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A morphometric approach to the taxonomic dilemma of *Zonozoe drabowiensis* Barrande, 1872 and *Zonoscutum solum* Chlupáč, 1999 (Upper Ordovician, Czech Republic)

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ABSTRACT

Zonozoe drabowiensis Barrande, 1872 and *Zonoscutum solum* Chlupáč, 1999 are rare and incompletely preserved arthropods from the Upper Ordovician of the Czech Republic. Their classification has been a subject of debate for over a century due to the limited number of specimens and the absence of clear diagnostic features. They were previously thought to belong to Aglaspidida, an extinct group of arthropods from the Cambrian and Ordovician, within Vicissicaudata, a branch of the larger arthropod clade Artiopoda that also includes trilobites. Herein, we used analyses of cephalic outline to quantify whether *Zonozoe* and *Zonoscutum* are morphologically more similar to vicissicaudates than other early Palaeozoic arthropods. We assembled a dataset of twenty-six cephalic outlines representing twenty-six early Palaeozoic species, including *Zonozoe*, *Zonoscutum*, five euchelicerates, six aglaspidids, three cheloniellids, and a selection of other artiopodans. We quantified their shape using elliptical Fourier analysis. Principal component analysis (PCA) and linear discriminant analysis (LDA) place *Zonozoe* and *Zonoscutum* within and close to the vicissicaudatan morphospace, clearly distinguishing them from euchelicerates and non-vicissicaudatan artiopodans. These data support the most conservative classification of *Zonozoe* and *Zonoscutum* within Artiopoda, while strengthening the case for a more specific affinity with Vicissicaudata, helping to resolve a 150-year-old taxonomic uncertainty. More broadly, this study demonstrates the value of outline-based morphometrics in testing systematic hypotheses when discrete characters are unavailable or scarce, offering a reproducible tool for re-evaluating other problematic fossils.

Key words: *Zonozoe drabowiensis*, *Zonoscutum solum*, elliptical Fourier analysis, Vicissicaudata, Artiopoda

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46

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INTRODUCTION

Zonozoe drabowiensis Barrande, 1872 and *Zonoscutum solum* are enigmatic arthropods known from the Letná and the Libeň Formations of the upper Ordovician of the Czech Republic (Chlupáč, 1965, 1999b; Rak et al., 2009; Vokáč & Grigar, 2024). Barrande (1872) originally described *Zonozoe* as an arthropod, specifically as a large carapace of an ostracod (Barrande, 1872). Later on, Novák in his unpublished manuscript (Novák, 1887) considered *Zonozoe* to be a merostomate arthropod close to Synziphosurina (Chlupáč, 1963, 1965, 1999b; Rak, 2009) . Since then, these fossils have not received much attention until the second half of the twentieth century. Chlupáč, 1963 assigned *Zonozoe* into the group Aglaspidida (Walcott, 1911) – a group of extinct marine arthropods, known from the Cambrian and Ordovician strata. However, this assignment remains uncertain (Chlupáč, 1963). It should also be noted that at that time Aglaspidida was considered as one of the basal-most groups within Xiphosura. Subsequent studies have revisited the taxon, reiterating its general association with Aglaspidida and/or the Merostomata, but always with a low degree of confidence (Chlupáč, 1965; Hou, 1997; Chlupáč, 1999a; Rak et al., 2009). As for *Zonoscutum*, the only fossil ascribed to this species was described in Chlupáč (1999a), who tentatively assigned it to Aglaspidida.

During the one hundred and fifty years since the discovery of *Zonozoe*, and twenty-five years for *Zonoscutum*, their classification has been complicated by two main factors. Firstly, the material ascribed to both *Zonozoe* and *Zonoscutum* is scarce, incomplete and not well preserved (Ortega□Hernández et al., 2013; Van Roy et al., 2022). There are currently only eight known specimens of *Zonozoe* and one of *Zonoscutum*, all of which are isolated moulds of cephala (Chlupáč, 1999b; Rak et al., 2009; Vokáč & Grigar, 2024), preserved in quartzose sandstones of the Libeň and Letná Formations. In most cases, the specimens preserve only the general vaulted cephalon outline with a raised longitudinal region terminating with a ridge bearing what is a vague indication of the eyes (Rak et al., 2009; Van Roy et al., 2022). The only exception is a single specimen of *Zonozoe* preserving what has been referred to as glabellar furrows (Rak et al., 2009)

