus* (Psocomorpha: Caeciliusetae), **(F)** *Metylophorus nebulosus* (Psocomorpha: Psocetae). Renders not to scale. **Red arrows** show position of anterior tentorial pit. **Yellow arrow** in (F) shows the ventrolateral expansion of the postclypeus in *Metylophorus*. **Abbreviations**: **acl**, anteclypeus; **ata**, anterior tentorial arm; **esr**, epistomal ridge; **ess**, epistomal sulcus; **fr**, frons; **lb**, labrum; **pcl**, postclypeus.

upon which they base their theory (Posnien and Bucher, 2010), the authors interpret (according to their figure S8) the entire lateral region of the clypeus of *Tribolium castaneum* as the "intercalate". However, this stands in contrast to the study of Posnien and Bucher (2010) which shows based on expression and interference patterns of *labial* in the larva of *T. castaneum* that the intercalary segment contributes cuticle to the region dorsad the mandible but not to the clypeus or the anterior tentorial pit (Fig. 1b) (*). This difference in the location of the intercalary sclerite between the developmental evidence (Posnien and Bucher, 2010, b) and its interpretation by Nel et al. (2025) undermines the authors' proposed solution to the head problem, as the tenebrionid beetle *T. castaneum* is the central empirical and model case for justifying the broader comparisons. Moreover, an identifiable "intercalate" sclerite is absent in all adult or larval beetles studied in detail in the last decades (*) including, for instance, the Archostemata (Beutel et al., 2008), a morphologically key taxon (Boudinot et al., 2023).

The situation in the fossil †*M. beatificus* is unclear for different reasons, beside the observation that an extinct species of one of the most specialized groups of insects with regard to head morphology is a questionable choice for reconstructing ancestral conditions in Hexapoda (~). In Fig. 2A of Nel et al. (2025), the light green "intercalary sclerite" is placed directly above the anteclypeus and only a small portion is dorsad the mandible. However, in their supplementary figures S2G and H, the intercalary segment is exclusively above the mandible and the "eupostclypeus" covers the complete area above the anteclypeus (*). We are thus unsure about the exact position of the "intercalary sclerite"; *i.e.*, the spatial diagnosis of this hypothetical sclerite is ambiguous as defined and illustrated. In both cases, the respective structure that is defined as the intercalary sclerite lies (at least partially) above (dorsad) the mandible which speaks against a clypeal interpretation (~). The situation becomes even more difficult to interpret as neither the anterior mandibular articulation nor the anterior tentorial pit—which would strongly help to define the clypeus—are shown in the figures. Considering these uncertainties, †*Moundthrips* almost certainly does not provide the necessary information to illuminate the mouthpart homologies of Hemiptera and Thysanoptera, as claimed by Nel et al. (2025).

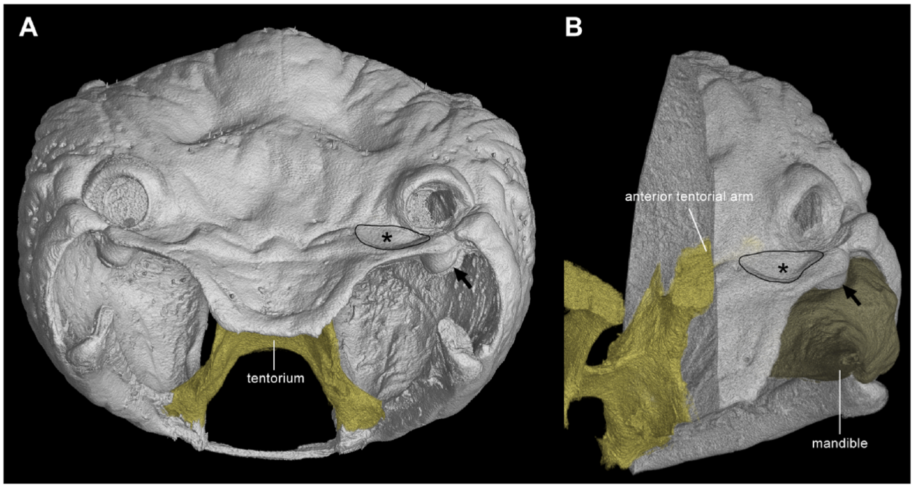

Fig. 3. Volume rendering of larval *Ithonia* sp. (Ithonidae) (data from Li et al., 2022). **(A)** frontal view showing the head capsule with the tentorium highlighted (yellow), (**B**) frontal view of the right half of the head capsule, illustrating the positions of the anterior tentorial arm and pit, the putative intercalary region (asterisk), and the mandible (dark green). Assuming that the "intercalate" is present across all Neuropteroidea as labeled by Nel et al. (2025) for Megaloptera, then the supposed sclerite fails their definition, as it is distant from the mandible and does not form the dorsal mandibular articulation.

2.2. On the "intercalate" sclerite: the interpretations

In addition to the unclear localization of the "intercalate" assumed by Nel et al. (2025) in their key fossil and conflicting identification of the genal region in the tenebrionid beetle *Tribolium* compared to the foundational study of Posnien and Bucher (2010), the authors also report this presumptive sclerite in several other species and lineages. These other taxa are important as the evolutionary hypothesis of Nel et al. (2025) requires that the "intercalate" is in the groundplans of the Polyneoptera and Pterygota specifically and other orders of the Hexapoda more broadly. Taking the other interpreted taxa on a case-by-case basis, we observe a consistent pattern of false positive identification.

The structure identified as the intercalate in their preferred model (Gryllidae) is the lateral region of the postclypeus. The multiple published studies about the cephalic skeleton of *Gryllus* (Yuasa, 1920; Crampton, 1921a; Walker, 1933; Ferris, 1942; DuPorte, 1946) are congruent with Fig. 4a and c of Nel et al. (2025): the postclypeus is well separated from the ventral anteclypeus but there is no separation of the lateral parts of the postclypeus from its mesal part (*). This is also what Nel et al. (2025) vaguely describe for crickets ("although not completely delimited medially"). This situation is also found in other gryllids and gryllotalpids (Ferris, 1942; Strenger, 1942; Gapud, 1968). Thus, we follow all previous authors working of this group in not seeing evidence of a distinct sclerite in the lateral regions of the postclypeus in crickets themselves (~). More broadly, the existence of distinct lateral postclypeal regions in the ancestral groundplan of the Polyneoptera is not supported (~). Such regions are absent from all other polyneopteran lineages (*), including Plecoptera (Hoke, 1924), Zoraptera (Matsumura et al., 2015), Dermaptera (Giles, 1963; Neubert et al., 2017), Grylloblattodea (Crampton, 1926; Walker, 1931, 1933; Wipfler et al., 2011), Phasmatodea (Friedemann et al., 2011), and Dictyoptera (Wipfler et al., 2016). A unique, unpigmented but also not distinctly separated area found laterad this location in Mantophasmatodea is likely an autapomorphy (~), as suggested by the absence in the sister taxon Grylloblattodea and other related groups (*) (Baum et al., 2007).

Regarding Odonata (their Fig. 5a, S6D–F), the "separation" of their lateral intercalary sclerites on the clypeus of *Aeshna* are in reality the strongly developed attachment ridges of the anterior cibarial dilators (*) (Short, 1955). In other odonatans, they are by far not as distinctly developed and not externally visible (*), a condition also found in Ephemeroptera (*) (Asahina, 1954; Staniczek, 2001; Blanke et al., 2012). The heterogeneity of the authors' assumed intercalary sclerite is highlighted, moreover, by their interpretation of large elliptical postclypeal regions in Psocodea (their Fig. 5f, g). The only presumed evidence for such elliptical "intercalates" in this order is a putative region of campaniform sensilla, the homology of which Nel et al. explicitly recognize as uncertain. Otherwise, no internal ridge or external line or suture separates those elliptical, highlighted regions in Psocodea (*) (Fig. 2). The lateral subdivisions of the psocodean postclypeus are absent across the order (*) (Yoshizawa, 2005). Attachment ridges (*Aeshna*) and putative campaniform sensilla regions (Psocodea) are not homologous landmarks.

