Morphometric and taxonomic analysis of trilobite *Acanthopyge haueri* (Barrande, 1846) from the Middle Devonian (Eifelian) of the Barrandian area (Czech Republic)

Petr Budil, Matěj Šilinger, Catherine Crônier, Václav Vokáč, Jiří Frýda & Brian D.E. Chatterton



A comprehensive study of morphological variability in *Acanthopyge haueri* (Barrande, 1846), the genotype species of *Acanthopyge* Hawle & Corda, 1847 from the Middle Devonian (Eifelian) of the Barrandian area (Czech Republic), is presented. Two different methods were used to assess variability: classical biometric analysis and landmark-based morphometrics. The data show notable morphological variability within a supposedly well-defined species. All measured parameters are variable, and some of these characters, previously considered to be of generic significance, show substantial variation. Early holaspid specimens of *A. haueri* are less variable, whereas larger ones show much greater variability which, however, may partially also reflect diagenetic and tectonic deformation. Prominent allometry is observed during development: early holaspid specimens obviously have less vaulted cephala with less prominent lobation; pygidia are almost sub-circular, with relatively shorter post-axial ridge and relatively long and straight marginal spines. In contrast, large specimens have prominent vaulting of the cranidium (especially median lobe), relatively longer pygidia with often a semi-elliptic to elongate, sub-triangular outlines, relatively shorter marginal spines, a relatively longer (sag.) post-axial ridge, and distinctly vaulted lateral lobes of the pygidium, while the axis is only moderately vaulted. However, the observed variability may reflect the broad stratigraphic range of *A. haueri*, which may comprise several subspecies or distinct species that cannot yet be differentiated. The new material allows an amendment to the description of Lower Devonian (upper Emsian) *Huginarges*? *pervasta* (Přibyl, Vaněk & Hörbinger, 1986), a species previously poorly known. The morphology of *H.*? *pervasta* is intermediate between *Acanthopyge* and *Huginarges* Basse *in* Basse & Müller, 2004. Early holaspid specimens of *A. haueri* are morphologically similar to *H.*? *pervasta*, including a relatively shorter postaxial pygidial ridge. The abrupt appearance of abundant *Acanthopyge* probably reflects the partial release of niche habitats following the extinction of many shallow-water scutelluid trilobites during the early Eifelian Basal Choteč Event. It is possible that *A. haueri* evolved from the *H.*? *pervasta* group through predominant peramorphosis. The decline of *Acanthopyge* is related to the early Givetian Kačák anoxic Event, although some representatives apparently survived into the early Givetian. • Key words: Lichida, *Acanthopyge*, Devonian, systematics, taphonomy.

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Petr Budil (corresponding author) & Jiří Frýda, Faculty of Environmental Science, Czech University of Life Sciences, Kamýcká 129, Praha 6, 165 21, Czech Republic & Czech Geological Survey, Klárov 3, Praha 1, 118 00, Czech Republic; phacopidina1@gmail.com • Matěj Šilinger, Museum of the Bohemian Karst, Husovo náměstí 87, Beroun, 266 01, Czech Republic; *Charles University, Faculty of Science, Institute Geology and Palaeontology, Albertov 6, Praha 2, CZ -128 43, Czech Republic • Catherine Crônier, Univ. Lille, CNRS, UMR 8198 Évo-Éco-Paléo, 59000 Lille, France • Václav Vokáč, Ke Kukačce 21, 312 00 Plzeň, Czech Republic • Brian D.E. Chatterton, Department of Earth and Atmospheric Sciences, University of Alberta, Edmonton, Alberta T6G 2E3, Canada*

Representatives of *Acanthopyge* Hawle & Corda, 1847 are typical and significant components of some Middle Devonian (Eifelian) trilobite associations. *Acanthopyge* belongs to the large and important group of Devonian trochurine lichids that includes *Acanthopyge*, *Huginarges* Basse *in* Basse & Müller, 2004 (*sensu* van Viersen 2021 = *Lobopyge* Přibyl & Erben, 1952), *Jasperia* Thomas & Holloway, 1988, and the poorly known *Nipponarges* Kaneko, 1984 (as well as the newly established but in our opinion rather problematical *Rheicarges* Basse & Müller,

2023). The origin of the group was probably during the late Silurian (see Thomas & Holloway 1988).

In the Prague Basin of the Barrandian area, Bohemia (part of the remnants of the Perunica Microcontinent, *sensu* Havlíček *et al.* 1994 and Fatka & Mergl 2009), the type species of *Acanthopyge*, *A. haueri* (Barrande, 1846), is common particularly in the shallow-water Acanthopyge Limestone of Eifelian age (see Vaněk 1959; Thomas & Holloway 1988; Chlupáč 1988, 1993, 1998a, b; Chlupáč *et al*. 1986). *Acanthopyge* forms an important component of the moderately diverse *Acanthopyge–Phaetonellus* Trilobite Assemblage (*sensu* Chlupáč 1983a), characterized by locally abundant occurrence of its exoskeletal sclerites (or *Karbous–Acanthopyge* Community, *sensu* Havlíček & Kukal 1990). A supposedly relative *Huginarges*? *pervasta* (Přibyl, Vaněk & Hörbinger, 1986) is a rare component of the *Orbitoproetus – Scabriscutellum* Trilobite Assemblage (*sensu* Chlupáč 1983a) in the underlying Suchomasty Limestone of latest Emsian age.

Common, but formally undescribed representatives of *Acanthopyge* are known from Morocco (Northwestern Gondwana). These specimens of *Acanthopyge* occur in the El Otfal Formation of the Eifelian age; some other representatives of *Acanthopyge* sensu stricto were gathered by Koppka & van Viersen (personal communication) in the Jorf Area. One of us (BDEC) has collected specimens from Middle Devonian rocks of the M'ader area, on the slopes of a distinctive bioherm known as Aferdou, near Mrakib.

In contrast, most previously reported occurrences of *Acanthopyge* s.s. from other palaeocontinents, especially from Laurentia, belong to *Jasperia* (Thomas & Holloway, 1988). The exception is an occurrence of a poorly known form apparently closely related to *A. haueri* from the Eifelian of Kazakhstan (Maximova 1979). Another important but poorly known taxon is Givetian *A.*? *granulosa* (Roemer, 1852) known from the Rhenish Mountains.

Representatives of this genus (together with other taxa such as *Thysanopeltis* Hawle & Corda, 1847) could be considered as useful supplementary stratigraphical markers for the uppermost Emsian and especially for the Eifelian Basal Choteč Event (*Thysanopeltis* likely first appears in the Eifelian). The disappearance of *Acanthopyge* in the latest Eifelian in Perunica, and probably also along the northern margin of Gondwana, can possibly be linked to environmental changes associated with the Kačák Event that caused major extinction of trilobite faunas (see Chlupáč & Kukal 1988; Chlupáč 1983a, 1988, 1994, 1998a).

The rare occurrence of *A.*? *granulosa* (Roemer, 1852) in the middle Givetian of the Rhenohercynian Belt (*fide* Basse & Müller 2004) and occurrences in Morocco in the lower Givetian can nevertheless indicate that the genus could have survived this major, global decline in trilobite diversity. An early Givetian (pre-Taghanic) occurrence of *Acanthopyge* was further discussed by Basse & Müller (2023), but Givetian findings remain scarce or problematic. A post-Kačák Event decline of the genus is apparent.

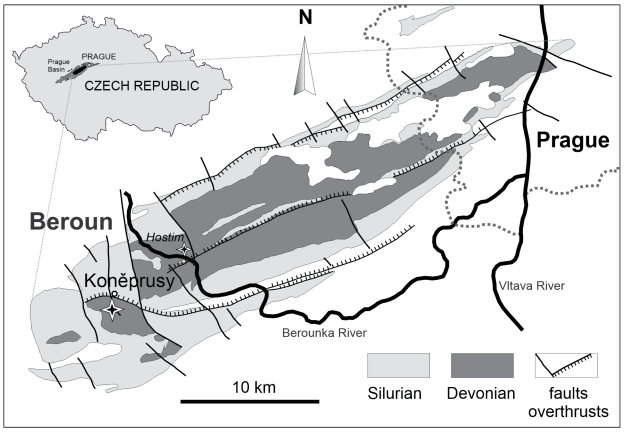


Figure 1. Sketch map showing the distribution of Devonian rocks in the Barrandian area. The position of the studied locality (Koněprusy area) is indicated by a star.

The last comprehensive revision of *Acanthopyge* was undertaken by Thomas & Holloway (1988). Since then, new taxa have been discovered, and older species (mostly of doubtful systematic position) have been described and assigned to this genus especially by Vaněk (2002), and Vaněk & Valíček (2002); additional taxa have been discussed by Kim (1997) and Basse & Müller (2004). As a result, the systematics of this genus need to be revised. As a first step, we review herein the considerable morphological variability observed in topotypes of the type species, *A. haueri*, and in *H.*? *pervasta*, here considered as its putative ancestor. The newly observed variability of features previously considered as diagnostic for *A. haueri* helps to improve the definition of type species and thus has implications for the concept and diagnosis of the genus.

Geological setting

The type species of *Acanthopyge*, *Lichas haueri* Barrande, 1846, occurs in Bohemia solely in the eponymous Acanthopyge Limestone, a shallow-water facies of the Eifelian Choteč Formation, established by Svoboda & Prantl (1949). The Acanthopyge Limestone is confined to the small, geographically limited Koněprusy area (see Chlupáč 1983a, b, 1998a, b, Chlupáč *et al*. 1986; Hladil 1993; among others; see Figs 1, 2). *H.*? *pervasta* (Přibyl *et al*., 1986) occurs in the same area (though much rarer than *A. haueri*) in the underlying Suchomasty Limestone, of late Emsian age, defined by Chlupáč (1957a). The Koněprusy area represents a part of a synsedimentary

(most probably tectonically) uplifted submarine elevation (*cf.* Hladil 1995, 1997; Hladil & Slavík 1997; Chlupáč 1996, 1998a, b) with well-developed local bioherms in the late Emsian and Eifelian. No true reefs are, however, recorded after the Pragian, when a reef *s.s.* was developed close to or within the area, with its marginal, peripheral, and possibly core parts preserved in the Koněprusy Limestone facies (for discussion see Chlupáč 1957a, b, 1959, 1977, 1983a, b, 1998a, b; Chlupáč *et al*. 1977, 1986 Havlíček & Kukal 1990; Hladil & Gabašová 1993; Hladil 1995, 1997; Hladil & Slavík 1997; Mergl 2014, 2022).

All three of the above-mentioned facies, *e.g*. Pragian Koněprusy, Upper Emsian Suchomasty, and Eifelian Acanthopyge limestones (locally also Roblín Member of the Srbsko Formation, of Givetian age, and perhaps even younger sediments; for review see Chlupáč 1996) are involved in the fabrics of neptunian dykes – fissure fillings in the supposed reef core that were periodically infilled by younger formations (see Chlupáč 1977, 1983a, b, 1996, 1998a, b; Chlupáč *et al*. 1986). These extensional fissures originated under congruent tectonics in an uplifting area (Chlupáč 1996) and presented a specific protected environment within a shallow, high energy setting that offered shelter and a nutrient-rich food source, suitable also to provide protection for the animals while they were soft shelled after moulting. The neptunian dykes were thus inhabited by enriched trilobite communities, especially harpetids, proetids, scutelluids, and lichids (Chlupáč 1983a). The rare *H.*? *pervasta* is much more common in the neptunian dykes than in the "normal" Suchomasty Limestone, and local accumulations or clusters of isolated shields of *A. haueri*, are also present in the neptunian dykes (Chlupáč 1996, p. 203).