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and a specimen of *Zonoscutum* preserving similar structures but in a different position (Chlupáč, 1999a). Secondly, the classification of *Zonozoe* and *Zonoscutum* has been further complicated by the complex history of the classification of aglaspidid arthropods themselves, especially during the second half of the twentieth century. Their overall dorsal morphology led several authors to consider the aglaspidids as an order of the subclass Xiphosura (Størmer, 1955), grouping Aglaspidida with Xiphosura and Eurypterida, as part of the Merostomata (Raasch, 1939; Størmer, 1944; Eldredge & Smith, 1974) or to consider Aglaspidida as the sister group to chelicerates (Weygoldt and Paulus, 1979). This is in contrast to more recent aglaspidid phylogenies, which emphasize ventral anatomical features as key to understanding their true affinities (Briggs et al., 1979; Hesselbo, 1992; Ortega□Hernández et al., 2013; Lerosey-Aubril, Paterson, et al., 2017; Lerosey-Aubril, Zhu, et al., 2017). Currently, they have been placed within the broader clade Artiopoda, as part of the clade Vicissicaudata (Ortega□Hernández et al., 2013; Lerosey-Aubril, Paterson, et al., 2017; Lerosey-Aubril, Zhu, et al., 2017). Until very recently, the absence of strong defining characteristics for the clade has made Aglaspidida prone to being used as a wastebasket taxon (Plotnick & Wagner, 2006). This could be the case for the poorly preserved *Zonozoe* and *Zonoscutum*, which lack strong anatomical evidence supporting placement within aglaspidids. Other factors that led previous workers to assign *Zonozoe* and *Zonoscutum* to Aglaspidida are likely not only the general similarity between their cephala, but also the known (or suspected) presence of aglaspidids in the same paleogeographic region (Chlupáč, 1963, 1965; Van Roy, 2005; Ortega-Hernandez et al., 2010) and the weak resemblance with other arthropod groups (e.g. position of the eyes and glabella if compared with trilobites).

Later authors commenting on *Zonozoe* and *Zonoscutum* decided to have a more parsimonious approach. (Ortega□Hernández et al. 2013) opted for the exclusion of those taxa from an extensive phylogenetic analysis of Vicissicaudata due to the lack of compelling taxonomically relevant features. (Van Roy et al., 2022), instead, revised *Zonozoe* and *Zonoscutum* to critically assess their possible affinity with *Triopus draboviensis* (Barrande, 1872). In their re-examination of the

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material, the authors did more than simply dismiss the affinity with *Triopus*; they advanced a conservative and more parsimonious taxonomic classification for both *Zonozoe* and *Zonoscutum*. They suggested that, at most, the fossils could be broadly classified as Artiopoda, and argued that any attempt to refine the classification beyond that level would be unwarranted (Van Roy et al., 2022). Known only from cephalic moulds, both *Zonozoe* and *Zonoscotum* lack the diagnostic features of Vicissicaudata, all of which are post-cephalic (Lerosey-Aubril, Zhu, et al., 2017; Briggs et al., 2023). They also lack several defining traits of Aglaspidida, including all post-cephalic diagnostic characters, most notably the modified posterior appendages, as well as evidence of a biomineralized cuticle and dorsal ecdysial sutures (Ortega□Hernández et al., 2013; Lerosey-Aubril, Zhu, et al., 2017). As a result, they cannot be confidently classified through standard phylogenetic or comparative analysis (Ortega□Hernández et al., 2013; Van Roy et al., 2022), a conclusion fully supported by this study. While the enigmatic *Zonozoe* and *Zonoscutum* are unlikely to be key taxa in contributing to resolving the phylogeny of Aglaspidida, a more accurate assignment of this species to this group may yield valuable palaeoecological and paleobiogeographical insights.

In order to resolve the taxonomic dilemma surrounding *Zonozoe* and *Zonoscutum* more effectively, we adopted an alternative approach to phylogenetic analysis and classical comparative anatomy, focusing instead on the only reliably preserved feature in these fossils: the overall cephalic outline. We compared the outline of the cephalon of *Zonozoe* and *Zonoscutum* with twenty-four other arthropods. We implemented a principal component analysis (PCA) and linear discriminant analysis (LDA) on the study of the cephalic outline to extract the maximum morphological information from the limited material of *Zonozoe* and *Zonoscutum*. This methodology has been used in paleobiology to compare the outline of different fossils and can provide information on their taxonomy, ecology, and development (Gevirtz, 1976; Healy-Williams & Williams, 1981; Burke et al., 1987; Foote, 1989; Pates et al., 2021; Ma et al., 2023; Braig et al., 2024; Drage & Pates, 2024; Collantes & Pates, in press). A significant advantage of this methodology over landmark-based approaches is that it does not rely on discrete morphological characters, facilitating quantification of shape variation

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when such discrete characters are absent. Ultimately, our analysis provides a novel line of evidence toward supporting the systematic placement of problematic species. Both *Zonozoe* and *Zonoscutum* plotted within the Vicissicaudata area of morphospace, and thus the shape of their cephala concurs with a vicissicaudate affinity.

MATERIALS AND METHODS

Species involved in the study and the criteria of selection

In addition to one *Zonozoe* and one *Zonoscutum* specimen (Figure 1), five euchelicerates, five non-vicissicaudatans artiopodans and fourteen vicissicaudatans arthropods (including six aglaspidids and three cheloinellids), representing twenty-six species, were included in our study. The most complete and horizontally preserved specimen of *Zonozoe* (Lectotype NM L 23586) was chosen, while *Zonoscutum* is known from only one specimen (Holotype NM L 33021). The selection from the literature of the other taxa, was made following three main criteria: 1) to include Early Palaeozoic diversity from various geographic regions, but with particular emphasis on species coeval and sympatric to *Zonozoe* and *Zonoscutum* (e.g. *Paraeurypterus anatoliensis* (Lamsdell et al., 2013)); 2) to exclude taxa with aberrant cephalic outlines and favour those potentially related to *Zonozoe* and *Zonoscutum* (e.g. *Eozetetes gemmelli* (Edgecombe et al., 2017) and *Chlupacaris dubia* (Van Roy, 2005)); and 3) to maximize higher-level taxonomic diversity (e.g. *Carimersa neptuni* (Briggs et al., 2023) and *Lunataspis borealis* (Lamsdell et al., 2022)). A summary of the species and specimens included in the analysis, along with inventory numbers, geological age, geographic provenance, and references to the original sources from which raw images were obtained, is provided in Table 1, while the specimen sample, one for each high taxonomic group, is shown in Figure 1.