The authors' homology inferences for their sampled Formicidae (Camponotini: *Camponotus* sp., *Dinomyrmex gigas*; see their Fig. 5c, S6G) are incongruent with anatomical, mechanical, and evolutionary morphological studies on the ant head (*) (*e.g.*, Richter et al., 2020, 2022; Kang et al., 2023, among others). The structure labeled with a thick arrow by the authors as the secondary mandibular articulation is misidentified; it is in fact the lateral clypeal region (*) ("lateroclypeus" in myrmecological jargon). The lateroclypeal region is close to but is dorsad the secondary articulation (the "cranial mandibular condyle"). The regions labeled with asterisks as the intercalate in the ants are the clypeus *de facto* (*). The median ridge that appears to divide the supposed intercalates in the sampled ants is an apomorphy of some genera within the subfamily Formicinae (*) (Boudinot et al., 2022), while the supposed "eupostclypeus" of the ant is a specific flattening of the clypeus (*). Such ridges and flattening characterize some species or groups of species but are absent in the majority of lineages across the phylogeny of both stem and crown Formicidae (*) (Keller, 2011; Boudinot et al., 2020; Richter et al., 2022).

The other holometabolan example of Nel et al. (2025) (Megaloptera, their figure 5d, e) is not totally certain. Based on evaluation CT data of Megalopteran heads, we observe that the first defining condition of Nel et al. (2025) for the intercalate—that it is "the ventralmost part of the intercalate involved in the joint with the anterior/dorsal secondary mandibular articulation”—is not necessarily present in all Neuropteroidea (*). Specifically, the slightly differentiated posterolateral region of the clypeus in the larva of *Ithone* sp. (Neuroptera: Ithonidae), which corresponds in position to the “intercalate” label for Megaloptera, is very clearly distant from the dorsal mandibular articulation (*) (Fig. 3). An evolutionary morphological hypothesis for the partially differentiated lateral clypeal region in Megaloptera and other groups of Holometabola has already been provided by the Dijon school of insect anatomy, without invoking novel groundplan features of the insect head (*) (Bitsch, 1973).

Beyond the Pterygota, the authors' evidence for the existence of the intercalate in the apterygote grade is important to consider. The authors interpret the lateral clypeal region of Zygentoma as their proposed “intercalate” (their figure 7e). To date, however, no such sclerite has been observed and documented for the primarily wingless orders, including Zygentoma, Archaeognatha, or the entognathous taxa (*) (*e.g.*, Diplura: Blanke and Machida, 2016; Protura, Collembola, Archaeognatha: Blanke et al., 2015a, b; Zygentoma: Blanke et al., 2014). Besides this lack of evidence, the location proposed for cuticle of the intercalary segment would require that the identity-bearing epidermal cells migrate across the invagination of the anterior tentorial arm then invade the clypeus medially, substantially displacing the postclypeus. Evidence for this during development is lacking (*) (*e.g.*, Machida, 1981).

In sum, the adduced empirical evidence for the existence and location of Nel et al.'s supposed “intercalate” sclerite in Zygentoma and Pterygota is in conflict with previously established facts of anatomy. None of the provided species has a separate or distinctly delimited sclerite in the lateral postclypeal region (*), and the provided interpretations are inconsistent with the available morphological evidence. To reiterate: A distinct sclerite between the clypeus and anterior tentorial pit is absent from the groundplan of Hexapoda or Pterygota (~, *), contradicting the central requirement of the head theory proposed by Nel et al. (2025). At a higher level, the cricket head is not an “ideal generalized head of a chewing insect” (Nel et al., 2025, p. 13) (see also Boudinot et al., 2025 on the notion of “generalized” morphology).

2.3. On the “intercalate” sclerite: developmental evidence

Nel et al. (2025) did not take the available developmental evidence in Archaeognatha into consideration. Machida (1981) suggested that the intercalary segment is identifiable in Archaeognatha during embryogenesis, and that a process of continuous formation apparently connects it to the hypopharynx and its lobes, the lingua and superlingua (*). According to Machida (1981), the intercalary segment forms a paired anlage anterad the mandibular lobes and posterad both the mouth and the anlagen of the clypeolabrum and antenna (*). The rudiment grows posteriorly, extending to the maxillae and eventually to the labium, hence is positioned between the mandibular lobes and is identified by Machida as the hypopharynx. This potential hypopharyngeal anlage develops distal lobes, where the unpaired proximal portion is identified by Machida as the lingua and the distal, paired portions as the superlinguae (*).

While the otherwise overlooked observations of Machida (1981) signal closure to the search for ancestral head segments in the facial region of insects, they raise another pair of related and pressing yet underappreciated questions in comparison to crustaceomorphs (Crampton, 1921b, pp. 65, 66): (1) What is or are the homologous structures of the insect hypopharynx (including the lingua and superlinguae) in crustacean taxa, and (2) what is the “fate” of the paragnaths from the crustaceomorph progenitor to the most recent common ancestor of the Hexapoda? The hypopharynx is an unpaired tongue-like structure in the oral cavity between the paired mouthparts (Beutel et al., 2014). From this arise the paired superlinguae and an unpaired lingua, which occur in Ephemeroptera and the apterygote orders, excluding Zygentoma (Bitsch, 1973). The paragnaths on the other hand are a pair of appendage-like perioral lobes in crustaceomorphs that are opposable to the labrum (Schram and Koenemann, 2021; Wolff and Scholtz, 2006). None of these structures were considered in the work of Nel et al. (2025), representing an oversight with respect to the complexity of the head regionalization problem.

In the context of a cell lineage analysis of the paragnaths in *Orchestia* (Amphipoda), Wolff and Scholtz (2006) identify the structures arising from Machida's “intercalary segment” as elements of the sternal region of the mandibular segment based on the expression of *Deformed* (reinterpreted as the possible mandibular endites by Bruce and Patel, 2025). (They further state that the interpretation of lobes arising from the intercalary segment as elements of the hypopharynx is erroneous.) In contrast, Machida's hypothetical intercalary region expresses *labial*—the marker of the homologous second antennal segment in crustaceomorphs (Wolff and Scholtz, 2006; Bruce and Patel, 2025)—as shown by Economou and Telford (2009) and Posnien and Bucher (2010a), among other studies.

The results of Economou and Telford (2009) in particular suggest that the hypopharyngeal lobes are derivatives of the mandibular segment, hence potential homologs of the paragnaths of the crustaceomorphs. There remains conflict among the developmental studies, however, in that the hypopharyngeal lobes arise from a domain that also expresses the intercalary segment marker *labial*, although this would be congruent with the observations of Machida (1981). A multisegmental origin of the hypopharyngeal complex was the previously synthesized perspective for insects based on the developmental, muscular, and neural anatomical evidence available at the time (Bitsch, 1973). It is therefore clear that the problem of intercalary segment “fate” in insects is dependent on resolution of the hypopharyngeal complex via molecular developmental study coupled with renewed anatomical investigation, ideally on Archaeognatha and/or Zygentoma. These open questions further underscore the importance of restraint in drawing conclusions about the hexapod groundplan from isolated pieces of the developmental evolutionary puzzle.