Notes on sedimentology – The Eifelian Acanthopyge Limestone is characterized by a predominance of generally well washed grainstone/rudstone, crinoidal lime-

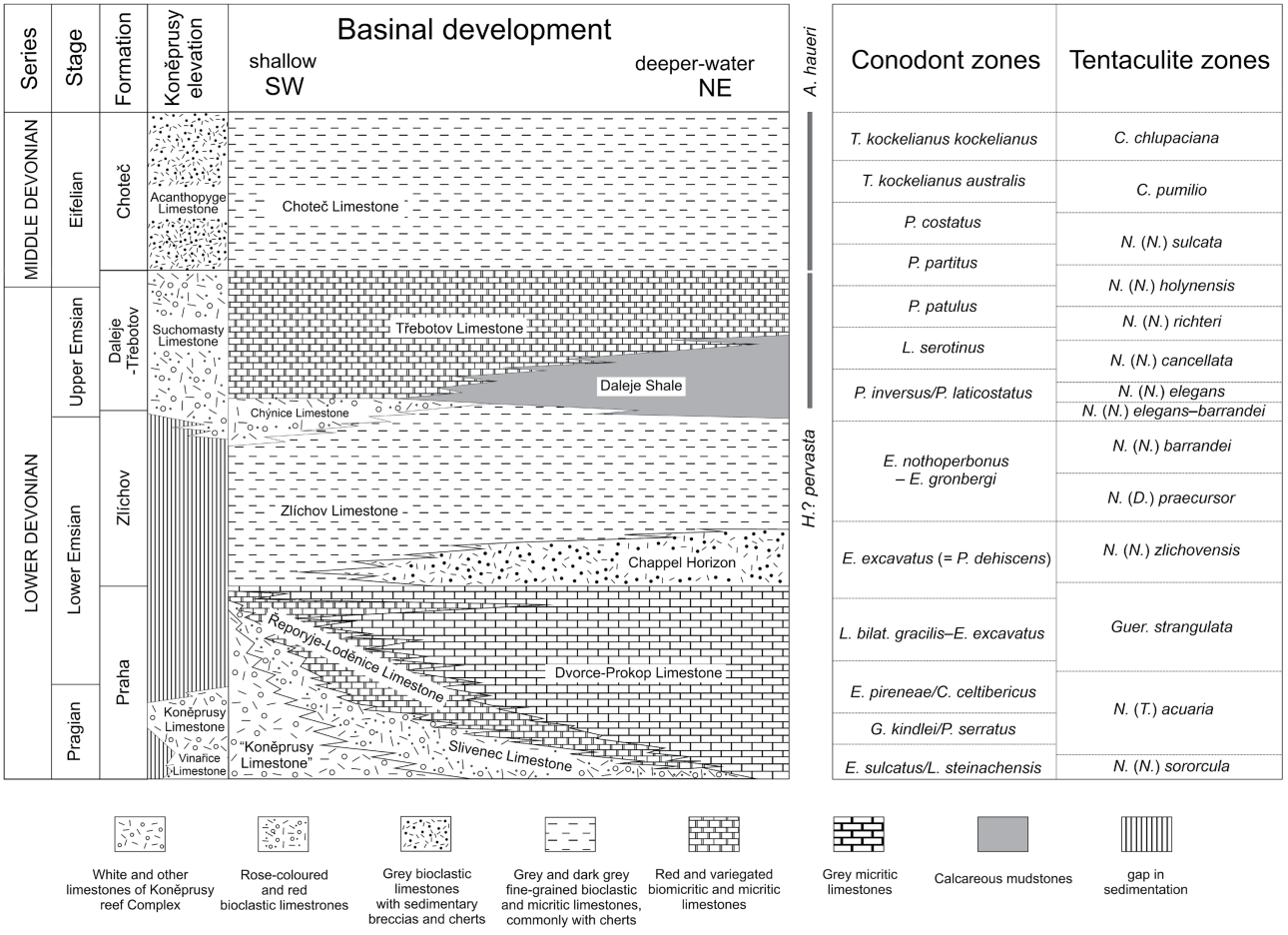


Figure 2. Pragian to Eifelian stratigraphy of the Prague Basin (after Chlupáč *et al.* 1998a, modified by Budil *et al*. 2009) with marked occurrences of *A. haueri* (Barrande, 1846) and *H.*? *pervasta* (Přibyl, Vaněk & Hörbinger, 1986). Conodont biozones of Pragian after Slavík (2004a, b), Slavík *et al*. (2007), and Carls *et al.* (2008). Upper Emsian to Eifelian biozones after Gradstein *et al.* (2012), Ferrová *et al*. (2012), Klapper & Vodrážková (2013) and Vodrážková *et al*. (2013).

stone and shallow-water carbonate facies (Havlíček & Kukal 1990, Galle & Hladil 1991). Grey, whitish, and less frequently red or pink color is typical for this limestone unit. Locally, irregular lenses or beds of white to yellowish carbonate mudstone ("Mydlák" facies) and sparites with abundant sponge remains are also present (Havlíček & Kukal 1990). The topmost sequence of the dark bedded limestone has been correlated by some authors with the basinal Kačák Member of the Srbsko Formation and with the onset of the late Eifelian–earliest Givetian Kačák Event (Hladil *et al*. 1992; Hladil 1993; Budil 1995; Mergl & Vohradský 2000; Mergl 2014, 2019, 2022; Mergl & Budil 2019; Vodrážková & Suttner 2020). The total thickness of the Acanthopyge limestones does not exceed 20 metres (Mergl 2022).

The Eifelian age of the Acanthopyge Limestone is well established, based on the occurrence of index goniatites (Chlupáč & Turek 1983), conodonts (Zikmundová & Kalvoda *in* Galle & Hladil 1991, Berkyová 2009), dacryoconarid tentaculites, and other fauna. The supposed Givetian age of the strata above the dark interval (in the uppermost part of the Acanthopyge Limestone) was originally indicated by typical tabulatomorphs and stromatoporoids (Hladil 1993), organisms not typically used for accurate age determination, but has been subsequently supported by tentaculites, conodonts, brachiopods and trilobites (*e.g*. Vodrážková 2004; Mergl 2019, 2022; Mergl & Budil 2019; Vodrážková & Suttner 2020). *Acanthopyge haueri* occurs in the Acanthopyge Limestone up to a level immediately below the dark colored interval that, most probably, corresponds to the onset of the Kačák Event.

Most of the Acanthopyge Limestone succession shows features of an extremely shallow-water (Havlíček & Kukal 1990), and dynamic environment with redeposition and fracturing of biomineralized particles. Such conditions were apparently unfavorable for the preservation of articulated trilobites. Only some phacopids, e.g. *Chotecops hoseri* (Hawle & Corda, 1847) and *C. breviceps* (Barrande, 1846) with well-developed coaptative structures are occasionally found articulated, whereas lichids or scutelluids are not. The absence of articulated specimens of *Acanthopyge* even in the more protected environment of neptunian dykes indicates that current energies within these crevices were still sufficient for local transportation and disarticulation of lichid shields. Thus, all known specimens of the type species *A. haueri*, are based on isolated cranidia, pygidia, hypostomes, and fragments of free cheeks and thoracic segments, with the exception of a newly described early holaspid cephalon with remains of attached free cheeks present (see below). This is the only articulated remain of *A. haueri* known to date from the Acanthopyge Limestone.

The Suchomasty Limestone, which yields the putatively ancestral form *H.*? *pervasta* (Přibyl, Vaněk & Hörbinger, 1986), shares (especially in its upper layers) several sedimentological features with the Acanthopyge Limestone. It lies, with a breccia interlayer (Chlupáč 1957, 1959), in the stratigraphic footwall of the Acanthopyge Limestone facies. It is of latest early to late Emsian in age and disconformably overlies the Pragian reefal Koněprusy Limestone. The Suchomasty Limestone is represented mostly by well-bedded, reddish, to reddish-brown, pink, purple and sometimes also grey, greenish, whitish and bluish, predominantly crinoidal grainstone/rudstone. The thickness of the Suchomasty limestones ranges from 15 to 25 metres. Sorting of bioclasts, lens-like fossil accumulations, stromatactis structures, and gradational bedding, together with heterogeneous sedimentological structures, indicate a shallow-water and high-energy environment (see Havlíček & Kukal 1990, Chlupáč 1998a, Mergl 2015). The age of the Suchomasty Limestone is confidently determined by dacryoconarid tentaculites (Chlupáč *et al*. 1979, 1986; Berkyová 2004; Ferrová *et al*. 2012), conodonts (Klapper 1977, Klapper *et al*. 1978, Chlupáč *et al.* 1986, Chlupáč 1998a, Berkyová 2009), and goniatites (Chlupáč & Turek 1983). The preservation pattern of *H.*? *pervasta*, despite its rarity and small size, is similar to that of *A. haueri* – articulated specimens are absent, and only rare isolated shields have been found.

Notes on trilobite assemblages – Acanthopyge haueri occurs within the *Acanthopyge–Phaetonellus* Trilobite Assemblage, described by Chlupáč (1983a) as highly diverse, confined to the Acanthopyge Limestone of the Choteč Formation (Eifelian). The assemblage is characterized by abundant occurrence of the indicative species *A. haueri* alongside *Phaetonellus planicaudus* (Barrande, 1846). Chlupáč (1983a) characterized this trilobite assemblage as shallow-water within the range of Benthic Assemblage 3 and possibly 2 *sensu* Boucot (1975). The *Acanthopyge–Phaetonellus* Assemblage includes representatives of the following trilobite families: Lichidae (*Acanthopyge*), Aulacopleuridae (*Aulacopleura*, *Aulacopleurina*, *Cyphaspides*, *Otarion*), Proetidae (*Erbenites*, *Koneprusites*, *Orbitoproetus*) and Tropidocoryphidae (*Alberticoryphe*, *Benesovella*, *Buchiproetus*, *Eremiproetus*, *Ignoproetus*, *Nagaproetus*, *Phaetonellus*, *Proetopeltis*, *Trautensteinproetus*, *Tropidocoryphe*), Styginidae (*Scabriscutellum*, *Thysanopeltis*), Cheiruridae (*Crotalocephalus*), Phacopidae (*Chotecops*), Odontopleuridae (*Isoprusia*, *Kettneraspis*, *Koneprusia*), and Harpetidae [*Kielania*, *Lioharpes* (*Fritchaspis*)], belonging to more than 35 species.

Huginarges? *pervasta* occurs as a rare part of the *Orbitoproetus–Scabriscutellum* Trilobite Assemblage, which was defined by Chlupáč (1983a). The assemblage is also highly diverse (about 50 species described) and characterized by very abundant occurrence of *Orbito-*

proetus orbitatus (Barrande, 1846) and abundant occurrence of *Scabriscutellum* (*S.*) *oblongum* (Hawle & Corda, 1847), *Scabriscutellum* (*S.*) *caelebs* (Barrande, 1852) and rare occurrence of *Scabriscutellum* (*S.*) *elongatum* (Barrande, 1846). Chlupáč (1983a) characterized this trilobite assemblage as shallow-water, within the range of Benthic Assemblage 3 (classification of Boucot 1975). The following families of trilobites are known from the *Orbitoproetus–Scabriscutellum* Assemblage: Lichidae (*Huginarges*?), Aulacopleuridae (*Conoparia*, *Cyphaspides*), Proetidae (*Buchiproetus*, *Cornuproetus*, *Gerastos* (*G.*), *Eremiproetus* (*E.*), *Myoproetus*, *Orbitoproetus*, *Tafilaltaspis*, *Unguliproetus*), Scharyiidae (*Scharyia*), Tropidocoryphidae (*Alberticoryphe*?, *Dalejeproetus*, *Ignoproetus*, *Phaetonellus*, *Proetopeltis*, *Trautensteinproetus*, *Tropidocoryphe*, *Quadratoproetus*, *Wolayella*), Styginidae (*Andegavia*, *Paralejurus*, *Scabriscutellum*), Cheiruridae (*Crotalocephalina*, *Crotalocephalus*), Phacopidae ("*Pedinopariops*", *Signatops*), Odontopleuridae (*Ceratocephala*, *Kettneraspis*, *Koneprusia*, *Leonaspis*, *Radiaspis*), Harpetidae (*Kielania*, *Reticuloharpes*).

Methods

Terminology and abbreviations. – Terminology follows Whittington & Kelly (1997), except where noted otherwise. Specimens with abbreviation CGS are housed in the collections of the Czech Geological Survey, Prague (Czech Republic), and specimens marked NM L are housed in the National Museum, Prague (Czech Republic). Specimens with the abbreviation SMF are housed in the collections of the Forschungsinstitut Senckenberg, Frankfurt am Main, Germany.

Illustration. – All trilobite specimens were examined using standard light microscopy of both external and internal surfaces (Microscope NIKON SMZ 1500, Leica S8APO). Photographs were taken using digital cameras NIKON D 300 and Olympus SZX-ILLB200 after coating the samples with ammonium chloride. Minute specimens were photographed using the National Museum's Keyence VHX-2000 digital microscope, and the resulting images were processed with the CombineZP PC program. Vector illustrations were prepared using Corel Draw X3, and photographs were enhanced in Corel Photo Paint X3.