Material and photography

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The studied material of *Zonozoe* and *Zonoscutum* is housed in the palaeontological collections of the National Museum, Prague (prefix NM L). The photographs of *Zonozoe* were taken using a Sony ILCE-7RM5 digital camera with associated DT 100mm F2.8 SAM lens under normal lighting conditions, using a stand and a sandbox to hold the sample in place and ensure the horizontality of both the camera and the specimen. Specimens were coated by ammonium chloride prior photography to enhance morphological details.

Geological settings of Zonozoe *and* Zonoscutum

The examined specimens of *Zonozoe* and *Zonoscutum* (Figure 1) come from the Ordovician deposits of the Prague Basin (Czech Republic, Barrandian area). All *Zonozoe* and *Zonoscutum* specimens represent internal moulds preserved as imprints in coarse quartzose sandstones, showing limited anatomical details. The majority of them were collected at the at Děd Hill near Beroun (five specimens) or in the fields between Trubín and Trubská villages near Králův Dvůr (one specimen, see (Drage et al., 2018) for details of the location), in the upper part of the Letná Formation (Chlupáč, 1965). One specimen (NM L 37385) was recovered from the Řevnice Quartzite Member within the Libeň Formation near Kařez (Rak et al., 2009). (Vokáč & Grigar, 2024) recently reported additional cephala of *Zonozoe* from the Řevnice Quartzite Member (Libeň Formation) near Starý Plzenec. The only known cephala of *Zonoscutum* comes also from the Letná Formation within the Barrandian area (Chlupáč, 1999a). It has been discovered in the fields between Trubín and Trubská Villages near Králův Dvůr.

The Libeň Formation is developed in three different members – the shallow water R□evnice Quartzite, the sequence of black shales deposited deeper sea below the wave base in anoxic conditions, and the pyroclastic material (Havlíček, 1998). The Letná Formation is generally composed of alternating quartzose sandstones, greywackes, siltstones, and occasional shales, with sandstones representing a shallow-water environment (Chlupác & Kukal, 1988; Kraft et al., 2023). *Zonozoe* and *Zonoscutum* have so far been discovered only in the shallow water facies of Libeň and

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Letná Formations. Both Letná and Libeň Formations are of Sandbian age (Upper Ordovician) (Kraft et al., 2023). From the palaeogeographical perspective, these formations within the Prague Basin were deposited in high-latitude area near the western margin of Gondwana (Kraft et al., 2023; Scotese, 2023).

Silhouette drawing, Principal component analysis (PCA), linear discriminant analysis (LDA)

We extracted silhouette drawings from photographs of selected specimens, either taken by the authors in museum collections or sourced from the literature (see Table 1 and Figure 1). Using Adobe Illustrator 2021, we manually traced each specimen's outline over the photograph, then exported the silhouette as a JPG file (Figure 3A). These image files served as input for the Momocs package in R (Bonhomme et al., 2014; RCoreTeam, 2024), which we used to perform the subsequent outline analyses. JPG files were imported and converted to outlines, scaled, centred, and sampled at 64 point resolution, and subjected to elliptical Fourier analysis. The function calibrate_harmonicpower_efourier was used to determine the number of harmonics required for 99.9% of the harmonic power. Elliptical Fourier coefficients were visualised using Principal Component Analysis. Linear Discriminant Analysis was used to model differences between the major groupings in the dataset (Artiopoda (non-Vicissicaudata), Euchelicerata, Vicissicaudata, *Zonozoe*, *Zonoscutum*).

RESULTS

EFA, Principal component analysis (PCA), linear discriminant analysis (LDA)

Fifteen harmonics were retained, providing 99.9% of the harmonic power for the dataset. Principal component analysis reduced the dimensionality of elliptical Fourier analysis results, with PC1 and PC2 explaining 88.3% of the variation (67.4% and 20.9% respectively). Higher principal components (PC3–PC26) explain <5% of the variation each, and <15% overall. Three slightly overlapping groups are observed in the PCA space: Euchelicerata, Vicissicaudata, and Artiopoda

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(not including Vicissicaudata) (Figure 3B). Euchelicerates cluster toward the lower left (negative PC1, with PC2 values from close to zero to negative), while non-Vicissicaudatan artiopodans occupy the area of the space with PC2 close to zero and positive PC1 values. Within Vicissicaudata, aglaspidids fall near the origin of morphospace (PC1, PC2 close to zero), except for *Tremaglaspis unite* (Fortey & Rushton, 2003), which plots with a negative PC1 value (Figures 3B and C). Cheloniellids form a tight cluster with positive PC2 values. Both *Zonozoe* and *Zonoscutum* lie within the upper region of the vicissicaudatan space. *Zonozoe* plots between the cheloniellid *Neostrabops martini* (Caster & Macke, 1952) and the aglaspidid *Aglaspis barrandei* (Hall, 1862)(Figures 3B and C), whereas *Zonoscutum* lies close to the cheloniellids *Triopus* and *Drabovaspis complexa* (Barrande, 1872)(Figures 3B and C).