2.4. On the “promandible” sclerite

Nel et al. (2025) claim the presence of a second sclerite in the insect groundplan which they refer to as “promandible”—a new name for the pleurostoma. According to these authors, this is an “external sclerite basal to the mandible, because it appears tightly linked to the mandible as shown in molting cricket larvae” (Nel et al., 2025, p. 4). The pleurostomal ridge that connects the anterior with the posterior mandibular articulation also gives origin to the anterior tentorial arms (*e.g.*, Hudson, 1945; Klass and Eulitz, 2007), while the posterior tentorial arms arise from the hypostomal and postoccipital ridge. In most insects with biting and chewing mouthparts there is a continuous supporting ridge that forms a ring around the head capsule, connecting the mandibular articulations and the tentorial pits. Mesally between the two anterior mandibular articulations this structure has been conventionally named the “epistomal ridge”, in between the anterior and posterior mandibular articulation the “pleurostomal” ridge, between the posterior mandibular articulation and the posterior tentorial pits the “hypostomal” ridge, and between the posterior tentorial pits the “postoccipital” ridge.

The tentorium and the ridge that rings the head capsule play a crucial role in deflecting the tremendous mechanical stress and strain created by the mandibles during biting (Blanke et al., 2017). The pleurostoma or subgena or mandibularia (Yuasa, 1920) or basimandibular sclerite (DuPorte, 1946, 1957) is the region below the pleurostomal ridge, while the area above it is referred to as the gena. In a few species such as *Gryllus*, the anterior tentorial pits are extremely enlarged and widened (“monstrous” in the words of Ferris, 1942), thus the anterior tentorial pit extends to the posterior mandibular articulation. As a consequence, the subgena is more pronounced than in other species. This situation, describe in *Gryllus* by Nel et al. (2025), is not found in most polyneopteran or pterygote lineages (*) (Ferris, 1942; Hudson, 1945; Klass and Eulitz, 2007; DuPorte, 1957) and thus not part of the polyneopteran, pterygote, or hexapod ground plan (~).

The pleurostomal ridge is clearly a supportive structure associated with the deflection of stress and strain (~) which strongly contrasts true segmentary boundaries which are always flexible (or weakened) areas (*) (see below). We found no evidence suggesting that the subgena (or its numerous other names such as promandible, pleurostoma, mandibularia) is a distinctive sclerite associated with the ancestral segmentation of the head capsule (~).

2.5. On head segmentation and the anterior tentorial arm

Nel et al. (2025, p. 12) claim that “the anterior tentorium is an intersegmental boundary [, which] is more parsimonious than to consider it originating *within* various segments” (emphasis original). Both parts of this claim hinge on assumptions that are not presently supported by material evidence. There are 14 examples of segmental boundaries that may be adduced for consideration: That between the head and thorax (1 boundary), those of the thoracic segments (2 boundaries), that between the thorax and abdomen (1 boundary), and those between the 11 ancestral segments of the abdomen (10 boundaries). These segmental boundaries are generally characterized by intersegmental membranes connecting the structural entities, particularly in their plesiomorphic condition, although they may be marked only by a suture of the cuticle and sometimes are absent altogether.

The anterior tentorial arm, in contrast, is a sclerotized apodeme in Archaeognatha, Zygentoma, and Pterygota, and is a ligamentous mesodermal endoskeletal structure in Collembola, Diplura, and Remipedia (the internal sclerotizations of Protura are of uncertain homology) (Koch, 2000; Fanenbruck, 2003; Richter et al., 2013). Apodemes are not *de facto* markers of segmental borders (*); they are supportive and muscle-bearing cuticular invaginations that have arisen where there is functional demand, which sometimes includes the boundaries between segments but may occur within the bounds of a sclerite. Other examples of such apodemes that serve as stabilizing elements and muscle attachment sites are the thoracic furcae, spinae, or the pleural arms. It should also be noted in this context that anterior tentorial arms are independently present in Myriapoda as apodemes, hence cannot categorically represent segmental borders retained from some deep arthropodan ancestor (Manton, 1964; Richter et al., 2013).

The search for evidence of dorsal head segmentation in insects requires refocusing on the supportive ridges on the head capsule. In contrast to ecdysial cleavage lines (weakenings of the cuticle that break during ecdysis) and syndeses (membranous connections that allow movements), ridges comprise infoldings of the cuticle to provide mechanical support or attachment sites for muscles. Examples in the head capsule include the epistomal, pleurostomal, hypostomal, circumantennal, circumocular, and postoccipital ridges. It is generally agreed that none of them coincides with any segmental border, but that they represent functional strengthening elements (Snodgrass, 1935; Strenger, 1952; Weber and Weidner, 1966; Posnien et al., 2010b) (*). Blanke et al. (2017) show how important those are for the mechanical stability of the head capsule during biting, including even the circumocular ridge. Further, strengthening ridges of the head have also independently arisen in Isopoda, which have convergently derived powerful mandibular bites (Manton, 1964).

The only structure among the various elements discussed in the past as the most plausible true segmental border is the postoccipital ridge (*)—a contention that remains highly debated (see, *e.g.*, DuPorte, 1957; Staniczek, 2000; Blanke et al., 2014), and an anatomical position that may be coincidental. The postoccipital ridge is a flange-like supporting structure encircling the foramen magnum, the biggest opening of the head capsule. This ridge is formed by a folding of the cuticle and is, in this regard, in line with several other ridges in the head capsule that surround openings or zones of weakness: (1) the circumantennal ridge encircles the antennal opening in the head capsule; (2) the circumocular ridge encloses the compound eyes (which are zones of distinctly weakened cuticle); and (3) the epistomal, pleurostomal, and hypostomal ridges run around the anterior and lateral part of the head capsule and include the mandibular and maxillary articulations and tentorial pits (see above). In Pterygota and some of the apterygote orders, the postoccipital ridge directly attaches to the hypostomal ridge, thus forming—along with the epistomal, pleurostomal, and hypostomal ridges—a continuous sclerotized supporting ring around the entire head capsule (Kristensen, 1975). Those ridges together thus form a functional unit and their separation into distinct ridges is based on man-made definitions. In our interpretation, the postoccipital ridge is thus in line with the other supporting ridges encircling openings in the head capsule and does not represent a segmental border retained from a deeper arthropodan ancestor (~).

We consider the search for ancestral segmental boundaries in the lines of the adult head capsule, overall, to be an endeavor unlikely to bear fruit (~). Whereas †Trilobita had clear metameric organization of the head in many cases, the head segmentation of the mandibulate ancestor was already reduced. Taking the Remipedia as example (Fanenbruck, 2006), the Kopfschild (“head shield”, = (dorsal) head capsule of Hexapoda) bears no clearly demarcated segmental boundaries (*). There are three faint transverse lines that are associated with the rostral remotors and first antennal muscles (anterior line), and the esophageal dilator, mandibular, maxillary, second maxillary, and suspensorial muscles (medial and posterior lines). These muscles are from five ancestral segments; whereas one would expect four lines to divide the muscles of five segments, only three are present, hence a direct or one-to-one segmental alignment between Remipedia and †Trilobita is not possible. This demonstrates the possibility that the distinct boundaries of the assumed ancestral metameric organization of the arthropod head may have been reduced one or more times among the Pancrustacea or other, more inclusive groups, and that the distinct ridges observed in the head of insects may be—and probably are—secondary (~).

Finally, the internal ridges that are present on the head capsule of Hexapoda are functional strengthening structures, rather than lines of weakness, as would be expected for segmental boundaries. While the development of these ridges must be patterned during embryogenesis somehow, they do not necessarily inform the question of deep ancestral segmentation of the adult insect head capsule. Especially accounting for the increased mechanical demand of true dicondylic mandibles within the Hexapoda (Blanke et al., 2017) and the likely independent origin of entognathous pouches between Diplura versus Protura and Collembola (Machida et al., 2025), we consider the tracing of head strengthening ridges to be informative within insects, but not for the origin and groundplan of insects themselves. Consequently, the interpretation of the anterior arms or any cephalic ridge as an original segmental border is unfounded (~). Careful reinterpretation of sufficiently well-preserved Paleozoic insect fossils may contribute to the resolution of these questions, with caveats about the difficulty of interpreting compression fossils (*e.g.*, Hörnschemeyer et al., 2013; Schädel et al., 2022) and the occurrence of unparsimonious patterns of morphological evolution (*e.g.*, Boudinot et al., 2023), among other potential pitfalls.