Statistics. – Statistical analyses were performed using the software PAST v.1.0-3.15. Graphs were generated with this program and Microsoft Excel 365.

Biometric parameters. – For the biometric evaluation of the variability of *Acanthopyge haueri*, we selected parameters that are preserved and readily measurable in most of the specimens studied (see Fig. 3A and its explanatory remarks). Some features are often covered by rock in bioclastic limestones and are difficult to prepare in larger numbers of individuals. For the quantitative evaluation of the cranidial width, for example, the parameter Cw_{max} was chosen, which reflects the maximum transverse (tr.) width across posterolateral lobes and not width of the cranidium itself. The biometric measurements of *A. haueri* involved an examination of 162 cranidia, 137 pygidia, and 50 hypostomes. The main constraint was the lack of precise stratigraphical affiliation for most measured specimens, which came mostly from museum collections. This represents a significant difficulty because the gathered data show notable morphometric variability. Unfortunately, it was not possible to obtain better new material in sufficient numbers, or material that could be located with greater stratigraphic precision. All sites where *Acanthopyge haueri* occurs are strictly protected; large-scale excavation work is not permitted there, and the number of new discoveries is thus severely limited.

The observed variation could reflect a wide range of factors. Morphological differences might result from examining different "hidden" species, gradual ontogenetic changes, or diagenetic alterations affecting different stratigraphic levels. The *Acanthopyge* limestones, however, constitute a lithologically relatively uniform unit in which bioclastic limestones of varying grain sizes and colors alternate with occasional interbeds of micritic limestones, in which *Acanthopyge* is absent or rare. We tried to minimize this range of factors by using only specimens without apparent deformation. In light of all the factors discussed above, the interpretative potential of the available material remains limited; the present analysis nonetheless provides new insights, while any future investigation based on newly acquired material would likely yield primarily incremental advances.

For our study, several specimens of other species of Lower Devonian trochurinae were included as comparative material: 8 cranidia and 11 pygidia of *H.*? *pervasta*, 3 cranidia of *H.*? *aigaion* (Vaněk, 2002) and 1 cranidium of *H.*? *parva* (Barrande, 1846). These species are very rare compared to *A. haueri* and documented only by fragmentary material (some individuals are unsuitable for biometric measurements), but they are very valuable as presumed closest relatives or even ancestors of *A. haueri*.

Landmark analysis. – In order to describe the morphology of *Acanthopyge*, a set of eleven landmarks was selected on both cranidia and pygidia to summarize their general shapes (see Fig. 3B and its explanatory remarks). Landmarks are homologous points whose number and position must be strictly identical for all examined individuals

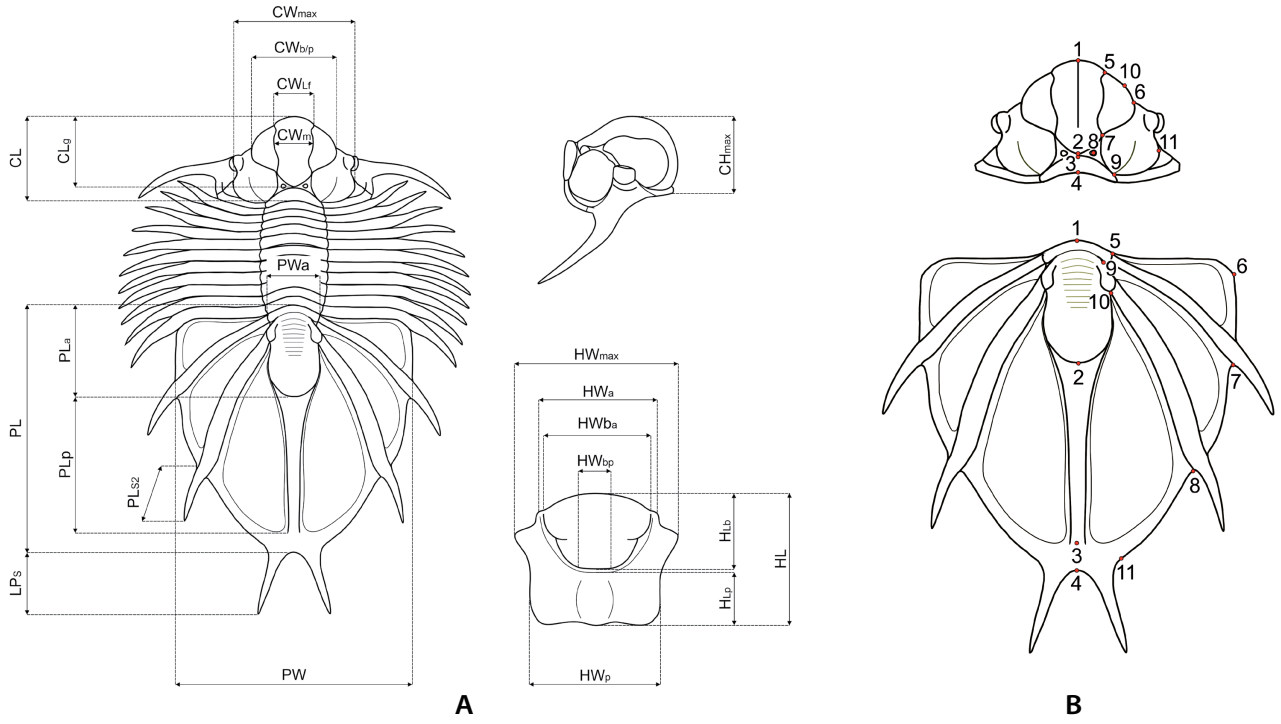


Figure 3. A – biometric parameters of an adult specimen of *Acanthopyge haueri* (Barrande, 1846). Key to abbreviations: CL – maximal sag. length of cranidium; CLg – sag. length of glabella; CWLf – width of Lf; CWm – width (tr.) of median glabellar lobe; CWb/p – maximal tr. width of bullar lobes at their contact with posterolateral cranidial lobes; CWmax – maximal tr. width of posterolateral lobes; CHmax – maximum height of cranidium; PL – sag. length of pygidium; Pla – sag. length of pygidial axis; PLp – sag. length of postaxial ridge; PW – tr. width of pygidium; PWa – tr. width of axis; PLs1,2,3 – relative length of 1st, 2nd and 3rd pygidial spine; LPS – exs. length of 3rd pygidial spine; HL – sag. length of hypostome; HLb – sag. length of hypostome body; HLp – length of posterior hypostomal margin; HWa – tr. width of anterior hypostomal margin (at anterior wings); HWmax – maximal tr. width of hypostome (at shoulders); HWp – tr. width of hypostomal posterior margin; HWba – maximal tr. width of anterior lobe of hypostome middle body; HWbp – posterior tr. width of posterior lobe of hypostome middle body. After Budil *et al*. (2016). • B – landmarks at the cranidium and pygidium of an adult specimen of *Acanthopyge haueri* (Barrande, 1846). Key to abbreviations: Cranidium: (1) – anterior margin of the glabella; (2) – posterior margin of the glabella; (3) – anterior margin of the occipital ring; (4) – posterior margin of the occipital ring; (5) – anterior projection of the longitudinal furrow into the anterior margin of cranidium in dorsal view; (6) – anterior projection of the axial furrow into the anterior margin of cranidium in dorsal view; (7) – contact of longitudinal and axial furrows; (8) – tubercle in S1; (9) – posterior contact of the occipital ring and cranidial margin; (10) – contact of the bullar lobe and the angle axis between landmarks 5, 7 and 6; (11) – contact of the facial suture and the angle axis between landmarks 6, 7 and 9. Pygidium: (1) – anterior margin of the pygidial axis; (2) – posterior margin of the pygidial axis; (3) – junction of postaxial ridge and posterior pygidial border; (4) – posterior margin of pygidium (except the spines); (5) – contact of axial furrow and anterior pygidial margin; (6) – point of maximal pygidial width (tr.); (7) – lateral pygidial margin at junction with posterior margin of the base of the first pygidial spine; (8) – lateral pygidial margin at junction with posterior margin of the base of the second pygidial spine; (9) – contact of posterolateral margin of first axial ring and base of first pleural ridge with axial furrow; (10) – contact of posterolateral margin of second axial ring and base of first pleural ridge with axial furrow; (11) – anterior junction of base of third pygidial spine with pygidial posterolateral margin.

(Bookstein 1991). In total, 17 pygidia and 19 cranidia of *A. haueri* and 6 pygidia and 1 cephalon of *H.*? *pervasta* were analyzed. The present analysis tests the validity of the species based on sufficiently preserved specimens from different stratigraphic levels and collections; it does not address interpopulation variability and should be interpreted with appropriate caution given the limited sample size. For comparison, several individuals of other species of trochurinae were included: one pygidium of *H. branikensis*, one pygidium of *H. docekali*, one pygidium and one cephalon of *Trochurus speciosus* Beyrich, 1845, four cranidia of *H.*? *parva* and two cranidia of *H.*? *aigaion*. The size of the comparative sample is limited by the need to ensure sufficient preservation of analysed specimens and the rarity of crucial species (*H. docekali*, *H.*? *parva* and *H.*? *aigaion*). In total, we were able to collect only a few specimens in these taxa; the majority of them are poorly preserved.

The x- and y- coordinates of landmarks were digitized using the optical image analyzer (tpsDig2). Landmarks were then standardized through Procrustes fitting (Dryden & Mardia 1998) to account for variation due to size, position, and rotation. Principal component analyses (PCA) were performed using PAST, and morphospaces were constructed to visualize shape variation. PCA subtracts mean shape from the dataset and identifies

directions of maximal shape variation (principal components), which can then be plotted to display multidimensional morphospace in two-dimensions.

Additionally, in order to compare size and shape variation among individuals, additional morphospaces were constructed, defined by both size, estimated by the centroid size of cranidia and pygidia, and shape, estimated by the first or second principal components, PC1 and PC2. These plots visualize relationships between size and shape and allow testing for correlations between size and principal component scores.

Note. – The angle at which the material is photographed significantly affects the measurements and the results of landmark analyses, especially in the case of strongly arched cranidia. Therefore, the dorsal orientation of cranidia during photography was verified with special care. Since all precautions were taken to minimize measurement errors, with certain reservations, we are of the opinion that 2D analysis yields relevant results under such conditions. Furthermore, a 2D *versus* a much more methodologically demanding 3D comparison on Phacopidae with similarly large depth of field showed that 2D analyses remain relevant, see Crônier *et al.* (2024).

Systematic palaeontology

Order Lichida Moore, 1959
Family Lichidae Hawle & Corda, 1847
Subfamily Trochurinae Phleger, 1936

Genus *Acanthopyge* Hawle & Corda, 1847
[= *Euarges* Gürich, 1901 and possibly *Niponnarges* Kaneko, 1984; see also Thomas & Holloway 1988]

Type species. – Subsequent designation by Reed (1902, p. 60 and Thomas & Holloway 1988, p. 221): *Acanthopyge Leuchtenbergii* Hawle & Corda, 1847 = *Lichas Haueri* Barrande, 1846, from the Acanthopyge Limestone (Middle Devonian, Eifelian), Czech Republic.

Diagnosis. – Trochurinae with cranidium having maximum width across the posterior part of fixigena. Pygidium with three pairs of long, marginal spines that are long, slender and rounded in cross section; first two pairs diverging strongly and protruding from rounded pleural ridges. Two pairs of narrow pleural furrows, meeting lateral margin in front of marginal spines; pleural and interpleural furrows almost straight, adjacent to the pleural ridges. Width to length ratio of pygidium (excluding marginal spines) varies from 0.9 to 1.3 in holaspid specimens (in juveniles, this ratio ranges from 1.3–1.5); axis comprising one third to two fifths of the anterior width of pygidium and one third to one half of pygidial sagittal (sag.) length. Postaxial ridge of pygidium prominent, rounded in cross section, bounded (exsag.) by narrow furrows, longer than or equal to 0.4 of sag. axial length. Posterolateral border of pygidium slightly vaulted (degree of prominence variable), often separated by a shallow furrow from the remainder of the pygidium.