Linear discriminant analysis is dominated by LD1 (83.1% of the trace), with LD2 (9.9%), LD3 (5.2%) and LD4 (1.9%) providing only a relatively small amount of information. Our LDA (Figure 3D) separates Eucheliceratа from all other taxa, but cannot separate vicissicaudates from non-vicissicaudate artiopodans (Table 2). Leave-one-out cross-validation was 45.7% (11/24). Non-Vicissicaudata artiopodans fall into the vicissicaudatans space while both *Zonozoe* and *Zonoscutum* plot at the upper part of the LDA space (Figure 3D).

DISCUSSION

Our outline analyses provide morphological support for an Artiopoda, most likely Vicissicaudata, affinity for both *Zonozoe and Zonoscutum*. This provides the first quantitative evidence placing these enigmatic taxa not only within Artiopoda, previously inferred through taxonomically weak morphological traits, but more specifically within Vicissicaudata. However, the PCA does not explicitly support an affinity with Aglaspidida, particularly in the case of *Zonoscutum.* Instead, both taxa are placed in an intermediate position between cheloniellids and aglaspidids (Figures 3B and C).

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Although our analysis places *Zonozoe and Zonoscutum* near the cheloniellid cluster, we interpret this proximity cautiously and do not suggest it as evidence of a closer affinity with cheloniellids than with other vicissicaudatans. Key differences in cephalic morphology, which are most apparent in three-dimensional views, are not fully captured by our two-dimensional dataset, and both *Zonoscutum* and cheloniellids follow in this case. They show, respectively, a highly vaulted and extremely flattened cephalon, which may have been more affected by this methodological constraint, respectively to what was retrieved for *Zonozoe* and the other involved taxa. We believe this is the explanation behind the results of our PCA, concerning *Zonoscutum* clustering closer to the well-defined cheloniellids *Triopus* and *Drabovaspis* than to any other taxa. Based on this, we consider our method less effective for taxa with extremely vaulted or flattened cephala, such as cheloniellids and *Zonoscutum*. This limitation might have been addressed by using 3D volume data, but such data are difficult to obtain for fossils held in collections across multiple continents, and will also be impacted by flattening during or after fossilisation. Thus, we broadly agree with (Van Roy et al., 2022), who rejected a close relationship between *Zonozoe*, *Zonoscutum*, and cheloniellids, especially with the coeval and sympatric *Triopus*.

The closest non-cheloniellid vicissicaudatan to *Zonoscutum*, on the other hand, is *Chlupacaris*, which we regard as a more likely relative, also due to both general morphological similarities and geographic context. Both *Zonoscutum* and *Chlupacaris* exhibit a highly vaulted cephalon, again, a feature not fully accounted for in outline-based 2D morphometric methods, yet they have been recovered closely. Moreover, during the Upper Ordovician, the Prague Basin was situated near the western margin of Gondwana (Kraft et al., 2023; Scotese, 2023) and, thus, shared a close position to Morocco from a paleogeographic point of view. For *Zonozoe*, the closest taxa in our PCA are the cheloniellid *Neostrabops* and the aglaspidid *A. barrandei*. Ortega-Hernández et al. (2013) assigned *Neostrabops* as the less derived Cheloniellida, on the basis of a shared “presence of rounded genal angles, the anterior boundaries of the trunk reflexed anterolaterally and a reduced head shield”.

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However, the absence of a well-developed thoracic axis, already led Van Roy (2006) to suggest it may represent the less derived form of the group. Other studies (e.g., Legg et al., 2013; Lerosey-Aubril, Zhu, et al., 2017) also placed *Neostrabops* as a basal cheloniellid, but again relied on limited synapomorphies. The lack of preservation of key traits, such as furcal rami or the morphology of terminal tergites, hinders reliable comparison with better-known forms like *Triopus* or *Cheloniellon calmani* (Broili, 1932). The proximity of *Zonozoe* and *Neostrabops* in our PCA may therefore reflect more on the uncertain taxonomy of *Neostrabops* than on *Zonozoe* itself. Both fall within the vicissicaudatan morphospace, closer to aglaspidids than to other cheloniellids. Based on our results, we suggest that the taxonomical assignment of *Neostrabops* could be reconsidered towards Aglaspidida after new investigations or, in a more parsimonious way, towards Xenopoda.

On the other hand, the close PCA placement of *Zonozoe* (and *Neostrabops*) with *A. barrandei* supports a possible affinity with aglaspidids. While we do not draw a definitive conclusion, this result is consistent with previous observations, such as the position of the eyes and glabellar furrows behind them, which, while not strongly diagnostic (Van Roy et al., 2022), align with our morphometric findings and the exclusion of a possible euchelicerate affinity retrieved in our analyses (Fig. 3).