2.6. *On the crustaceomorph comparisons*

The crustaceomorph outgroup comparisons of Nel et al. (2025) are insufficient to reconstruct the groundplan of the insect head (~). The lesser of the two issues is the labeling of the sampled species in their Fig. 8, which implies that the clypeus is either (a) the intercalate sclerite itself or (b) an evolutionary novelty (apomorphy) of the Hexapoda, arising between the labrum and the supposed intercalary sternite. We point out that Remipedia do not have a clearly identified sternite of the intercalary segment (*) (Fanenbruck, 2003) and that the clypeus and labrum arise together during development (*) (*e.g.*, Machida, 1981). Additionally an epistomal ridge between the clypeus and frons is clearly a derived condition within insects as it is absent in Protura, Collembola, Diplura and Archaeognatha (Bitsch and Bitsch, 2000) (*). In any case, further comparative investigation on these points is warranted.

Critically, the authors' contention that dicondyly is a symplesiomorphy of Hexapoda necessarily implies that it is a synapomorphy of Pancrustacea or some clade including Hexapoda therein. In other words, they claim that the defining synapomorphy of Zygentoma + Pterygota (dicondylic mandibles, hence the name Dicondylia) is a shared apomorphy with at least some other crustaceomorph Pancrustacea, presumably Malacostraca (or Peracarida) given their sampling. Besides implying the loss of the secondary mandibular articulation in Archaeognatha, the entognathous orders, and numerous crustaceomorph lineages, this conclusion overlooks the facts that: (a) Remipedia have mandibles without a secondary articulation (Koenemann et al., 2009) (*); (b) the mandibles of Collembola, Protura, Diplura, and Archaeognatha only have a single mandibular articulation proper (*), *i.e.*, they are monocondylic, without hinge-like motion (Blanke et al., 2015a); and (c) there is a continuous transition from mandibular interaction with surrounding sclerites to the highly derived second mandibular articulations from Archaeognatha through the Palaeoptera and Neoptera (*) (Blanke et al., 2015a, 2015b). It is therefore most likely that the malacostracan taxa chosen by the authors (Peracarida: Amphipoda, Isopoda) have evolved their dicondylic articulations independently of the Hexapoda (~).

The authors' conclusion that dicondyly is ancestral to Hexapoda is premature given their limited outgroup sampling (~). However, this conclusion is not premature in the sense that the dicondylic condition in Pterygota and some Malacostraca was recognized over a century ago (Boerner, 1909). Indeed, in the middle of the last century, Manton (1964) drew two pertinent conclusions on the evolution of mandibular mechanisms across Arthropoda: That hinge-like (dicondylic) mandibles enable powerful biting in contrast to "rolling chewing" (monocondylic) mandibles; and that such biting mechanisms occur in clearly "advanced" groups of crustaceomorphs and Hexapoda (*i.e.*, Isopoda, Decapoda, and Pterygota), whereas rolling chewing mechanisms are widespread phylogenetically, including within Malacostraca. It is also worth noting from Manton (1964) that virtually all groups with the plesiomorphic condition of rolling chewing mandibles experience some amount of physical interaction between the mandible and other structures, reducing the degrees of freedom in different ways, as confirmed by Blanke et al. (2014, Blanke et al., 2015a, 2015b)) for the apterygote orders.

Given that the available evidence points to dicondyly being almost certainly derived independently between crustaceomorphs and Hexapoda, we consider it unwarranted to exclude the name "Dicondylia" from future literature. We also think that it is unwarranted to argue, as Nel et al. have done, that this name should be dropped from use because the secondary mandibular articulation may not be a condyle in the strict sense. The suggested replacement name for Dicondylia, "Trisynaphata", is a pleasing sounding synonym, indicating the three-point articulation of the gonangulum assumed by the authors to be a synapomorphy of this clade. However, in their major anatomical contribution on the gonangulum, Klass and Matushkina (2012) demonstrated that although this sclerite is functionally important, the gonangulum lacks the clear phylogenetic signal assumed since Hennig, which those authors point out in direct contrast to the secondary mandibular articulation. Although the ICZN does not regulate these names, hence provides no concrete guidance, we argue that "Dicondylia" is the more appropriate label for Zygentoma + Pterygota, and that its continued usage will prevent confusion in the literature, lab, and classroom.

More useful in future study will be formal and detailed anatomical comparison of Hexapoda and Remipedia. This has already been found to be informative for the hexapodan groundplan, as shown by Fanenbruck (2003), Fanenbruck et al. (2004), and Boudinot (2018), and even earlier as intimated by the literature analysis of Moura and Christoffersen (1996). Together with Nel et al. and many active colleagues, we are very far from being the first ones to call for more detailed comparisons of apterygote insects and crustaceomorphs: "[Oh, to] what flights one may be led if [one] does not take the precaution of studying the modifications met with in the Crustacea and lower insects, before indulging in speculations concerning the interpretation of [insect] structures … in terms of crustacean anatomy!" – Crampton (1921b).

3. Summary and conclusion

Questioning assumptions about morphological homologies and evolutionary series is a fundamental task of higher-level morphological study. The work of Nel et al. (2025) is commendable in this regard, as the authors propose a bold, new theory of head organization across the insects, which requires critical reassessment of head homologies. Unfortunately, the solution proposed by the authors is, in our understanding, incompatible with the available evidence. We summarize the key points below.

For the occurrence of a hypothetical and distinct sclerite of the intercalary segment in the groundplan of the Hexapoda, the case outlined by Nel et al. (2025) centers on *T. castaneum* and †*Moundthrips*. However, the presented interpretation of *Tribolium* contradicts experimental gene expression data from Posnien and Bucher (2010), and the labeling of the fossil thripidan duplicates this questionable regional homologization, hence does not provide direct evidence. The ancillary support claimed for presence of the intercalate in the hexapod groundplan, based on the expanded taxon sampling, is questionable for different reasons, including: (a) reliance on misidentified sclerites and unsupported assumptions of groundplan conditions in larger groups (*e.g.*, Formicidae); (b) reliance on non-homologous landmarks for regional delimitation (*e.g.*, the putative campaniform sensilla field and the strengthening ridge of *Aeshna*); (c) the choice of taxa with derived frontoclypeal regions without reference to relatives with more

Table 1
Scan data of Psocodea specimens used in this study.

Taxon	Scan ID	SR source
Prionoglaris* cf. *stygia	**fsu_357_MW_Pso_50**	**DESY**
Germany, Bavaria: Heiligenstadt i. Ofr., cave entrance, coll. by hand, raised to adulthood from early instar nymph, N 49.87732, E 11.17114; 26.x.2024; leg. M. Weingardt.		
Lepidopsocidae gen. et sp. indet.	**FSU_297_MW_Pso_40_35_08_2024**	**DESY**
Germany, Thuringia: Jena, forest edge, grassland with apple trees, tray beating; 50°58′19.3″N11°37′39.9″E; 22.vii.2024; leg. M. Weingardt.		
***Liposcelis* sp.**	**FSU_256_MW_Pso_24_20_10_2023**	**DESY**
Germany, Thuringia: Jena, Kunitz, on stem of *Salix* sp., coll. by hand; 22.vii.2020, leg. M. Weingardt.		
‡*Amphientomum knorrei*	**FSU_158_Amphientomum_PMJ**	**DESY**
(East African?) Copal, Age: 390 ± 30 BP, Max. age: 565 years; see also Boudinot et al. (2024).		
Valenzuela flavidus	**KIT_MW01**	**KIT**
Germany, Thuringia: Jena, Kunitz, near agricultural field and grassland, area with several trees and shrubs above small stream, beat from deciduous tree using tray; 05.vii.2021; leg. M. Weingardt.		
Metylophorus nebulosus	**FSU_282_MW_Pso_47_42_08_2024**	**DESY**
Germany, Thuringia: Zeitzbach valley, between Stadtroda and Hermsdorf, ephemeral pools, diverse woody plants, tray beating; 24.vii.2024; 50°53′21″N11°47′32″E; leg. M. Weingardt.		

plesiomorphic conditions (*e.g.*, Gryllidae in the context of Polyneoptera or *Aeshna* among Odonata); and (d) inconsistent labeling, which reduces observational replicability (*e.g.*, Neuropteroidea). Further, developmental evidence from Archaeognatha indicates that the intercalary segment is involved in the as-yet unresolved homology problem of the hypopharyngeal complex, rather than frontoclypeal regionalization as proposed by the authors.