Remarks. – *Lichas decheni* Holzapfel, 1895 and *A*.? sp. ex gr. *A. pervasta* (*sensu* Basse & Müller 2004, pp. 98, 99; = *A*.? *decheni* fide Basse & Müller 2023, p. 97); and with some reserve *A. pervasta* (Přibyl, Vaněk & Hörbinger, 1986) (upper Emsian, Czech Republic), were recently affiliated to the new genus *Rheicarges* by Basse & Müller (2023). Their affiliation with *Acanthopyge* is in any case improbable. These species were formerly assigned to this genus, and we therefore consider it appropriate to explicitly note this here.

We adopt a more restricted concept of *Acanthopyge*, following the diagnosis of *Acanthopyge* (*Acanthopyge*) by Thomas & Holloway (1988). Transitional forms traditionally classified within *Acanthopyge* should instead be interpreted as representatives of *Huginarges* s.l., as defined by van Viersen (2021), see the discussion of *Huginarges* below. Thomas & Holloway (1988), however, proposed a wider concept of *Acanthopyge*, subdividing it into subgenera *A*. (*Acanthopyge*) Hawle & Corda, 1847, *A*. (*Lobopyge*) Přibyl & Erben, 1952 and *A*. (*Perunaspis*) Přibyl, 1949, and *A*. (*Jasperia*) Thomas & Holloway, 1988. We prefer to consider these taxa as separate genera, in accordance with Chlupáč (1983b), Přibyl *et al*. (1986), Pek & Vaněk (1989), Vaněk & Valíček (2002), and Basse & Müller (2004). However, they appear closely related, sharing similar glabellar morphology but differing in pygidial features (see also our landmark analysis results).

Acanthopyge seems to be well defined based primarily on its distinctive pygidial morphology: mostly posteriorly elongated axis occupying less than $^3/_5$ of the sag. length of the pygidium, with sharply projecting pleural ridges running into well-defined spines of circular to slightly elliptical cross-section. We suggest, but cannot confirm, that the genus *Nipponarges* Kaneko, 1984 may be a junior synonym of *Acanthopyge* (see also Thomas & Holloway 1988). Its type and only species, *Nipponarges mediosulcatus* Kaneko, 1984, is poorly documented and based on strongly deformed and flattened material, showing a very long (sag.) anterior cranidial border and different proportions of glabellar lobes.

The poorly documented species *Acanthopyge uralensis* Maksimova, 1979 (originally described as *Acanthopyge haueri uralensis*, see Maksimova 1979, p. 32, pl. 2, figs 2, 3) shares the same glabellar morphology as the type species of *Acanthopyge*, but differs in having a substantially wider pygidium. Its estimated width/length

ratio spans from 1.4 (based on measured photographs) to 1.75 (based on measurements discussed in the text), with a very short pygidial axis and postaxial ridge. These parameters were possibly the reason why Thomas & Holloway (1988) classified this species in the subgenus *Acanthopyge* (*Lobopyge*). This small paratype pygidium, however, is an early holaspid specimen (the length of its pygidium is only 4 mm). It cannot be excluded that these character states (high width/length ratio) result primarily from its relatively young ontogenetic stage. A similarly high ratio has been documented only very rarely in *A. haueri*, in the smallest measured pygidium from Hostim near Srbsko (PL = 2.3 mm; see Fig. 1) which has an estimated width/length ratio about 1.39. New topotypes of *A. uralensis* are needed to clarify its taxonomic status and possible merger with the nominal species.

It is also difficult to classify *Lichas granulosus* Roemer, 1852 as Roemer's original types have been lost (see Roemer 1852, p. 85, pl. 13, fig. 3; and 1855, p. 136(24), pl. 20(5), figs 8, 9, from the Givetian *Stringocephalus* Limestone of Harz, Germany). Basse & Müller (2004, pp. 99, 100, pl. 37, fig. 476) designated a pygidium that may be regarded as a neotype, corresponding to one of the specimens figured by Roemer [1855, pl. 20(5), fig. 8; not fig. 9]. However, the figured pygidium (Basse & Müller 2004, fig. 476) shows one extra pair of pygidial marginal spines, placed between the second pair and the posterior marginal spines, slightly closer to the latter. All other features are shared with *A. haueri*, including a moderately vaulted pygidial border, which can occur in *A. haueri*, in young holaspid specimens (Thomas & Holloway 1988, p. 226).

Roemer's original figure (1855, fig. 8) of *Lichas granulosus* depicts a pygidium that is reminiscent of *A. haueri*, with three pairs of marginal spines, and similar pygidial morphology. The only differences between *A.*? *granulosa* and *A. haueri* (based on Roemer's figures of 1852 and 1855) consist of a more rounded frontal part of the median lobe, smaller bullar and posterolateral lobes, possibly shallower pleural furrows, and more posterior inclination of the pygidial marginal spines in *A.*? *granulosa* (see also Vaněk 1959, p. 125 and Basse & Müller 2004, pp. 99, 100). It is questionable whether *Lichas granulosus* should be considered a *nomen dubium*, as type selection was not explicit. The specimen SMF 12942 may represent a different species rather than a teratological (or malformed) individual.

Vaněk & Valíček (2002) included *Acanthopyge aigaion* Vaněk, 2002, *Lobopyge docekali docekali* Vaněk, 1959, and *Acanthopyge pervasta* (Přibyl, Vaněk & Hörbinger, 1986) into *Acanthopyge*. Among these, *H.*? *pervasta* and poorly documented *H.*? *aigaion* seems to be most similar to *Acanthopyge* among Lower–Middle Devonian trochurines of the Barrandian area. However, we prefer to classify them within *Huginarges* sensu van Viersen (2021) = *Lobopyge* Přibyl & Erben, 1952 (see discussion below). They show an intermediate pygidial morphology with a relatively shorter postaxial ridge compared to *Acanthopyge*. Their pleural furrows meet the lateral margin in front of the marginal spines, and a vaulted posterolateral margin is present in most studied specimens, but the first discussed feature is imperfectly developed, often leaving a small space between the furrow and the ridge. In *A. pervasta*, the pygidial spines are longer and more slender than in most *Huginarges* species. Similar intermediate morphology occurs in other Lower-Middle Devonian trochurines; see discussion of *H.*? *pervasta* below and Thomas & Holloway 1988).

Differences between *Acanthopyge* and *Huginarges* remain somewhat ambiguous, with some species that are not readily assignable to either genus. Differences include:

1) Width to length ratio of the *Acanthopyge* pygidium varies from 0.9 to 1.3 (about 1.5 in *Huginarges*; see also Thomas & Holloway 1988, p. 225).

2) Postaxial ridge in *Acanthopyge* longer than or equal to 0.4 of sag. axial pygidial length (about 0.3 in *Huginarges*; see Thomas & Holloway 1988, p. 225).

3) Three pairs of long, marginal spines that are long, slender and rounded in cross section in *Acanthopyge* (they are generally shorter, flat to elliptical in cross section in *Huginarges*; see Thomas & Holloway 1988, p. 225).

4) First two pairs of pygidial marginal spines diverge strongly and protrude from equally rounded pleural ridges in *Acanthopyge* (the relation of pleural spines to the pleural ridges in *Huginarges* is much less perceptible).

5) Two pairs of narrow pleural furrows meet the lateral margin of the pygidium of *Acanthopyge* immediately in front of marginal spines (Thomas & Holloway 1988, p. 225) and run along the front of its pleural ridges, see Basse & Müller 2004, p. 37 (not meeting the pygidial lateral margin in *Huginarges*; see Thomas & Holloway, 1988, p. 225 and more or less distant from the pleural ridges; see Basse & Müller 2004, p. 37).

6) pleural and interpleural furrows are almost straight in *Acanthopyge* (they are slightly rounded in *Huginarges*). Together with these pygidial features, cranidia of *Acanthopyge* are generally much vaulted than of *Huginarges*, with a frontally protruding median lobe. Its bullar lobes are transversely much wider, and much vaulted. However, all cranidial features vary strongly in both genera.

Often, early holaspid specimens of *A. haueri* share numerous features with the putatively ancestral *Huginarges*. Even genus-level characters, such as axis/postaxial ridge form and pygidial outline, strongly vary within this supposedly well-defined species. Nevertheless, the typical *Acanthopyge* and *Huginarges* morphologies are sufficiently distinctive; see also Přibyl & Erben (1952) who

distinguished a *Lobopyge*-type and *Acanthopyge*-type morphology among Lower–Middle Devonian trochurines.

Species included. – *Acanthopyge uralensis* Maksimova, 1979, Eifelian, western part of the Polar Urals, Russian Federation (possibly conspecific with the type species, see discussion below); *Acanthopyge* sp. nov. 1, Eifelian, Morocco (specimens with sagittally shorter pygidium and very long, incurved pygidial spines); *A.* sp. nov. 2, Eifelian–Givetian, Morocco [specimens with extremely long pygidium (sag.) and rather short pygidial spines].

Species of uncertain generic assignment: *Acanthopyge*? *granulosa* (Roemer, 1852), Eifelian–Middle Givetian, Germany; *A.*? *mediosulcatus* (Kaneko, 1984), Eifelian, Japan.

Occurrence. – Uppermost Emsian–middle Givetian; Czech Republic, Germany, Russian Federation, Morocco, and ?Japan.

***Acanthopyge haueri* (Barrande, 1846)**
Figures 4; 5A, B, H–P; 6; 7

1846	*Lichas Haueri* Barr.; Barrande, p. 73.
1847	*Acanthopyge Leuchtenbergii* nobis; Hawle & Corda, p. 143, pl. 1, figs 5–7.
partim 1852	*Lichas Haueri* Barrande. – Barrande, p. 604, pl. 28, figs 39–44 (*non* pl. 28, fig. 38).
non 1890	*Lichas (Arges) Haueri* Barrande. – Novák, p. 121, pl. 2, fig. 10.
non 1881	*Lichas Haueri* Barrande. – Maurer, p. 21, pl. 1, fig. 20.
1901	*Lichas (Euarges) Haueri* Barrande. – Gürich, p. 527.
1909	*Lichas (Euarges) Haueri* Barrande. – Gürich, p. 151, pl. 47, fig. 2a, b.
1936	*Euarges haueri* (Barrande). – Phleger, p. 610.
1953	*Acanthopyge haueri* (Barrande). – Přibyl, p. 24.
1959	*Acanthopyge haueri* (Barrande). – Vaněk, pp. 120–125, pl. 5, figs 1–7, pl. 6, figs 3–6, 14–17.
1970	*Acanthopyge haueri* (Barrande). – Horný & Bastl, p. 192.
1983b	*Acanthopyge haueri* (Barrande). – Chlupáč, pl. 1, fig. 1.
1986	*Acanthopyge haueri* (Barrande). – Přibyl, Vaněk & Hörbinger, pl. 4, fig. 3.
1988	*Acanthopyge* (*Acanthopyge*) *haueri* (Barrande). – Thomas & Holloway, pl. 13, figs 274–279, 281.
1989	*Acanthopyge haueri* (Barrande). – Pek & Vaněk, p. 18.
1995	*Acanthopyge haueri* (Barrande). – Galle, Hladil & Isaacson, p. 223.
2002	*Acanthopyge haueri* (Barrande). – Vaněk & Valíček, p. 16.
2004	*Acanthopyge haueri* (Barrande). – Basse & Müller, p. 37, figs 466–468.

Types. — Lectotype cranidium, NM L 15148, selected by Šnajdr (1984, p. 169), figured by Hawle & Corda (1847, pl. 1, figs. 5) as *Acanthopyge Leuchtenbergii*, Barrande (1852, pl. 28, figs 40, 41), Šnajdr (1984, pl. 5, fig. 13) and discussed by Thomas & Holloway (1988, pp. 221, 222) from the Acanthopyge Limestone (Middle Devonian, Eifelian), Koněprusy near Beroun, Czech Republic, refigured herein in Fig. 4A.

Material. – 162 cranidia, 137 pygidia, and 50 hypostomes.