Our LDA results, though more influenced by predefined categories, provide additional insight. Euchelicerates are distinguished from Artiopoda, however vicissicaudatans and non-vicissicaudatans cannot be clearly separated (Figure 3D; Table 2). This was an unexpected finding for our outline data, given the superficial similarity in dorsal morphology between some early euchelicerates and vicissicaudatans like aglaspidids (e.g. *P. anatoliensis* and *T. unite*). Previous authors have even suggested the affinities of euchelicerates with aglaspidids based on such similarities, but our LDA analyses were able to discriminate the two groups. Both taxa of interest, *Zonoscutum* and *Zonozoe*, are positioned closer to vicissicaudatans than to non-vicissicaudatan artiopods, and are clearly separated from Euchelicerata. These results reinforce the more recent

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interpretation of aglaspidids, and by extension *Zonozoe* and *Zonoscutum*, as artiopodans, most likely vicissicaudatans.

CONCLUSION

Our outline□based morphometric analyses provide quantitative support for placing *Zonozoe* and *Zonoscutum* within Artiopoda, most likely as Vicissicaudata. Although they plot between cheloniellids and aglaspidids in the morphospace of two-dimensional carapace outlines, reflecting methodological limits when three□dimensional cephalic shape is compressed, both PCA and LDA consistently separate them from eucheliceratesWithin PCA space, they plot closest to vicissicaudatan artiopods. Taken together, these results support a vicissicaudatan affinity for these taxa. Overall, our method has proven to be a useful alternative for classifying arthropod fossils when discrete characters required for phylogenetic methods are absent. This is often the case with moulds, which rarely preserve fine anatomical details. While our approach is less precise than formal phylogenetic analysis, it allows for the inclusion of specimens that would otherwise be excluded from broader evolutionary or paleoecological studies. In our case, it provides evidence for the presence of non-cheloniellid vicissicaudatans in the Letná Formation, based on poorly preserved specimens that would likely be overlooked using only traditional qualitative methods.

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AUTHOR CONTRIBUTIONS

L.Lu. conceptualized the original idea and wrote the first draft of the manuscript. L.Lu., L.La. and L.C. collected the data. S.P. analysed the data. L.La. and L.C., and S.P. prepared the figures and wrote sections of the material and methods, results, and discussion. Y.L., J.B. and M.N. were involved in the discussion and final editing of the manuscript. All authors read and approved the final version of the manuscript.

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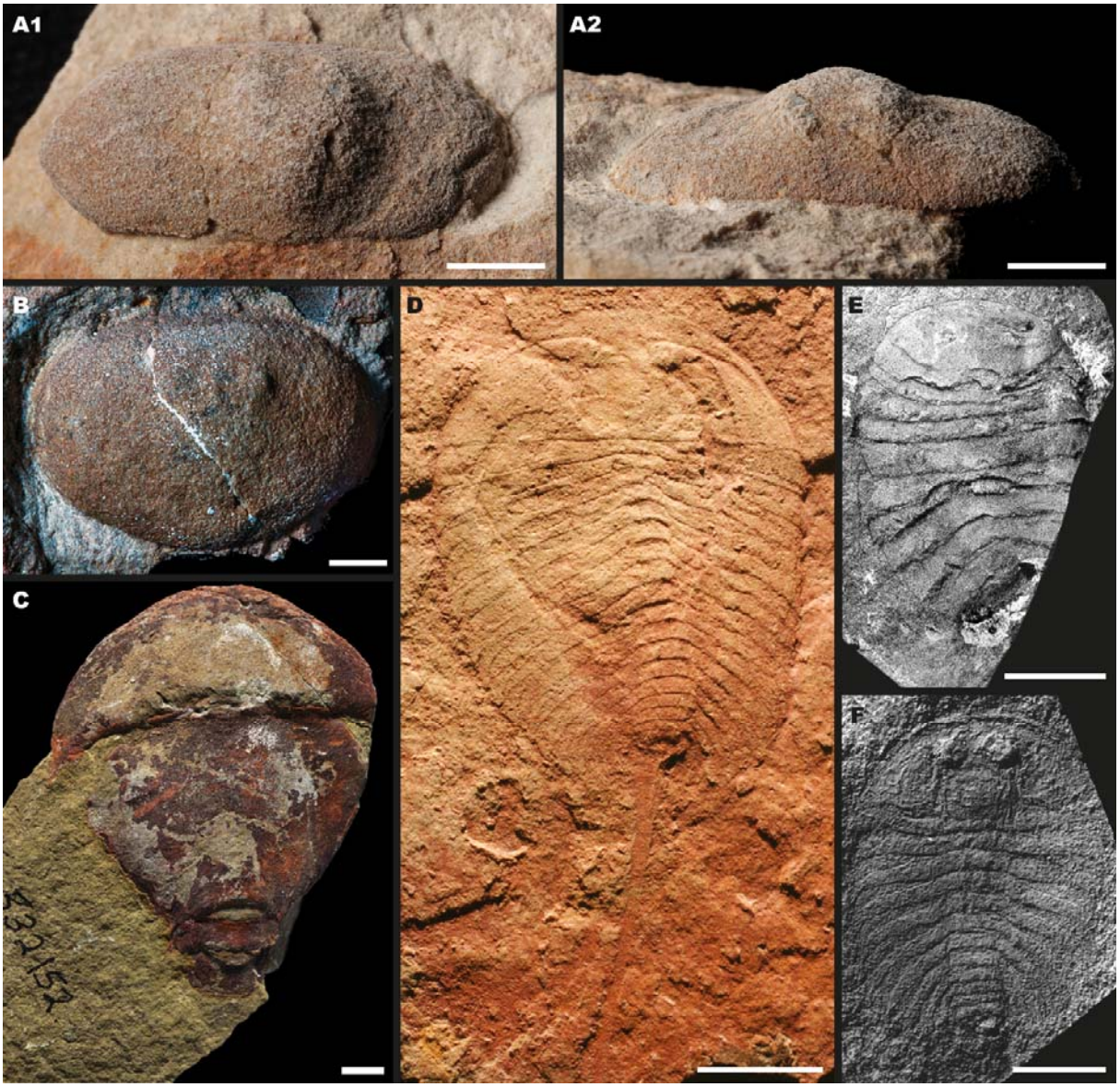