The Nel et al. reinterpretation of the head has two other key elements: the proposed "promandible" sclerite and the segmental significance of the anterior tentorial arms. The promandible is reasonably re-identified as the modified pleurostomal ridge, hence representing a mechanical reinforcement associated with mandible function, rather than an ancestral segmental sclerite. Likewise, the pleurostoma and other ridges—including the epistomal ridge, which is associated with the anterior tentorial arms—are strengthening structures rather than intersegmental membranes or sutures. Based on comparison among apterygote orders, crustaceomorph Pancrustacea, and other Arthropoda, we find it most likely that the transverse lines of the head representing the metameric organization of, *e.g.*, some †Trilobita, was reduced one or more times. The final claim of the authors is that dicondyly is a shared primitive character of both Hexapoda and Malacostraca, which disregards the monocondylic state of Remipedia, many other crustaceomorphs, and most apterygote orders, and overlooks known transitional conditions. Consequently, their proposal to reject the clade name "Dicondylia" is based on assumptions from limited sampling and overstates the importance of the gonangulum.

To conclude, we reiterate our agreement with the authors that comparative morphology is necessary, but we are compelled to disagree that there has been "a lack of progress for decades in the exploration of comparative morphology for the insect head" (Nel et al., 2025, p. 3). As a counterpoint see, for example, Koch (2000, 2001), Fanenbruck (2006), Beutel et al. (2008, 2011), Wipfler et al. (2011), Blanke et al. (2015a, b), Blanke and Machida (2016), Richter et al. (2019), Boudinot et al. (2021), Li et al. (2023), Meira et al. (2024), Fabian et al. (2025), and Weingardt et al. (2025), among numerous others. In general, we urge caution with drawing broad, new conclusions about insect head homologies without considering all lines of evidence and the well-developed state of research and knowledge. We hope that the text we present here may serve as a useful reference for problems of insect head evolution down the line.

4. Materials and methods

4.1. Synchrotron scanning: DESY

Five Psocodea (*Prionoglaris* cf. *stygia*, Lepidopsocidae Gen. sp., *Liposcelis* sp., ‡*Amphientomum knorrei*, *Metylophorus nebulosus*) were scanned at the imaging beamline P05 of storage ring PETRA III (Haibel et al., 2010; Greving et al., 2014; Wilde et al., 2016) at DESY (Hamburg, Germany) (Table 1). The parameters of the scan were as follows: effective pixel size (binned) 0.913 mm, photon energy of ca. 18 keV, sample to detector distances of 50 mm, using a 50 MP CMOS camera system, 4001 projections, exposure time of 350 ms. The parameters for both scans are as follows: effective pixel size (binned) 1.285 mm, photon energy of ca. 18 keV, sample to detector distance of 100 mm, using a 20 MP CMOS camera system, 3501 projections, exposure time of 250 ms.

4.2. Synchrotron scanning: KIT

Synchrotron X-ray microtomography (SR-μ-CT) on specimen *Valenzuela flavidus* (Psocodea: Caeciliusidae) (scan code KIT_MW01) was performed at the Imaging Cluster of the KIT Light Source (Karlsruhe Institute of Technology) using a filtered polychromatic X-ray beam produced by a 1.5 T bending magnet with a spectrum peak of about 15 keV (Table 1). The beam was filtered with 0.5 mm aluminum. We employed a fast indirect detector system consisting of an LSO:Tb scintillator (Cecilia et al., 2011) and a diffraction-limited optical microscope (Optique Peter, Lentille, France; Douissard et al., 2012) coupled to a 12-bit pco.dimax high-speed camera with 2016 × 2016 pixels (dos Santos Rolo et al., 2014). The specimens were scanned in 95 % ethanol.

For each scan, we acquired 3000 projections at 70 fps at × 10 optical magnification, resulting in an effective pixel size of 1.22 μm, respectively. The control system concert (Vogelgesang et al., 2016) was used for automated data acquisition and online reconstruction of tomographic slices for data quality assurance. Final 3D tomographic reconstructions were performed by tofu (Faragó et al., 2022) and additionally included phase recovery (Paganin et al., 2002), ring removal, 8-bit conversion, and mixing of phase and absorption 3D reconstructions to increase the contrast between the background and homogeneous regions while highlighting the edges.

4.3. Computer-based 3D reconstruction

Before segmentation, the scans from DESY were cropped, sampled, and transformed to 8 bit using Fiji (Schindelin et al., 2012) and Dragonfly (Object Research Systems, Montreal, Quebec, Canada). The segmentation was performed using Amira Ver. 6.0.1 and 6.1.1 (Thermo Fisher Scientific, Hillsboro, USA). After segmentation, the materials were exported as tif stacks using the Amira macro "Multi Export" (Engelkes et al., 2018). For 3D Phong rendering, we used VGStudio Max Ver. 3.4 (Volume Graphics, Germany). The final renders are presented in central perspective, while renders in parallel perspective were used to create scale bars.

5. Figures

The figures were assembled using Adobe Photoshop (v. 24.1.0) and Adobe Illustrator (v. 27.2) for lettering and finalizing (Adobe Systems Incorporated, San Jose, CA, USA).

CRediT authorship contribution statement

Brendon E. Boudinot: Writing – original draft, Visualization, Validation, Resources, Project administration, Methodology, Investigation, Conceptualization. **Rolf G. Beutel:** Writing – original draft, Investigation, Conceptualization. **Michael Weingardt:** Writing – original draft, Visualization, Methodology, Investigation. **Thomas van de Kamp:** Software, Resources, Methodology, Data curation. **Jörg U. Hammel:** Software, Resources, Methodology, Data curation. **Di Li:** Writing – review & editing, Validation, Investigation. **Adrian Richter:** Writing – review & editing, Investigation. **Benjamin Wipfler:** Writing – original draft, Investigation, Conceptualization.

Declaration of competing interest

The authors declare no competing interests.

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References

Asahina, S., 1954. A Morphological Study of a Relic Dragonfly *Epiophlebia superstes* Selys (Odonata, Anisozygoptera). The Japan Society for the Promotion of Science, Tokyo.

Baum, E., Dressler, C., Beutel, R.G., 2007. Head structures of *Karoophasma* sp. (Hexapoda, Mantophasmatodea) with phylogenetic implications. J. Zool. Syst. Evol. Res. 45, 104–119.

Bernot, J.P., Owen, C.L., Wolfe, J.M., Meland, K., Olesen, J., Crandall, K.A., 2023. Major revisions in pancrustacean phylogeny and evidence of sensitivity to taxon sampling. Mol. Biol. Evol. 40, msad175.

Beutel, R.G., Ge, S.Q., Hörnschemeyer, T., 2008. On the head morphology of *Tetraphalerus*, the phylogeny of Archostemata and the basal branching events in Coleoptera. Cladistics 24, 270–298.