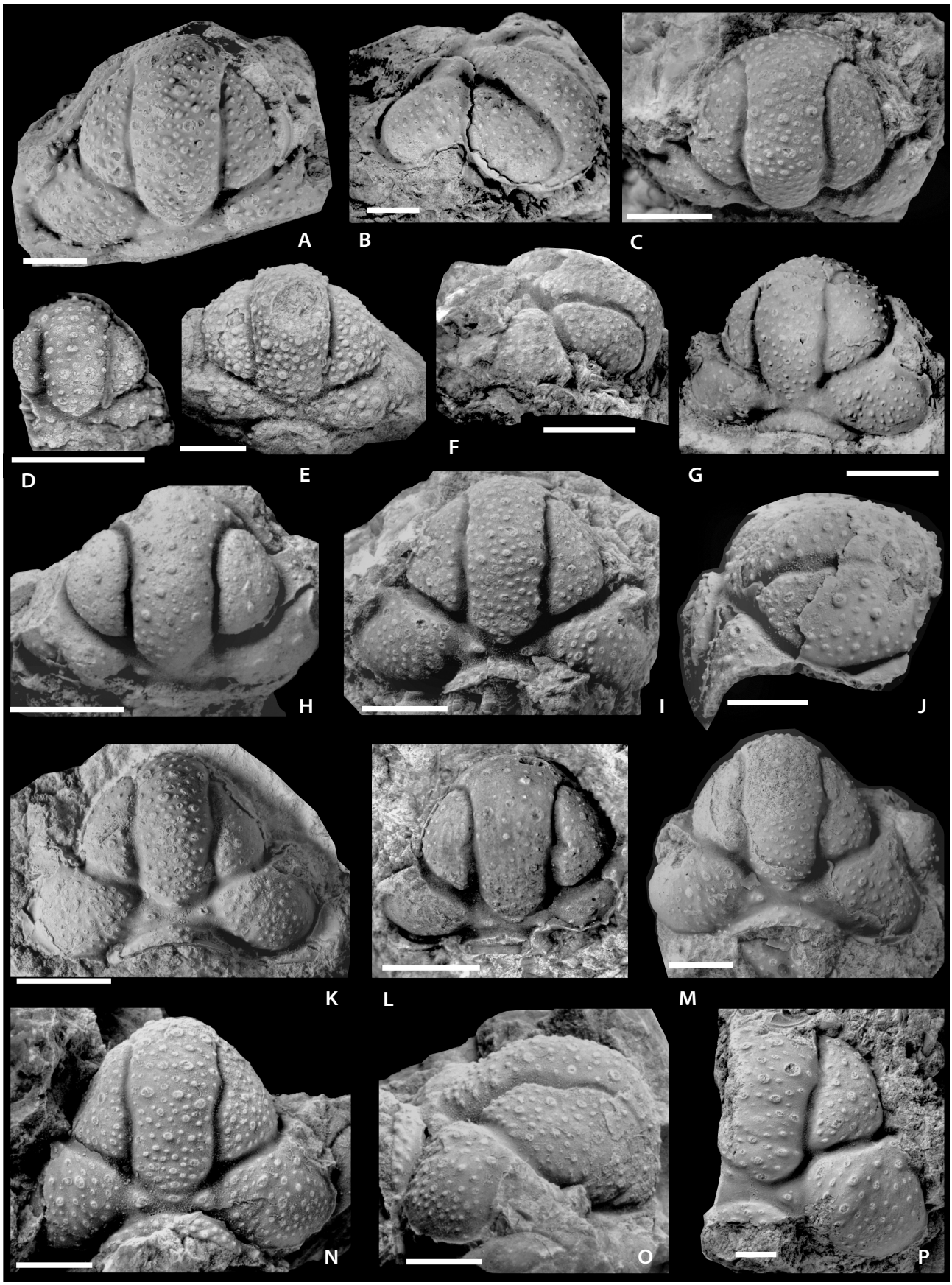
Diagnosis. – *Acanthopyge* with width to length ratio of pygidium (excluding marginal spines) varying from 1.03 to 1.36. Axis comprises one third to two fifths anterior width of pygidium and approximately half of sagittal length.

Description. — Exoskeleton of moderate dimensions (CL up to 23 mm, PL up to 40 mm). Strongly vaulted cranidium of sub-trigonal outline, its width/length ratio attains 1 (in smallest specimens) to 1.73. Longitudinal furrows almost parallel, exsagitally directed, narrow but deeply impressed. They form an inconspicuous abaxial projection in their middle part, where an adaxial impression in bullar lobes adjoins (prominence of this projection strongly varies). Occipital furrow and especially first glabellar furrow (S1) wide (sag.) and shallow, S1 with paired supra-occipital nodes. The median glabellar lobe vaulted, mildly expanding frontally. Anterior border narrow (sag.) but present, although in the dorsal view it is overlapped by the median lobe. Bullar lobes are prominent, kidney-shaped, vaulted. Posterolateral cranidial lobes are strongly vaulted, sub-trigonal in outline, dorsolaterally protruding into the long (always broken off because of their fragility) eye socles that, however, possess a robust base that is, in most cases, preserved. Occipital lobe is very narrow (sag.), wide (tr.), and moderately vaulted. Free cheeks are poorly known. Their adaxial base is vaulted and wide, their posterior margin is, however, concavely cut out. As a continuation of the anterior margin, genal spines protrude laterally, making a posteriorly bent arch (see Fig. 5A, B). The posterior border of free cheeks is (based on this poorly preserved young specimen) probably flat, inconspicuous. The surface of cephalon (excluding the abaxial part of free cheeks) is covered by sparse but prominent granules of very variable density and diameter, in some cases, some of the granules are spinose, especially on the median lobe and posterolateral cranidial lobes. The distribution pattern of granules is haphazard; only on elevated parts of the median lobe, bullar lobes and posterolateral lobes, larger granules randomly occur between smaller granules. The ventral structures of cephalon, except the hypostome, are poorly known. Cephalic doublure is very narrow and flat. Rostrum is unknown. Hypostome is conterminant,

of wide trapezoidal outline, with three posterior lobes (shorter median and slightly longer lateral lobes). The anterior outline is widely arched. The lateral border is almost straight, modestly vaulted and with small but prominent shoulders, inclined together with the border laterally. The posterior margin of the hypostome is sinusoidal. Middle body of the hypostome is moderately vaulted, subdivided by differently prominent transverse furrow into more vaulted anterior and posterior parts. The posterior border is wide and strongly vaulted in the axial part. The surface of the middle body is covered by sparse large granules of strongly variable diameter and density (for some extremes, see Fig. 7). Thorax is incompletely known, and no articulated remains have been gathered so far. The axis is moderately vaulted, narrow (sag.), wide (tr.), see Vaněk (1959, p. 123; this author observed extremely narrow pleural furrows subdividing the pleurae into two equal, very narrow parts). Vaněk's observation could not be confirmed because of the scarce material at our disposal. The surface of thoracic segments is smooth. Pygidium is relatively large (compared to cephalon), of elongated semi-elliptical to semioval outline, with straight anterior margin, its width/length ratio attains 1.03 to 1.36. Articulating half-ring is narrow (sag.) but prominent, separated from the axis by a very deep furrow. Pygidial axis is narrow (tr.; about 0.3 of the pygidial width), with very variable width and vaulting (especially in large specimens, pygidial axis is only moderately vaulted and lateral pygidial lobes notably overreach it). Only one complete, well-defined axial ring is present, with slightly distended and posterolaterally redirected lateral lobes. In some specimens (this feature is very variable), further indistinct, up to 8–10 fine and narrow rings defined by sculpture are distinguishable (this feature is often better preserved in small holaspid pygidia). The postaxial ridge is narrow (tr.), up to twice as long as the axis but this ratio strongly varies in studied material. Generally, in smaller specimens, the postaxial ridge is shorter but this is not ubiquitous. At the posteriormost end of the postaxial ridge, inconspicuous arcuate widening of this ridge appears in some specimens. Pleural bands subtrigonal, mildly to prominently vaulted (especially the posterior ones in large specimens). Pleural and interpleural furrows deep, almost straight, reaching the lateral pygidial margin along the bases of the pygidial marginal spines. Two pairs of narrow ridges are slightly posteriorly bent to lateral margin, and they protrude into very long, needle-like marginal spines that are circular in cross-section. These spines are only very slightly bent posteriorly (forming an almost inconspicuous half-arch). Relative length of these spines, however, strongly varies between different individuals. Generally, in early holaspid specimens, spines are longer but exceptions are common. In addition, in most specimens, these spines are more or less broken off. The posterior part of the pygidium protrudes into the proximal third part of marginal spines with flatter bases that are elliptical in cross-section. The spines, however, soon change distally into narrow, needle-like spines that are circular in cross-section. Pygidial border is almost absent in some specimens but is moderately vaulted and relatively prominent in others (mostly younger/smaller ones, as already stated by Thomas & Holloway 1988, p. 226), with shallow border furrow in these cases. The surface of pygidium is covered by sparse granules of different diameters, which haphazardly cover the entire surface of pygidium with the exception of furrows. Even some marginal spines and postaxial ridge bear fine, often spinose granules.

Measurements. – Sagittal length of the lectotype cranidium (CL) is 17.37 mm, maximal tr. width of cranidium (Cwmax) attains 24.8 mm. Average sag. length of adult cranidia attains about 14 mm (maximal values 21.37 mm), average sag. length of adult pygidia attains about 20 mm (maximal values 40.29 mm); note that the length measurement done by Vaněk (1959, p. 124) on its invalid lectotype pygidium SBNM Br-576 = NM L 15150 is erroneous – almost twice its actual value, meanwhile its width measurement is correct. Some of the specimens figured by Vaněk (1959) are re-figured here. On the Vaněk's figures, measurements are often sketched and the photographs were made with the use of obsolete photographic equipment and their quality is thus variable.

Figure 4. A–C, E–P – *Acanthopyge haueri* (Barrande, 1846). Choteč Formation, Acanthopyge Limestone, Eifelian, Koněprusy near Beroun. Scale bar represents 5 mm. A – lectotype cranidium, selected by Šnajdr (1984, p. 169), figured by Hawle & Corda (1847, pl. 1, fig. 5) as *Acanthopyge Leuchtenbergii*, Barrande (1852, pl. 28, figs 40, 41), Šnajdr (1984, pl. 5, fig. 13) and discussed by Thomas & Holloway (1988, pp. 221, 222) NM L 15148, dorsal view. B – cranidium, internal mold with partially preserved exoskeleton, NM L 17202, lateral view. C, F, I – cranidium NM L 46872; C – frontodorsal view; F – lateral view; I – dorsal view. E – cranidium NM L 46877, dorsal view. G – cranidium NM L 46902, posterodorsal, right lateral view. H – cranidium NM L 46873, frontodorsal view. J – incomplete cranidium NM L 46870, right lateral view. K – cranidium NM L 46862, dorsal view. L – cranidium NM L 15147, dorsal view. M – cranidium NM L 46863, dorsal view. N–O – cranidium NM L 46884; N – dorsal view; O – right lateral view. P – incomplete cranidium NM L 46883, dorsal view. • D – *Acanthopyge*? sp. Unknown formation, allegedly from the Zlíchov Limestone (Emsian), most probably rather Acanthopyge Limestone. Cranidium of smallest early holaspid specimen of Lower–Middle Devonian trochurine known (CL = 3.41 mm), NM L 46899, dorsal view. Specimen was marked as "*Acanthopyge* cf. *aigaion* by Vaněk MS", the specimen come from the Geological Institute of the Bohemian University = Charles University (leg. O.P. Novák 1882).


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Remarks. – As noted in discussion of the genus, probably the most similar species to the *A. haueri* is the possibly conspecific *A. haueri uralensis* Maximova, 1979 from the Karpinsky Horizon of the Yurtishchian Regional Stage, western part of the Polar Urals, poorly documented *A.*? *granulosa* Roemer, 1852 from the Stringocephalus Limestone of Harz, and one of the as yet formally undescribed Moroccan forms from the El Otfal Formation.

Acanthopyge haueri is documented by several hundreds of available specimens (only part of them, however, can be used for biometric study). It occurs almost exclusively in the Acanthopyge Limestone (Middle Devonian, Eifelian), in the Koněprusy area. Vaněk (1959, p. 125), discussed an occurrence near the Hostim, in the Choteč Limestone of the same age (this unique finding was confirmed by Chlupáč 2003, p. 304). This material was rediscovered in 2025 in the collection of Ivo Chlupáč housed in the Czech Geological Survey. A well-preserved juvenile pygidium (smallest known, PL = 2.3 mm) preserved with the fragment of larger cephalon is figured here as Fig. 7C, meanwhile three other fragments of cephala and pygidia provide only limited information.