Figure 1. Representative cephala of *Zonozoe drabowiensis*, *Zonoscutum solum*, euchelicerate arthropods, vicissicaudatan cheloniellids, vicissicaudatan aglaspidids, and non-vicissicaudatan artiopodans featured in this study. A1, *Zonozoe drabowiensis*, dorsal view; A2, *Zonozoe drabowiensis*, frontal view; B, *Zonoscutum solum*, dorsal view, modified from Van Roy et al. (2022); C, unnamed Xiphosura from the Fezouata biota, modified from Lamsdell & Ocon (2025). D, *Eozetetes gemmelli*, modified from (Edgecombe et al., 2017); E, *Neostrabops martini*, modified from (Caster & Macke, 1952); F, *Aglaspis barrandei*, modified from (Hesselbo, 1992). Scale bar equals 5 mm.

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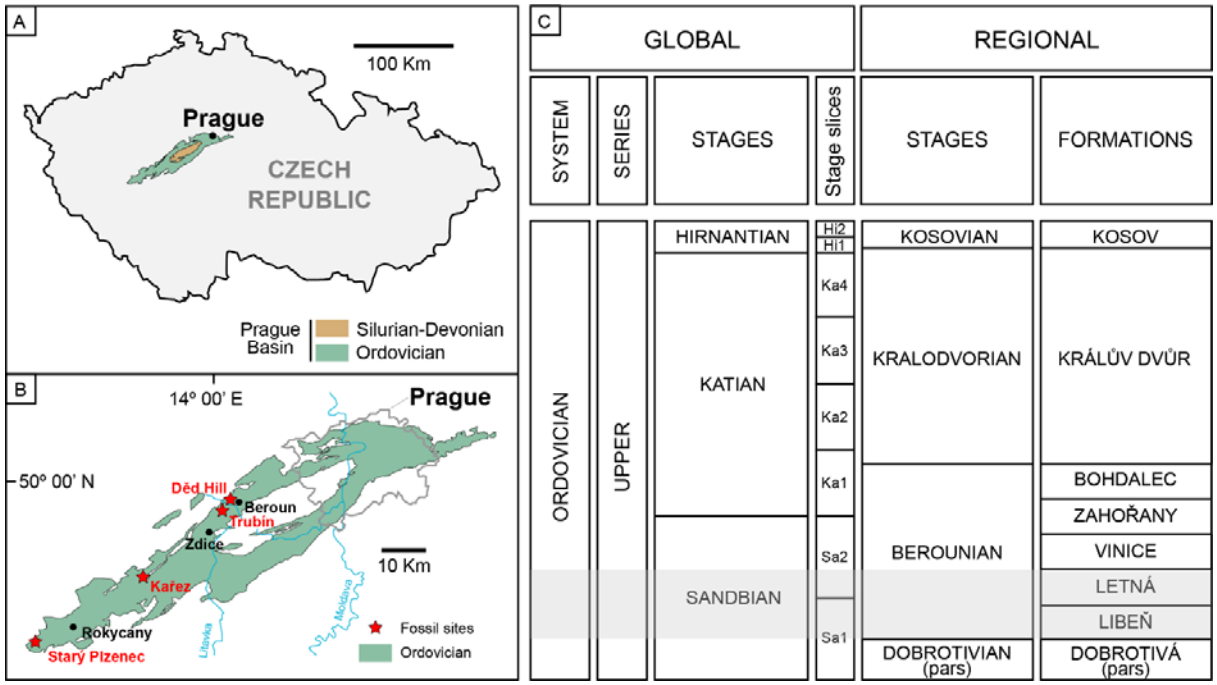


Figure 2. geographical and stratigraphical position of the localities where *Zonozoe drabowiensis* and *Zonoscutum solum* were collected. A; map of the Czech republic, B; stratigraphical column of the upper Ordovician (modify after (Van Roy et al., 2022)).