Beutel, R.G., Friedrich, F., Hörnschemeyer, T., Pohl, H., Hünefeld, F., Beckmann, F., et al., 2011. Morphological and molecular evidence converge upon a robust phylogeny of the megadiverse Holometabola. Cladistics 27, 341–355.

Beutel, R.G., Friedrich, F., Yang, X.K., Ge, S.Q., 2014. Insect Morphology and Phylogeny: a Textbook for Students of Entomology. Walter de Gruyter, Berlin.

Bitsch, J., 1973. Morphologie de la tête des insectes. A. Partie générale. In: Grassé, P. P. (Ed.), Traité De Zoologie, vol. 8. Masson et Cie, Paris, pp. 3–100. Part 1.

Blanke, A., Wipfler, B., Letsch, H., Koch, M., Beckmann, F., Beutel, R., Misof, B., 2012. Revival of Palaeoptera—head characters support a monophyletic origin of Odonata and Ephemeroptera (Insecta). Cladistics 28, 560–581.

Blanke, A., Koch, M., Wipfler, B., Wilde, F., Misof, B., 2014. Head morphology of *Tricholepidion gertschi* indicates monophyletic Zygentoma. Front. Zool. 11, 1–20.

Blanke, A., Rühr, P.T., Mokso, R., Villanueva, P., Wilde, F., Stampanoni, M., et al., 2015a. Structural mouthpart interaction evolved already in the earliest lineages of insects. Proc. R. Soc. Lond. B Biol. Sci. 282, 20151033.

Blanke, A., Machida, R., Szucsich, N.U., Wilde, F., Misof, B., 2015b. Mandibles with two joints evolved much earlier in the history of insects: dicondyly is a synapomorphy of bristletails, silverfish and winged insects. Syst. Entomol. 40, 357–364.

Blanke, A., Machida, R., 2016. The homology of cephalic muscles and endoskeletal elements between Diplura and Ectognatha (Insecta). Org. Divers. Evol. 16, 241–257.

Blanke, A., Watson, P.J., Holbrey, R., Fagan, M.J., 2017. Computational biomechanics changes our view on insect head evolution. Proc. R. Soc. Lond. B Biol. Sci. 284, 20162412.

Boerner, C., 1909. Neue Homologien zwischen Crustaceen und Hexapoden. Die Beissmandibel der Insecten und ihre phylogenetische Bedeutung. Archi- und Metapterygota. Zool. Anz. 34, 100–125.

Boudinot, B.E., 2018. A general theory of genital homologies for the Hexapoda (Pancrustacea) derived from skeletomuscular correspondences, with emphasis on the Endopterygota. Arthropod Struct. Dev. 47, 563–613.

Boudinot, B.E., Perrichot, V., Chaul, J.C., 2020. †*Camelosphecia* gen. nov., lost ant-wasp intermediates from the mid-Cretaceous (Hymenoptera, Formicoidea). ZooKeys 1005, 21.

Boudinot, B.E., Moosdorf, O.T.D., Beutel, R.G., Richter, A., 2021. Anatomy and evolution of the head of *Dorylus helvolus* (Formicidae: Dorylinae): Patterns of sex- and caste-limited traits in the sausagefly and the driver ant. J. Morphol. 282 (11), 1616–1658.

Boudinot, B.E., Borowiec, M.L., Prebus, M.M., 2022. Phylogeny, evolution, and classification of the ant genus *Lasius*, the tribe Lasiini and the subfamily Formicinae (Hymenoptera: Formicidae). Syst. Entomol. 47, 113–151.

Boudinot, B.E., Yan, E.V., Prokop, J., Luo, X.Z., Beutel, R.G., 2023. Permian parallelisms: reanalysis of †Tshekardocoleidae sheds light on the earliest evolution of the Coleoptera. Syst. Entomol. 48, 69–96.

Boudinot, B.E., Bock, B.L., Weingardt, M., Tröger, D., Batelka, J., Li, D., et al., 2024. Et latet et lucet: Discoveries from the Phyletisches Museum amber and copal collection in Jena, Germany. Dtsch. Entomol. Z. 71, 111–176.

Boudinot, B.E., Casadei-Ferreira, A., Wöhrl, T., Probst, R.S., Lieberman, Z.E., Czekanski-Moir, J., Richter, A., 2025. Ecomorphology of ants. In: Betz, O. (Ed.), Insect Ecomorphology. Academic Press, Oxford, pp. 469–524.

Bruce, H.S., Patel, N.H., 2025. preprint. Molecular basis of arthropod appendage diversity. bioRxiv.

Cecilia, A., Rack, A., Douissard, P.-A., Martin, T., dos Santos, R.T., Vagovič, P., Hamann, E., van de Kamp, T., Riedel, A., Fiederle, M., Baumbach, T., 2011. LPE grown LSO: Tb scintillator films for high-resolution X-ray imaging applications at synchrotron light sources. Nucl. Instrum. Methods Phys. Res. 648, 321–S323.

Chipman, A.D., 2025. The development and evolution of arthropod tagmata. Proc. R. Soc. Lond. B Biol. Sci. 292, 20242950.

Crampton, G.C., 1921a. The sclerites of the head, and the mouthparts of certain immature and adult insects. Ann. Entomol. Soc. Am. 14, 65–110.

Crampton, G.C., 1921b. The phylogenetic origin of the mandibles of insects and their arthropodan relatives: a contribution to the study of the evolution of the Arthropoda. J. N. Y. Entomol. Soc. 29, 63–100.

Crampton, G.C., 1926. The affinities of *Grylloblatta* indicated by a study of the head and its appendages. Psyche 33, 77–84.

Crampton, G.C., 1928. The evolution of insects, chilopods, diplopods, crustacea and other arthropods indicated by a study of the head capsule. Can. Entomol. 60, 129–141.

dos Santos Rolo, T., Ershov, A., van de Kamp, T., Baumbach, T., 2014. In vivo X-ray cine-tomography for tracking morphological dynamics. Proc. Natl. Acad. Sci. USA 111, 3921–3926.

Douissard, P.-A., Cecilia, A., Rochet, X., Chapel, X., Martin, T., van de Kamp, T., Helfen, L., Baumbach, T., Luquot, L., Xiao, X., Meinhardt, J., Rack, A., 2012. A versatile indirect detector design for hard X-ray microimaging. J. Instrum. 7, P09016.

DuPorte, E.M., 1946. Observations on the morphology of the face in insects. J. Morphol. 79, 371–417.

DuPorte, E.M., 1957. The comparative morphology of the insect head. Annu. Rev. Entomol. 2, 55–70.

Economou, A.D., Telford, M.J., 2009. Comparative gene expression in the heads of *Drosophila melanogaster* and *Tribolium castaneum* and the segmental affinity of the *Drosophila* hypopharyngeal lobes. Evol. Dev. 11, 88–96.

Engelkes, K., Friedrich, F., Hammel, J.U., Haas, A., 2018. A simple setup for episcopic microtomy and a digital image processing workflow to acquire high-quality volume data and 3D surface models of small vertebrates. Zoomorphology 137, 213–228. https://doi.org/10.1007/s00435-017-0386-3.

Fabian, B., Schneeberg, K., Löwe, S., Bauernfeind, R., Beutel, R.G., 2025. Transformations of head structures during the larval development of the black soldier fly *Hermetia illucens* (Stratiomyidae, Diptera). J. Morphol. 286, e70048.

Fanenbruck, M., 2003. Die Anatomie des Kopfes und des cephalen Skelett-Muskelsystems der Crustacea, Myriapoda und Hexapoda: Ein Beitrag zum phylogenetischen System der Mandibulata und zur Kenntnis der Herkunft der

Remipedia und Tracheata. Dissertation, Ruhr-Universität Bochum.