Notes on ontogeny: The collections of the National Museum in Prague offered several early holaspid cranidia of Lower–Middle Devonian trochurine trilobites labeled as *A. haueri* that had not yet been previously documented. These are preserved in pale grey to whitish bioclastic limestone. Unfortunately, these specimens were collected in the 19th century and thus lack a reliable locality or stratigraphic affiliation. The locality label is Koněprusy, which spans from the late Lochkovian to the Givetian in age. In our opinion, the vast majority of these specimens are juveniles of *H.*? *parva*, a species known from the reef and peri-reef facies of the Koněprusy Limestone. These specimens were distinguished from *A. haueri* using landmark analysis (see yellow dots in Fig. 15; *cf.* Fig. 5C–G). Only one of these small specimens probably belongs to *A. haueri* due to its difference in having much smoother vaulting of the cranidium: the specimen (NM L 46864, Fig. 5A, B) has attached free cheeks with eyes, but is heavily damaged and composed of two poorly glued parts; it cannot be used for landmark or biometric analysis.

Occurrence. – *Acanthopyge haueri* occurs almost exclusively in the Acanthopyge Limestone (Middle Devonian, Eifelian), in the Koněprusy area. The outcrops are located between the peak of Zlatý kůň (475 m above sea level) and the southern part of the Červený Lom quarry below the southern slope of Kobyla hill (472 m above sea level). The most significant localities of Acanthopyge Limestone with the documented occurrence of *A. haueri* are: (1) Old collector's pits and remains of "peasant" limestone mining located at the top of Zlatý kůň, which were briefly described and illustrated by Chlupáč (1983b, pl. 1, fig. 1); (2) Herget's quarry – occurrences of accumulations of disarticulated exoskeletons in the infillings of neptunic dykes penetrating the underlying Suchomasty Limestone. From this locality, lumachelle of well-preserved pygidia and cranidia was illustrated by Chlupáč (1983a, pl. 2, fig. 3); (3) Preisler's quarries near the Koněprusy–Bykoš road; (4) VČS quarry – east (Voskop) – outcrops just below the Koněprusy–Bykoš road. Červený Lom quarry – in a few thick (approx. 20 cm) layers of light gray, bioclastic limestones stratigraphically situated approximately 5 m above the lithologically sharp boundary between Suchomasty and Acanthopyge limestones (Emsian–Eifelian). Only four findings – an almost complete early holaspid pygidium plus fragments of cephala and pygidia (mentioned by Vaněk 1959 and Chlupáč 2003) comes from the Choteč Limestone of the same age in Hostim near Srbsko (see Fig. 1).

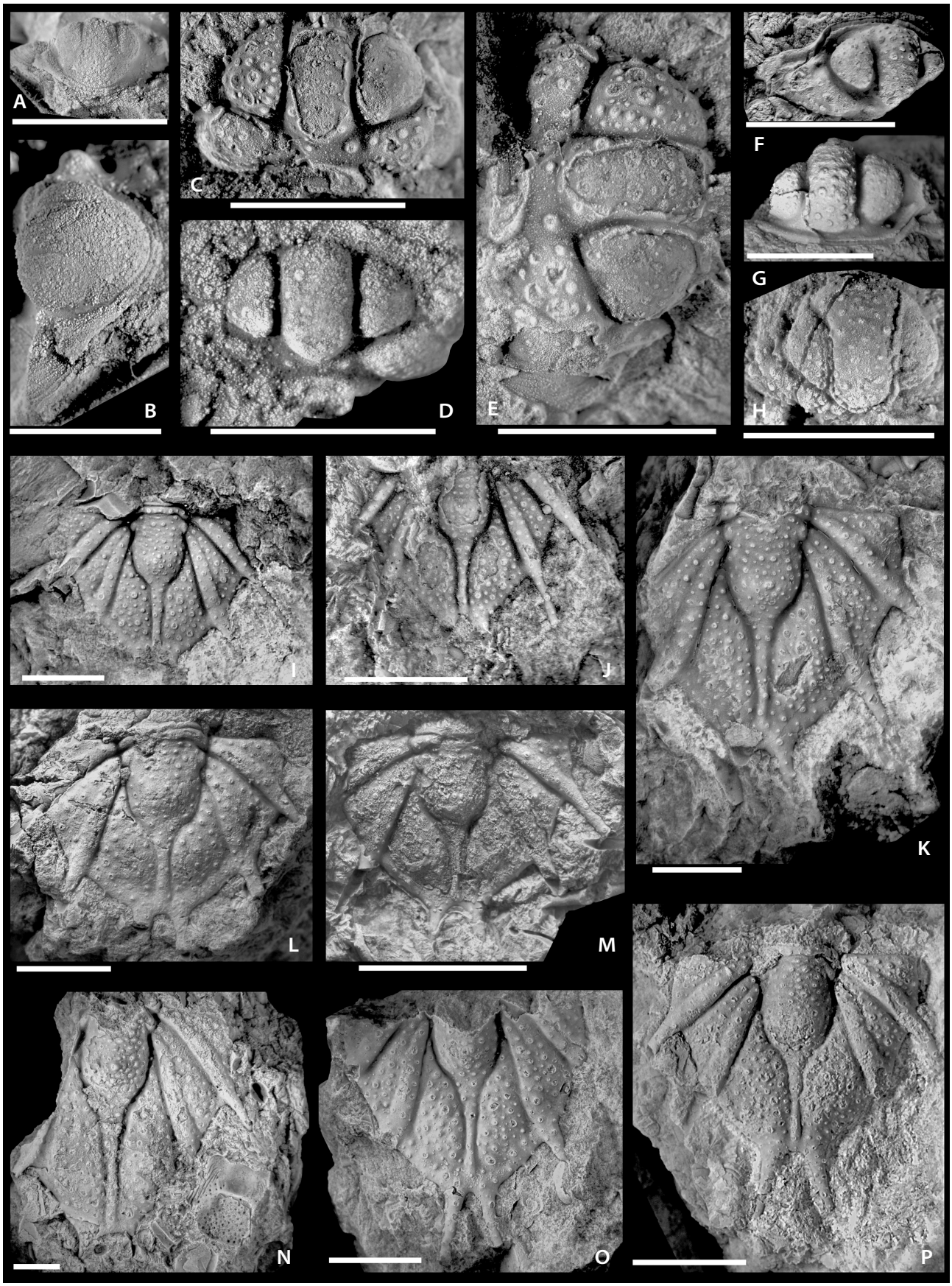
Genus *Huginarges* Basse *in* Basse & Müller, 2004

Type species. – *Huginarges mathesiorum* Basse *in* Basse & Müller, 2004 from the upper Emsian in the Rhenish Mountains.

Diagnosis. – Basse *in* Basse & Müller (2004), see also discussion of van Viersen (2021, pp. 178, 179).

Remarks. – In general, we follow approach of van Viersen (2021) and van Viersen & Müller (2024, pp. 93, 94) in use of the name *Huginarges* Basse in Basse & Müller, 2004 as a substitute name for the invalid trilobite genus

Figure 5. A, B, H–P – *Acanthopyge haueri* (Barrande, 1846). Choteč Formation, Acanthopyge Limestone, Eifelian, Koněprusy near Beroun). Scale bar represents 5 mm with exception of B, D which represents 3 mm. A, B – cranidium of early holaspid specimen with attached free cheeks, NM L 46864; A – frontal view; B – right dorsolateral view. H – cranidium of early holaspid specimen, NM L 46866, dorsal view. I – pygidium NM L 46859, dorsal view. J – pygidium figured by Vaněk (1959) in pl. 5, fig. 3, NM L 17203, dorsal view. K – pygidium NM L 46860, dorsal view. L – pygidium NM L 46861, dorsal view. M – pygidium NM L 46862, dorsal view. N – incomplete pygidium of large specimen with negative counterpart of the hypostome NM L 17196, figured by Vaněk (1959) in pl. 5, fig. 6, dorsal view. O – pygidium NM L 46863, right lateral view. P – early holaspid pygidium NM L 46861, dorsal view. • C–G – *Huginarges*? *parva* Beyrich, 1845. Devonian of Koněprusy area, exact stratigraphical affiliation uncertain (probably Koněprusy Limestone). C, E – cranidium of early holaspid specimen with exposed doublure of right free cheek NM L 46867; C – dorsal view; E – dorsolateral view. D – cranidium of the smallest early holaspid specimen known (estimated CW = 4 mm), NM L 46865, dorsal view. F – cranidium of early holaspid specimen with attached left free cheek, NM L 46869, left dorsolateral view. G – cranidium of early holaspid specimen with attached left free cheek, NM L 46869, frontal view.


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Lobopyge Přibyl & Erben, 1952 (contrary to the opinion of Özdikmen, 2009). Recently, Basse & Müller (2023) presented a much narrower concept of *Huginarges* and proposed as a third name substituting for *Lobopyge* – new name *Branikarges* Basse & Müller 2023. We are aware that the morphology of the pygidium in the type species of the genus *Huginarges – H. mathesiorum* is distinctive ("*Trochurus*-like") – see Basse *in* Basse & Müller (2023) – especially with its markedly vaulted pygidial border and depressions posterolaterally bordering the postaxial ridge, and we understand the approach of Basse & Müller (2023). However, arguments of van Viersen (2021) that *Huginarges* is the appropriate name are largely justified. Even in the overview of representatives of the originally conceived genus *Huginarges* (Basse & Muller 2004, pl. 36, figs 450–453), considerable variability in diagnostic characters on the pygidium is evident. These distinctive features occur in various expressions in many taxa traditionally classified in the genus "*Lobopyge*" occurring since the Upper Ordovician. In our opinion, the question of relationships within Early Devonian trochurines of the former genus "*Lobopyge*" is too poorly understood to allow taxonomic conclusions at the level of genera. Since this question will probably require a thorough phylogenetic analysis based on careful descriptive study to be answered (which is beyond the scope of this differently focused study), we leave it open.

The question of the origin of *Acanthopyge* is closely related to the topic of our study. We assume that it is closely related to *H.*? *pervasta*-like forms. Some such species were accommodated within the new genus *Rheicarges* Basse & Müller, 2023 by its authors (Basse & Müller 2023, p. 97). Although the arguments for establishing this new genus are compelling overall, a similar key concern remains, which could diminish the clarity of the classification. For this reason, we are provisionally following broader concept of van Viersen (2021) and of van Viersen & Müller (2024). If the genus *Rheicarges* were shown to be valid, it would be reasonable to redefine it to cover just the transitional forms between original "*Lobopyge*" and *Acanthopyge*. However, this step goes beyond the aims of this contribution, which focuses on the study of the variability of the type species of *Acanthopyge – A. haueri* and uses the species *H.*? *pervasta* mainly as a comparative "outgroup", allowing for comparison of intraspecific and interspecific variability of *A. haueri*. For the purposes of this contribution, we provisionally retain *H.*? *pervasta* as a doubtful member of *Huginarges*, although it almost certainly belongs to the *Huginarges–Rheicarges* group characterised by a mosaic of *Acanthopyge*-like features (*e.g.* slightly longer postaxial part of the pygidium, and especially narrow pleural ridges and long, narrow and slender pygidial spines). A separation of such taxa into distinct taxonomic unit is also questionable as these "intermediate" taxa occur from the late Emsian up to the Givetian in Northern Gondwana, Perunica, and the basins lying close to Laurentia (Rheic Devonian).