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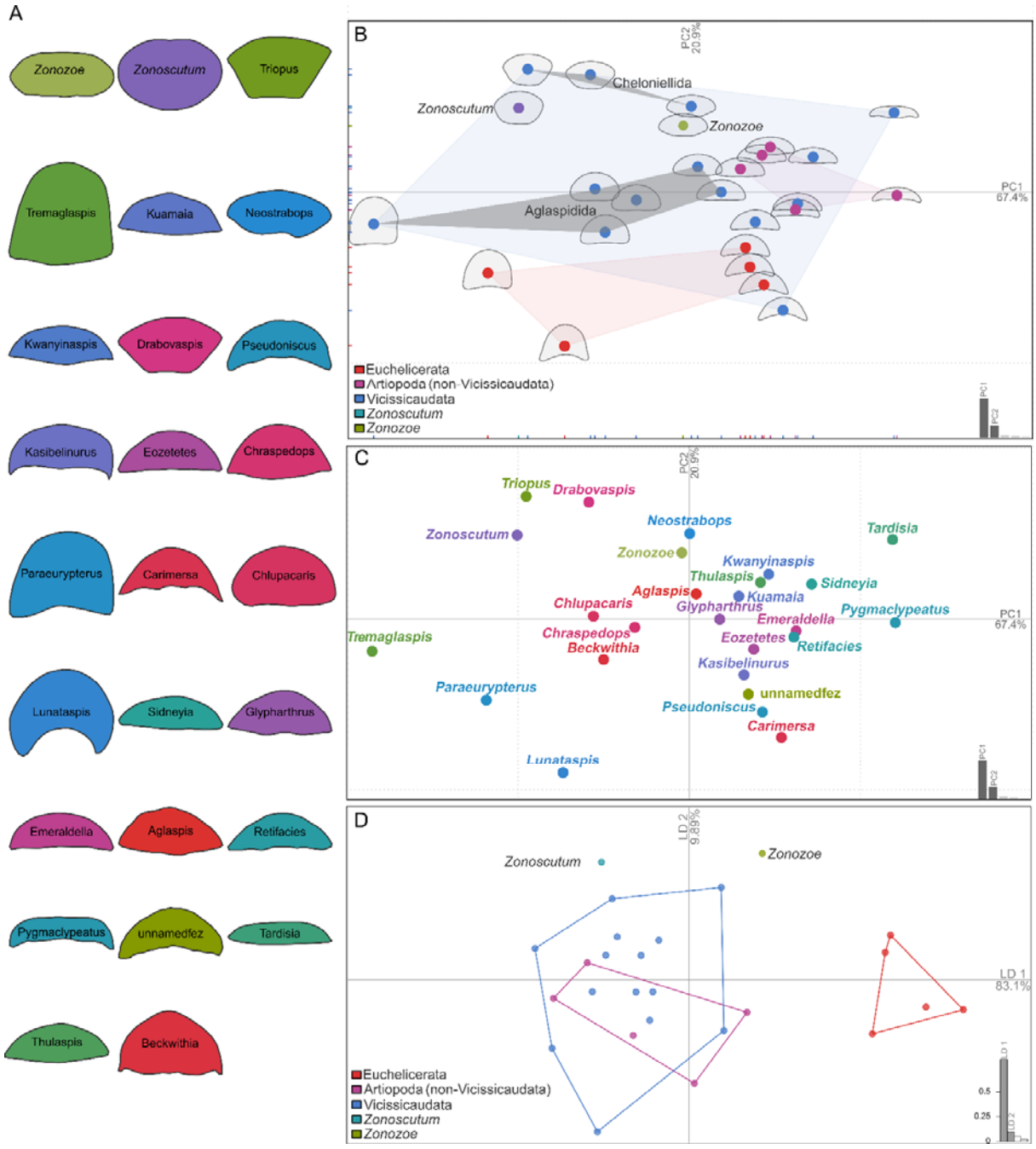


Figure 3. Data and Results of Principal Component Analysis and Linear Discriminant Analysis of elliptical Fourier coefficients. A, Cephalic outline of *Zonozoe drabowiensis*, *Zonoscutum solum* and the other specimens involved in the study; B, position of *Zonoscutum* and *Zonozoe* in relation to major taxonomic groupings: Euchelicerata, Artiopoda (not including Vicissicaudata), and Vicissicaudata. Grey convex hulls show subgroups within Vicissicaudata, specifically Aglaspidida and Cheloniellida. Coloured marks along x and y axis indicate PC1 and

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PC2 values of individual specimens plotted in the space, with positions of specimens shown by filled circles. Grey outlines show variation in cephalic outline across PC1 and PC2. Histogram in bottom right shows amount of variation explained by PC1, PC2, and PC3-5; C, results by individual outline of PCA analyses. Abbreviation 'unnamedfez' refers to an unnamed Xiphosura from the Fezouata biota (Van Roy et al., 2010; Lamsdell & Ocon, 2025); D, Position of *Zonoscutum* and *Zonozoe* in relation to major taxonomic groupings: Eucheliceratа, Artiopoda (not including Vicissicaudata), and Vicissicaudata in Linear Discriminant space. Coloured circles show positions of individual specimens. Histogram in B, C and D the shows the proportion of the trace for each linear discriminant.