Fanenbruck, M., Harzsch, S., Wägele, J.W., 2004. The brain of the Remipedia (Crustacea) and an alternative hypothesis on their phylogenetic relationships. Proc. Natl. Acad. Sci. USA 101, 3868–3873.

Fanenbruck, M., 2006. Die Anatomie des Kopfes und des cephalen Skelett-Muskelsystems der Crustacea, Myriapoda und Hexapoda. Die Mitteilungen der Deutschen Zoologischen Gesellschaft, pp. 9–16.

Faragó, T., Gasilov, S., Emslie, I., Zuber, M., Helfen, L., Vogelgesang, M., Baumbach, T., 2022. Tofu: a fast, versatile and user-friendly image processing toolkit for computed tomography. J. Synchrotron Radiat. 29, 916–927.

Ferris, G.F., 1942. Some observations on the head of insects. Microentomology 7, 25–62.

Friedemann, K., Wipfler, B., Bradler, S., Beutel, R.G., 2011. On the head morphology of *Phyllium* and the phylogenetic relationships of Phasmatodea (Insecta). Acta Zool. 93, 184–199.

Fusco, G., Minelli, A., 2013. Arthropod segmentation and tagmosis. In: Minelli, A., Boxshall, G., Fusco, G. (Eds.), Arthropod Biology and Evolution. Springer, Berlin, pp. 197–221. https://doi.org/10.1007/978-3-642-36160-9_9.

Gapud, V.P., 1968. The external morphology of the head and mouthparts of some philippine Orthoptera. Philipp. Entomol. 1, 11–32.

Giles, E.T., 1963. The comparative external morphology and affinities of the Dermaptera. Trans. R. Entomol. Soc. Lond. 115, 95–164.

Greving, I., Wilde, F., Ogurreck, M., Herzen, J., Hammel, J.U., Hipp, A., Friedrich, F., Lottermoser, L., Dose, T., Burmester, H., Müller, M., Beckmann, F., 2014. P05 imaging beamline at PETRA III: first results, 2014. In: Stuart, R.S. (Ed.), Proceedings of SPIE 9212 – Development in X-ray Tomography IX. https://doi.org/10.1117/12.2061768. San Diego, USA, 92120O-8.

Haibel, A., Ogurreck, M., Beckmann, F., Dose, T., Wilde, F., Herzen, J., Müller, M., Schreyer, A., Nazmov, V., Simon, V., Last, A., Mohr, J., 2010. Micro- and nano-tomography at the GKSS imaging beamline at PETRA III, 2010. In: Stock, S.R. (Ed.), Proceedings of SPIE 7804 – Developments in X-ray Tomography VII, San Diego, USA, 78040B. https://doi.org/10.1117/12.860852.

Hoke, G., 1924. The anatomy of the head and mouth-parts of Plecoptera. J. Morphol. 38, 347–385.

Hörnschemeyer, T., Haug, J.T., Bethoux, O., Beutel, R.G., Charbonnier, S., Hegna, T.A., Koch, M., Rust, J., Wedmann, S., Bradler, S., Willmann, R., 2013. Is Strudiella a Devonian insect? Nature 494 (7437), E3–E4.

Hudson, G.B., 1945. A study of the tentorium in some orthopteroid Hexapoda. J. Entomol. Soc. South Afr. 8, 71–90.

Kang, V., Püffel, F., Labonte, D., 2023. Three-dimensional kinematics of leaf-cutter ant mandibles: not all dicondylic joints are simple hinges. Philos. Trans. R. Soc. Lond. B Biol. Sci. 378, 20220546.

Keller, R.A., 2011. A phylogenetic analysis of ant morphology (Hymenoptera: Formicidae) with special reference to the poneromorph subfamilies. Bull. Am. Mus. Nat. Hist. 2011, 1–90.

Klass, K.D., Eulitz, U., 2007. The tentorium and anterior head sulci in Dictyoptera and Mantophasmatodea (Insecta). Zool. Anz. 246, 205–234.

Klass, K.D., Matushkina, N.A., 2012. The exoskeleton of the female genitalic region in *Petrobiellus takunagae* (Insecta: Archaeognatha): Insect-wide terminology, homologies, and functional interpretations. Arthropod Struct. Dev. 41, 575–591.

Koch, M., 2000. The cuticular cephalic endoskeleton of primarily wingless hexapods: ancestral state and evolutionary changes. Pedobiologia 44, 374–385.

Koch, M., 2001. Mandibular mechanisms and the evolution of hexapods. Ann. Soc. Entomol. Fr. 37, 129–174.

Koenemann, S., Olesen, J., Alwes, F., Iliffe, T.M., Hoenemann, M., Ungerer, P., et al., 2009. The post-embryonic development of Remipedia (Crustacea)—additional results and new insights. Dev. Gene. Evol. 219, 131–145.

Kristensen, N.P., 1975. The phylogeny of hexapod “orders”. A critical review of recent accounts. J. Zool. Syst. Evol. Res. 13, 1–44.

Lev, O., Edgecombe, G.D., Chipman, A.D., 2022. Serial homology and segment identity in the arthropod head. Integr. Org. Biol. 4, obac015.

Li, D., Friedrich, F., Jandausch, K., Pohl, H., Liu, X., Beutel, R.G., 2022. Unearthing underground predators: The head morphology of larvae of the moth lacewing genus *Ithone* Newman (Neuroptera: Ithonidae) and its functional and phylogenetic implications. Syst. Entomol. 47, 618–636.

Li, D., Jandausch, K., Pohl, H., Yavorskaya, M.I., Liu, X., Beutel, R.G., 2023. Cephalic anatomy highlights morphological adaptation to underground habitats in a minute lacewing larva of *Dilar* (Dilaridae) and conflicting phylogenetic signal in Neuroptera. Insect Sci. 30 (5), 1445–1463.

Machida, R., 1981. External features of embryonic development of a jumping bristletail, *Pedetontus unimaculatus* Machida (Insecta, Thysanura, Machilidae). J. Morphol. 168, 339–355.

Machida, R., Fukui, M., Tomizuka, S., Ikeda, Y., Sekiya, K., Masumoto, M., 2025. Embryology cannot establish the “Protura-sister”. Proc. Natl. Acad. Sci. USA 122, e2423813122.

Manton, S.M., 1964. Mandibular mechanisms and evolution of arthropods. Philos. Trans. R. Soc. Lond. B Biol. Sci. 247, 1–183.

Matsumura, Y., Wipfler, B., Pohl, H., Dallai, R., Machida, R., Mashimo, Y., et al., 2015. Cephalic anatomy of *Zorotypus weidneri* New, 1978: new evidence for a placement of Zoraptera. Arthropod Syst. Phylo. 73, 85–105.

Meira, O.M., Beutel, R.G., Pohl, H., van de Kamp, T., Almeida, E.A., Boudinot, B.E., 2024. Bee morphology: A skeletomuscular anatomy of *Thyreus* (Hymenoptera: Apidae). J. Morphol. 285, e21751.

Misof, B., Liu, S., Meusemann, K., Peters, R.S., Donath, A., Mayer, C., Frandsen, P.B., Ware, J., Flouri, T., Beutel, R.G., et al., 2014. Phylogenomics resolves the timing and pattern of insect evolution. Science 346, 763–767.

Moura, G., Christoffersen, M.L., 1996. The system of the mandibulate arthropods: Tracheata and Remipedia as sister groups, “Crustacea” nonmonophyletic. J. Comp. Biol. 1, 95–113.

Nel, P., Engel, M.S., Soriano, C., Pont, S., Jacquelin, L., Dollinger, L., et al., 2025. Unraveling the insect head: Segmentation and pancrustacean homologous. Arthropod Struct. Dev. 87, 101462.