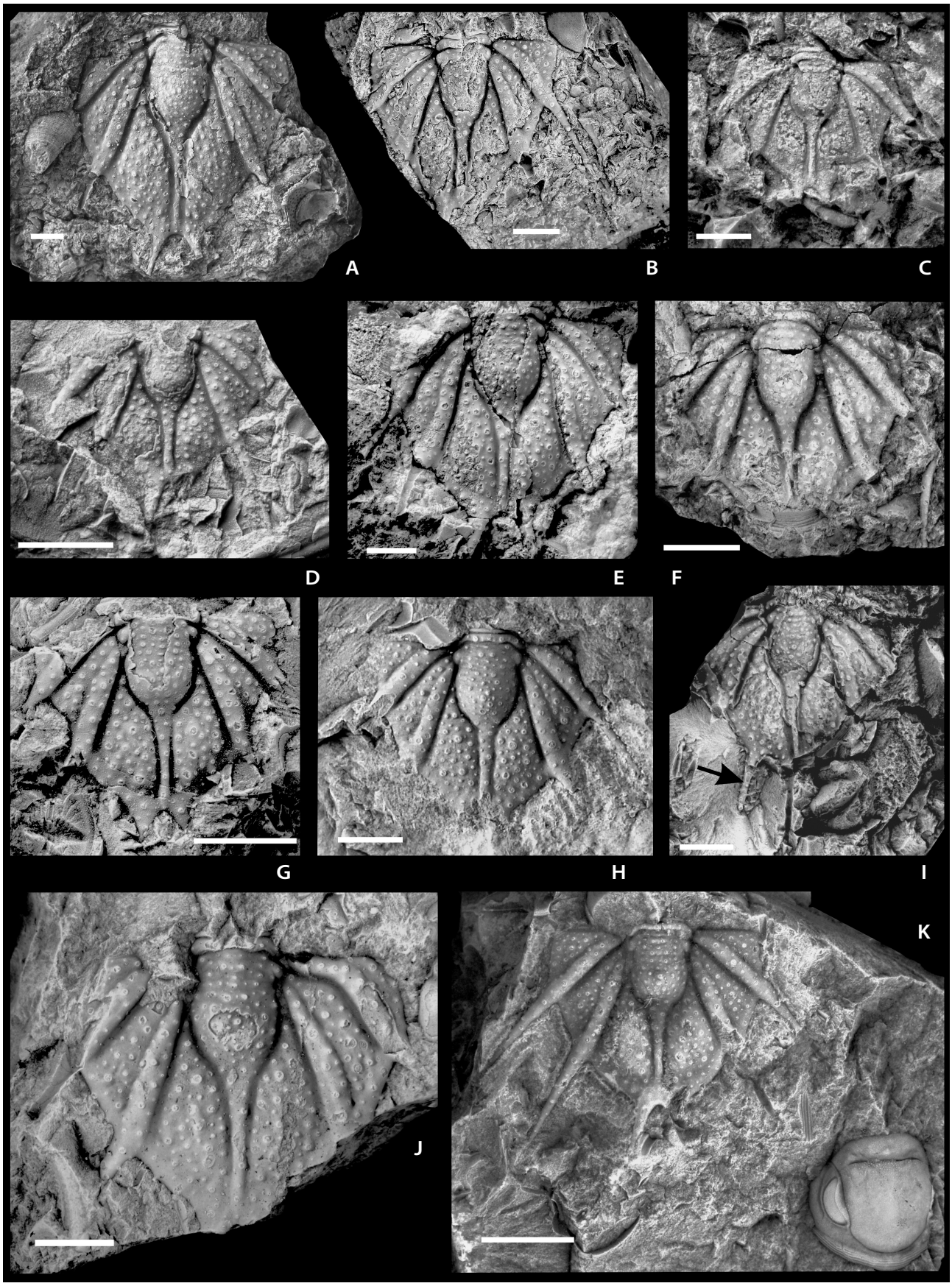
Ebach & Ahyong (2001) previously examined the phylogeny of *Huginarges* (= *Lobopyge*) in some detail, providing a diagnosis for the genus and coding for phylogenetic analysis for 33 of 38 named species that could be assigned to this genus (none from Morocco or other parts of North Africa). They included in their cladistic analysis, however, only 23 of the named species, as the others could only be coded for less than 45% of their characters. They provided 15 characters for their analysis. We follow, however, only part of their results, see also comments of van Viersen (2021).

Species included. – See the list of species for *Lobopyge* of Ebach & Ahyong (2001), respectively for *Acanthopyge* (*Belenopyge*) of Corbacho & Kier (2013); see also discussions in Basse *in* Basse & Müller (2004) and van Viersen (2021).

***Huginarges*? *pervasta* (Přibyl, Vaněk & Hörbinger, 1986)**
Figure 8

1986 *Acanthopyge pervasta* sp. n.; Přibyl, Vaněk & Hörbinger, pl. 4, fig. 2.
1989 *Acanthopyge pervasta* Přibyl, Vaněk & Hörbinger. – Pek & Vaněk, p. 18.
2002 *Acanthopyge pervasta* Přibyl, Vaněk & Hörbinger. – Vaněk & Valíček, p. 16.
2013 *Acanthopyge* (*Belenopyge*) *pervasta* Přibyl, Vaněk & Hörbinger. – Corbacho & Kier, p. 6.
2023 *Acanthopyge pervasta* Přibyl *et al*. – Basse & Müller, p. 97.

Figure 6. A–K – *Acanthopyge haueri* (Barrande, 1846). Choteč Formation, Acanthopyge Limestone, Eifelian, Koněprusy near Beroun (Koněprusy – Mnienian = Měňany in Fig. 6I). The scale bar represents 5 mm. A – pygidium of large specimen, invalid lectotype of Vaněk (1959, pl. 5, fig. 5), NM L 15150, dorsal view. B – pygidium with prominently sub-triangular outline NM L 46875, unpublished and invalid lectotype of *Acanthopyge Leuchtenbergii* Hawle & Corda, 1847, selected from original chirotypes by Přibyl & Vaněk (unpublished paper = Vaněk 1959), dorsal view. C – pygidium of early holaspid specimen, NM L 46887, dorsal view. D – pygidium NM L 46880, dorsal view. E – pygidium NM L 46879, dorsal view. F – pygidium with partially exposed doublure, NM L 46858, dorsal view. G – pygidium NM L 46886, dorsal view. H – pygidium NM L 46864, dorsal view. I – pygidium of the malformed specimen. Arrow indicates inserted marginal spine without relation to the pleura. Determined by A. Frič as *Lichas* sp. n., NM L 46874, dorsal view. J – pygidium NM L 17197 figured by Vaněk (1959) in pl. 5, fig. 7, dorsal view. K – pygidium of early holaspid specimen NM L 46860, dorsal view.


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Type. – Holotype, incomplete pygidium, NM L 21554 figured by Přibyl *et al.* (1986, pl. 4, fig. 2), re-figured herein as Fig. 8A, B, Suchomasty Limestone (Lower Devonian, upper Emsian, Dalejan Regional Stage), Koněprusy near Beroun, outcrop near house on Zlatý kůň hill *fide* Přibyl, Vaněk & Hörbinger (1986), Czech Republic.

Material. – 12 cranidia, 18 pygidia, and 2 hypostomes

Diagnosis. – *Huginarges* with sag. slightly more elongated pygidium than in typical *Huginarges*, its length/width ratio attains 1.38–1.4. Axis is of *Acanthopyge*-like morphology and occupies about $^{3}/_{5}$ of the pygidium length. Postaxial ridge prominent, longer than in typical *Huginarges* but shorter than in *Acanthopyge*, slightly vaulted, and does not reach posterior pygidial margin. Pygidial pleural ribs are narrow, moderately vaulted, limited by tightly adjacent shallow furrows. Only slightly curved pleural furrows do not reach the pygidial margin in some specimens. The pygidium surface between the ribs is slightly vaulted or flat; pygidial spines are long, slender, of *Acanthopyge* type – *e.g*. circular in cross section. Dimensions of the exoskeleton are minute in all specimens.

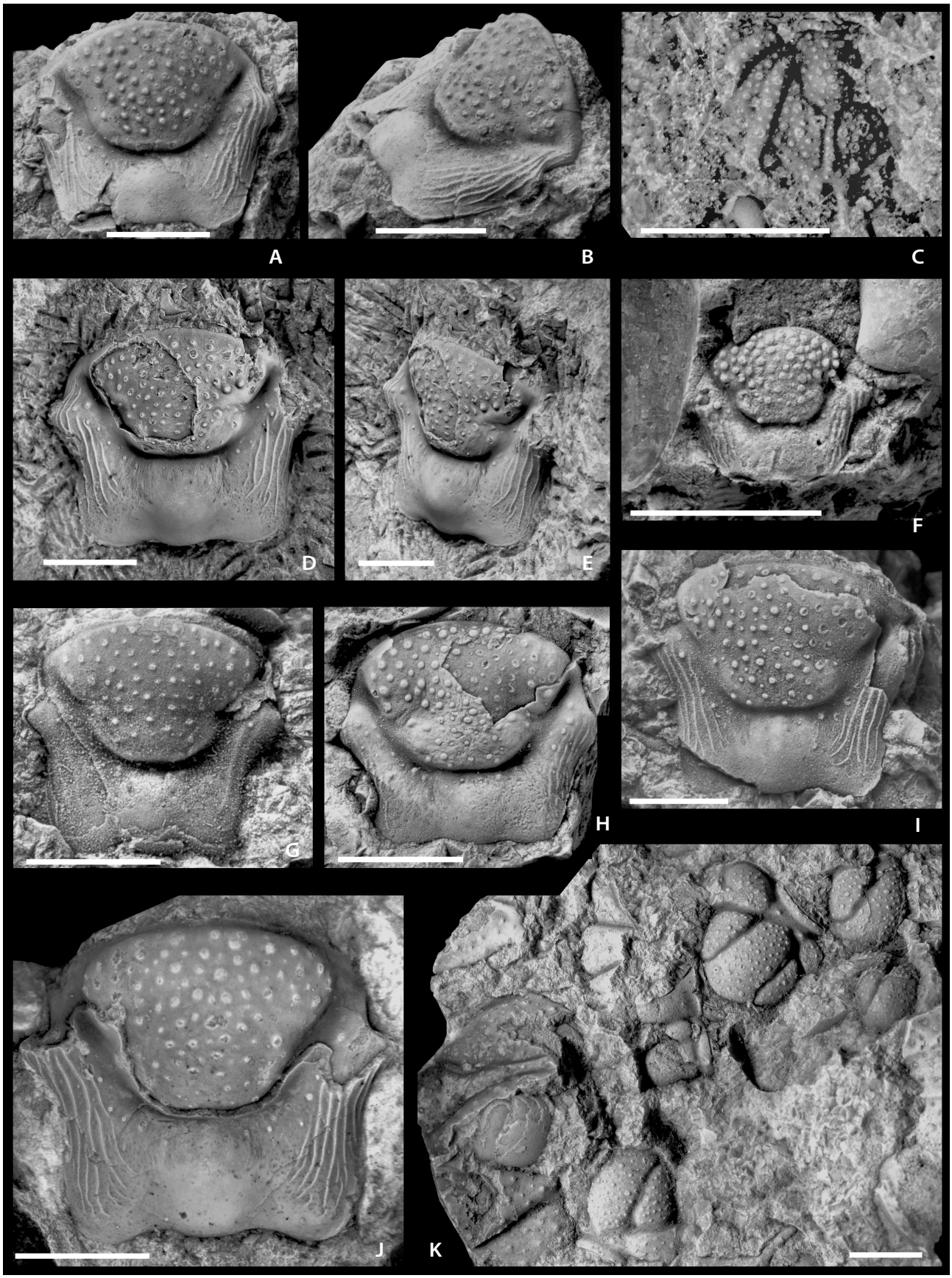
Measurements. – Sagittal estimated length of the holotype pygidium NM L 21554 (PL) is about 10.76 mm, maximal tr. width of this pygidium (PW) attains 14.8 mm. Average sag. length of adult cranidia in *H*.? *pervasta* (CL) about 8 mm (maximal value is 10.39 mm), average sag. length of adult pygidia (PL) about 9 mm (maximal value is 14.22 mm).