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344 **Table 1.** List of specimens used for the outline analyses.

Species	Number	Age and origin	Clade	Reference	Figures
Zonoscutum solum	NM L 33021	Upper Ordovician, Czech Republic	Suspected Aglaspidida	(Van Roy et al., 2022)	Fig. 8C
Zonozoe drabowiensis	NM L 23586	Upper Ordovician, Czech Republic	Suspected Aglaspidida	Present work	Fig. 1E
Beckwithia typa	BPM 1060	Late Cambrian, Utah	Aglaspidida	(Lerosey-Aubril, Paterson, et al., 2017)	Fig. 9F
Chlupacaris dubia	NMSG.2005.103.1	Upper Ordovician, Morocco	Aglaspidida	(Van Roy, 2005)	Fig. 3A
Tremaglaspis unite	NHMIA56	Upper Ordovician, Wales	Aglaspidida	(Fortey & Rushton, 2003)	Fig. 1B
Glypharthrus trispinicaudatus	NIGPAS 165044	Late Cambrian, South China	Aglaspidida	(Lerosey-Aubril, Paterson, et al., 2017)	Fig. 3 G
Chraspedops modesta	MPM 11938	Late Cambrian, US	Aglaspidida	(Hesselbo, 1992)	Fig. 18, 4
Aglaspis barrandei	AMNH 39193	Late Cambrian, Wisconsin	Aglaspidida	(Hesselbo, 1992)	Fig. 2, 5
Xiphosura from Fezouata	YPM IP 532152	Lower Ordovician, , Morocco	Eucheliceratа	(Lamsdell & Ocon, 2025)	Fig. 2, 7
Paraeurypterus anatoliensis	MTANHMSETR 10-İZ-01-1	Upper Ordovician, Turkey	Eucheliceratа	(Lamsdell et al., 2013)	Fig. 3A
Lunataspis borealis	MM I-4583	Upper Ordovician, Canada	Eucheliceratа	(Lamsdell et al., 2022)	Fig. 2, 1
Pseudoniscus falcatus	UK. NHMUK PI	Early Silurian, Scottland	Eucheliceratа	(Bicknell & Pates, 2020)	Fig. 9A
Kasibelinurus amicorum	AM F68969	Devonian, Australia	Eucheliceratа	(Bicknell & Pates, 2020)	Fig. 11A
Kwanyinaspis maotianshanensis	ELI-12004001	Early Cambrian, South China	Artiopoda	(Zhang & Shu, 2005)	Fig. 2A-D
Pygmaclypeatus daziensis	YKLP 11427	Early Cambrian, South China	Artiopoda	(Schmidt et al., 2025)	Fig. 1A
Thulaspis tholops	MGUH 34172a	Early Cambrian, North Greenland	Artiopoda	(Berks et al., 2023)	Fig. 1A
Retifacies abnormalis	JS-840	Early Cambrian, South China	Artiopoda, Trilobitomorpha	(Lin et al., 2024)	Fig. 1A
Kuamaia lata	YKLP 17296	Early Cambrian, South China	Artiopoda, Helmetiidae	(O'Flynn et al., 2024)	Fig. 2A
Emeraldella brocki	USNM 136641	Middle Cambrian, Canada	Artiopoda, Vicissicaudata	(Stein & Selden, 2012)	Fig. 3B
Tardisia broedeae	FMNH PE 88856	Late Carboniferous, Illinois	Artiopoda, Vicissicaudata	(McCoy et al., 2025)	Fig. 1D
Eozetetes gemmelli	SAM P48369a	Early Cambrian, Australia	Artiopoda, Vicissicaudata	(Edgecombe et al., 2017)	Fig. 2A
Carimersa neptuni	OUMNH PAL-C.376503	Early Silurian, England	Artiopoda, Vicissicaudata	(Briggs et al., 2023)	Fig. 1A
Sidneyia minor	YKLP 12435	Early Cambrian, South China	Artiopoda, Vicissicaudata	(Du et al., 2023)	Fig. 2A
Triopus draboviensis	NM L 16736	Upper Ordovician, Czech Republic	Cheloniellida	(Van Roy et al., 2022)	Fig. 2B
Drabovaspis complexa	NM L 23577	Upper Ordovician, Czech Republic	Cheloniellida	(Van Roy et al., 2022)	Fig. 9A
Neostrabops martini	25560	Late Cambrian, Missuri	Cheloniellida	(Caster & Macke, 1952)	Fig. 2

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346 **Table 2.** Cross validation table following Linear Discriminant Analysis, showing the classification
347 of groups and the class accuracy. Class accuracy and classification not performed for *Zonoscutum*
348 and *Zonozoe* as they are represented only by a single specimen.

	Euchelicerata	Non-Vicissicadata	Vicissicaudata	*Zonoscutum*	*Zonozoe*	Class accuracy
Euchelicerata	4	0	0	0	1	80%
Non-Vicissicadata	1	0	4	0	0	0%
Vicissicaudata	0	4	7	2	1	50%

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