Neubert, D., Simon, S., Beutel, R., Wipfler, B., 2017. The head of the earwig *Forficula auricularia* (Dermaptera) and its evolutionary implications. Arthropod Syst. Phylo. 75, 99–124.

Ortega-Hernández, J., Janssen, R., Budd, G.E., 2017. Origin and evolution of the panarthropod head–a palaeobiological and developmental perspective. Arthropod Struct. Dev. 46, 354–379.

Paganin, D., Mayo, S.C., Gureyev, T.E., Miller, P.R., Wilkins, S.W., 2002. Simultaneous phase and amplitude extraction from a single defocused image of a homogeneous object. J. Microsc. 206, 33–40.

Posnien, N., Bucher, G., 2010a. Formation of the insect head involves lateral contribution of the intercalary segment, which depends on *Tc-labial* function. Dev. Biol. 338 (1), 107–116.

Posnien, N., Schinko, J.B., Kittelmann, S., Bucher, G., 2010b. Genetics, development and composition of the insect head – A beetle's view. Arthropod Struct. Dev. 39, 399410.

Posnien, N., Hunnekuhl, V.S., Bucher, G., 2023. Gene expression mapping of the neuroectoderm across phyla–conservation and divergence of early brain anlagen between insects and vertebrates. eLife 12, e92242.

Regier, J.C., Shultz, J.W., Zwick, A., Hussey, A., Ball, B., Wetzer, R., et al., 2010. Arthropod relationships revealed by phylogenomic analysis of nuclear protein-coding sequences. Nature 463, 1079–1083.

Richter, S., Stein, M., Frase, T., Szucsich, N.U., 2013. The arthropod head. In: Minelli, A., Boxshall, G., Fusco, G. (Eds.), Arthropod Biology and Evolution. Springer, Berlin, pp. 223–240.

Richter, A., Keller, R.A., Rosumek, F.B., Economo, E.P., Garcia, F.H., Beutel, R.G., 2019. The cephalic anatomy of workers of the ant species *Wasmannia affinis* (Formicidae, Hymenoptera, Insecta) and its evolutionary implications. Arthropod Struct. Dev. 49, 26–49.

Richter, A., Garcia, F.H., Keller, R.A., Billen, J., Economo, E.P., Beutel, R.G., 2020. Comparative analysis of worker head anatomy of *Formica* and *Brachyponera* (Hymenoptera: Formicidae). Arthropod Syst. Phylo. 78, 133–170.

Richter, A., Boudinot, B., Yamamoto, S., Katzke, J., Beutel, R.G., 2022. The first reconstruction of the head anatomy of a Cretaceous insect, †*Gerontoformica gracilis* (Hymenoptera: Formicidae), and the early evolution of ants. Insect Syst. Divers. 6, 4.

Savigny, J., 1816. Mémoires sur les animaux sans vertèbres. G. Dufour, Paris.

Schädel, M., Yavorskaya, M., Beutel, R.G., 2022. The earliest beetle †*Coleopsis archaica* (Insecta: Coleoptera)–morphological re-evaluation using Reflectance Transformation Imaging (RTI) and phylogenetic assessment. Arthropod Syst. Phylog. 80, 495–510.

Schindelin, J., Arganda-Carreras, I., Frise, E., Kaynig, V., Longair, M., Pietzsch, T., et al., 2012. Fiji: an open-source platform for biological-image analysis. Nat. Methods 9, 676–682.

Scholtz, G., Edgecombe, G.D., 2006. The evolution of arthropod heads: reconciling morphological, developmental and palaeontological evidence. Dev. Gene. Evol. 216, 395–415.

Schram, F.R., Koenemann, S., 2021. Evolution and Phylogeny of Pancrustacea: a Story of Scientific Method. Oxford University Press, Oxford.

Schwentner, M., Combosch, D.J., Nelson, J.P., Giribet, G., 2017. A phylogenomic solution to the origin of insects by resolving crustacean-hexapod relationships. Curr. Biol. 27, 1818–1824.

Short, J.R.T., 1955. The morphology of the head of *Aeshna cyanea* (Müller) (Odonata: Anisoptera). Trans. R. Entomol. Soc. Lond. 106, 197–211.

Snodgrass, R.E., 1935. Principles of Insect Morphology. Cornell University Press, Ithaca, New York.

Staniczek, A.H., 2000. The mandible of silverfish (Insecta: Zygentoma) and mayflies (Ephemeroptera): its morphology and phylogenetic significance. Zool. Anz. 239, 147–178.

Staniczek, A., 2001. Der Larvenkopf von *Oniscigaster wakefieldi* McLachlan, 1873 (Insecta: Ephemeroptera: Oniscigastridae). Dissertation, Eberhard-Karls-Universität, Tübingen.

Strenger, A., 1942. Funktionelle Analyse des Orthopterenkopfes. Zool. Jahrb. Syst. 75, 1–72.

Strenger, A., 1952. Die funktionelle und morphologische Bedeutung der Nähte am Insektenkopf. Zoologica 127, 1–18.

Vogelgesang, M., Farago, T., Morgeneyer, T.F., Helfen, L., dos Santos Rolo, T., Myagotin, A., Baumbach, T., 2016. Real-time image-content-based beamline control for smart 4D X-ray imaging. J. Synchrotron Radiat. 23, 1254–1263.

Walker, E.M., 1931. On the anatomy of *Grylloblatta campodeiformis* Walker 1. Exoskeleton and musculature of the head. Ann. Entomol. Soc. Am. 24, 519–536.

Walker, E.M., 1933. On the anatomy of *Grylloblatta campodeiformis* Walker 2. Comparisons of head with those of other orthopteroid insects. Ann. Entomol. Soc. Am. 26, 309–344.

Weber, H., Weidner, H., 1966. Grundriß der Insektenkunde. Gustav Fischer Verlag, Stuttgart.

Weingardt, M., Liang, F., Boudinot, B.E., Hammel, J.U., Bock, B.L., Yoshizawa, K., Beutel, R.G., 2025. The first detailed morphological treatment of a Cretaceous psocid and the character evolution of Trogiomorpha (Insecta: Psocodea).

Arthropod Struct. Dev. 85, 101409.

Wilde, F., Ogurreck, M., Greving, I., Hammel, J.U., Beckmann, F., Hipp, A., Lottermoser, L., Khokhriakov, I., Lytaev, P., Dose, T., Burmester, H., Müller, M., Schreyer, A., 2016. Micro-CT at the imaging beamline P05 at PETRA III. AIP Conf. Proc. 1741, 030035. https://doi.org/10.1063/1.4952858.

Wipfler, B., Machida, R., Mueller, B., Beutel, R.G., 2011. On the head morphology of Grylloblattodea (Insecta) and the systematic position of the order, with a new nomenclature for the head muscles of Dicondylia. Syst. Entomol. 36, 241–266.

Wipfler, B., Weissing, K., Klass, K., Weihmann, T., 2016. The cephalic morphology of the American cockroach *Periplaneta americana* (Blattodea). Arthropod Syst. Phylo. 74, 267–297.

Wolff, C., Scholtz, G., 2006. Cell lineage analysis of the mandibular segment of the amphipod *Orchestia cavimana* reveals that the crustacean paragnaths are sternal outgrowths and not limbs. Front. Zool. 3, 1–14.

Yoshizawa, K., 2005. Morphology of Psocomorpha (Psocodea: 'Psocoptera'). Ins. Matsum. (N.S.) 62, 1–44.

Yuasa, H., 1920. The anatomy of the head and mouthparts of Orthoptera and Euplexoptera. J. Morphol. 33, 251–307.

Zrzavý, J., Štys, P., 1997. The basic body plan of arthropods: insights from evolutionary morphology and developmental biology. J. Evol. Biol. 10, 353–367.