Remarks. – Although Přibyl *et al.* (1986) described *H*.? *pervasta* as a representative of *Acanthopyge*, we cannot accept this classification. A general cephalic architecture of *H*.? *pervasta* corresponds to that of late *Huginarges* s.l. (see van Viersen 2021, fig. 2c) rather than to the *Acanthopyge* (with the reservations noted above – the cephalic architecture of *Acanthopyge* and *Huginarges* is very similar), meanwhile its pygidial architecture combines features typical of *Huginarges* – medium-long postaxial ridge, long and wide axis and pleural furrows that sometimes do not reach lateral margin of the pygidium, with axial architecture and especially marginal pygidial spines typical for *Acanthopyge* (long, slender and circular in cross-section, even at their bases). In *H*.? *pervasta*, the pleural furrows, although considerably shallowed adaxially, almost meet the lateral margin in front of the marginal spines in a few specimens but not in all individuals (compare Fig. 8A–C, E, F, I, J, Q–S). In larger specimens of *H*.? *pervasta*, the pygidium becomes elongated (sag.) and relatively larger than in typical *Huginarges*. Such morphology of *H*.? *pervasta* is reminiscent of the type *Lichas decheni* Holzapfel, 1895 and especially of other species now also assigned to *Rheicarges*, such as *R. schneideri* Basse & Müller, 2023 (see Basse & Müller 2023, pl. 31, figs 1–5, 8, 9). It cannot be excluded that *H*.? *pervasta* belongs to this genus (if it is valid, see discussion above). In summary, we consider *H*.? *pervasta* as an intermediate form, a putative ancestor for *A. haueri* (see also original diagnosis of Přibyl *et al*. 1986 and discussion on p. 274) but still belonging to *Huginarges* and/or the *Rheicarges* (if it is valid) clade. This assumption is indirectly supported by the stratigraphic occurrence of *H*.? *pervasta* in the upper Suchomasty Limestone, lying stratigraphically immediately below the first occurrence of *A. haueri* and also by the similar morphology that young holaspid specimens of *A. haueri* share with *H*.? *pervasta*.

Huginarges? *pervasta* is also closely related to *H. bassei* (Chatterton & Gibb 2010) and *H. estevei* (Corbacho & Kier 2013) from Lower Devonian of Morocco (and, in our opinion, to other possible species of *Rheicarges*) – these species share similar pygidial architecture: the shape and length of the short postaxial ridge, the outline of the pygidium (much elongated in *H*.? *pervasta*), but above all the long and slender pygidial spines with a circular cross-section (these are flatter in *H. estevei*). *Huginarges bassei* is much closer to *H*.? *pervasta* in terms of the shape of the pygidial spines and pleural ridges on the pygidium. A sole pygidium of a similar form was collected by Raimund Feist in the Lower Devonian strata of the Carnic Alps. It is stored in the palaeontological collections of Geosphere Austria under the reference number GEOLBA 1998-1-61.

Occurrence. – *Huginarges*? *pervasta* occurs exclusively in the Suchomasty Limestone (Lower Devonian, upper Emsian, Dalejan Regional Stage), especially in its upper part, in the Koněprusy area. The most significant localities of Suchomasty Limestone with documented occurrence of *H*.? *pervasta* are: (1) Zlatý kůň – old collector's pits and remains of "peasant" limestone mining located above the

Figure 7. A–K – *Acanthopyge haueri* (Barrande, 1846). Choteč Formation, Acanthopyge Limestone, Eifelian, Koněprusy near Beroun; Choteč Limestone, Hostim in Fig. 7C. The scale bar represents 5 mm (2.5 mm in D). A, B – large hypostome NM L 46900; A – dorsal view; B – right lateral view. C – early holaspid pygidium (smallest known specimen), CGS ICh 7300, dorsal view. D, E – large hypostome figured by Thomas & Holloway (1988) in pl. 13, fig. 275, BM 42421; D – dorsal view; E – right dorsolateral view. F – early holaspid hypostome, NM L 46882, dorsal view. G – exfoliated hypostome NM L 46878, dorsal view. H – hypostome NM L 46881, dorsal view. I – hypostome NM L 46885, dorsal view. J – large hypostome NM L 17193, figured by Vaněk (1959) in pl. 6, fig. 5, dorsal view. K – accumulation of several cranidia, ČGS JV 2258d, dorsal view.


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upper edge of the Jírův quarry, in a still visible excavated probe exposure by the road in front of the Herget's quarry, established by Přibyl, Vaněk & Hörbinger in 1983, and restored by Vaněk & Vokáč in 1995, and (2) The rock debris (quarry spoil – waste rock) on the southern edge of the Červený lom Quarry.

Biometric analysis

All material of *A. haueri* and *H.*? *pervasta* is preserved as almost non-deformed internal molds, sometimes with remains of the original exoskeleton, preserved in bioclastic limestone. Because of the highly dynamic depositional environment, most spines are broken off and the exoskeleton is often damaged. Therefore, classical biometric analysis was used to supplement landmark analysis, which can be affected by incomplete material. For biometric analysis, all specimens were measured using a digital micrometric caliper-square. Each measurement was repeated twice, and the average values were used. Some exoskeletal parts were partially broken. If damage affected no more than 10% of the left and/or right portion of measured carapace, bilateral symmetry estimation was applied (*e.g.* the values measured on the undamaged part of the exoskeleton were doubled). Such incomplete measurements were repeated three times and the average values were calculated. Despite this, the final dataset is relatively incomplete, although in many specimens the measured parameters were sufficiently preserved. This especially applies to the pygidial marginal spines, which are incomplete in more than 95% of the specimens. In cranidia, maximum cranidial width (CWmax) was measured at the lateral margin of the posterolateral lobes, rather than at the true posterolateral margin (at the crossing of the genal suture), as this part of the exoskeleton is only very rarely preserved in Bohemian material.

Cranidial parameters

Considering the cranidial parameters, namely CL to CWmax/CL ratios (see Fig. 3) for *A. haueri*, *H.*? *pervasta*, *H.*? *aigaion*, and *H.*? *parva*, measured values show considerable variability in *A. haueri* (see Fig. 9). Although the material for the other species is limited, it shows that these species cannot be reliably distinguished based solely on these ratios. Cephalon length (CL) to CWmax/CWbp ratios (Fig. 10) yield results nearly identical to those in Fig. 9. This confirms both the high variability of *A. haueri* and the overlapping ranges with the other species. A boxplot of CWmax/CWbp values (Fig. 13B) further illustrates this overlap: the middle 50% of the values for *A. haueri* coincide with those for *H.*? *pervasta* and are very close to the values for *H.*? *aigaion*. The values for both poorly documented species lie within the range of variability of *A. haueri*, and five specimens of *H. haueri* appear as outliers.

Pygidial parameters

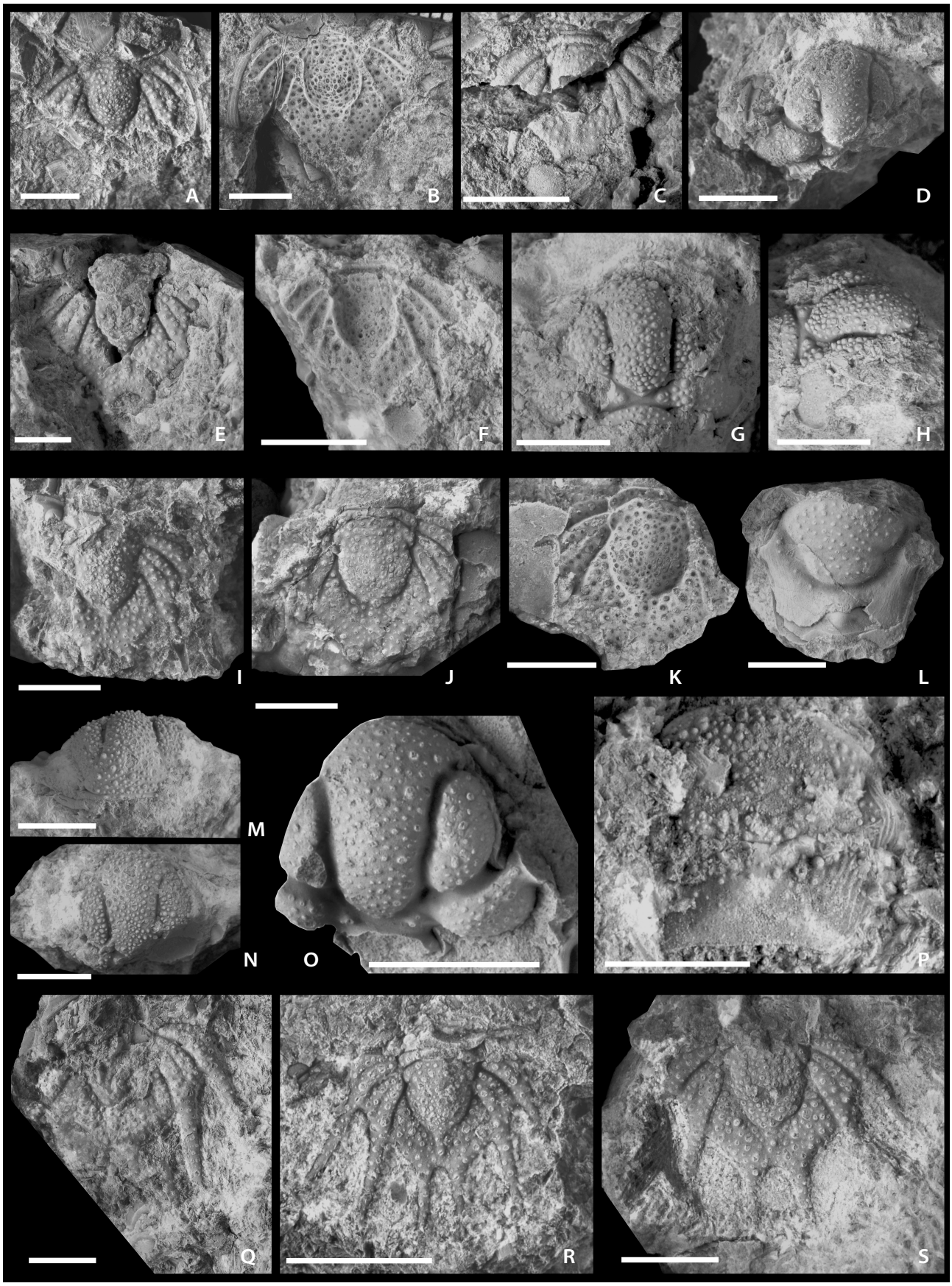
Considering the pygidial parameters, namely PL to PLp/PLa ratios (see Fig. 3) for *A. haueri* and *H.*? *pervasta*, the measured values for early holaspid individuals of *A. haueri* and large specimens of *H.*? *pervasta* are similar, they form two distinguishable clusters (Fig. 11). The range of this ratio is noticeably greater in *A. haueri* than in *H.*? *pervasta*.

The PL to PW/PL ratios plot (Fig. 12) shows some overlap between smaller individuals of *A. haueri* and larger individuals of *H.*? *pervasta*. However, the differences in variability remain, and the overlap is only partial. The boxplot (Fig. 13D) of PW/PLa supports this pattern, with the mean values for the two species clearly distinct, with *H.*? *pervasta* showing a wider range of values than *A. haueri*. Three specimens of *H. haueri* are identified as outliers (Fig. 13D). The measured values indicate two partially overlapping clusters.

Pygidial spine ratios

Pygidial length (PL) *versus* PLs1–3/PL ratios in *A. haueri* shows for all three spines a statistically significant (p-value < 0.05) but still weak (R^2 = 0.15–0.28) trend towards smaller PLs/PL ratio with increasing PL, meaning large individuals (large pygidial length) tend to have

Figure 8. A–S – *Huginarges*? *pervasta* (Přibyl, Vaněk & Hörbinger, 1986). Zlíchov Formation, Suchomasty Limestone, Upper Emsian, Koněprusy near Beroun. Scale bar represents 5 mm. A – holotype, incomplete pygidium, NM L 21554a figured by Přibyl, Vaněk & Hörbinger (1986) in pl. 4, fig. 2. B – negative counterpart of the holotype (so far unknown), NM L 21554b, dorsal view. C – paratype pygidium, NM L 21555, dorsal view. D – cranidium NM L 46865, dorsal view. E – damaged pygidium NM L 46866, dorsal view. F – negative counterpart of pygidium, NM L 46867, dorsal view. G, H – cranidium NM L 46868, dorsal view G – dorsal view; H – right lateral view. I – incomplete pygidium NM L 46874, dorsal view. J, K – incomplete pygidium NM L 46869; J – internal mould, dorsal view; K – negative counterpart, dorsal view. L – hypostome NM L 46870, dorsal view. M, N – incomplete small cranidium NM L 46871; M – frontal view; N – dorsal view. O – incomplete cranidium NM L 46872, dorsal view. P – incomplete hypostome NM L 46873, dorsal view. Q – incomplete large pygidium RŠ1023, dorsal view. R – well preserved pygidium with long spines, CGS RŠ1024, dorsal view. S – larger pygidium CGS RŠ1025, dorsal view.


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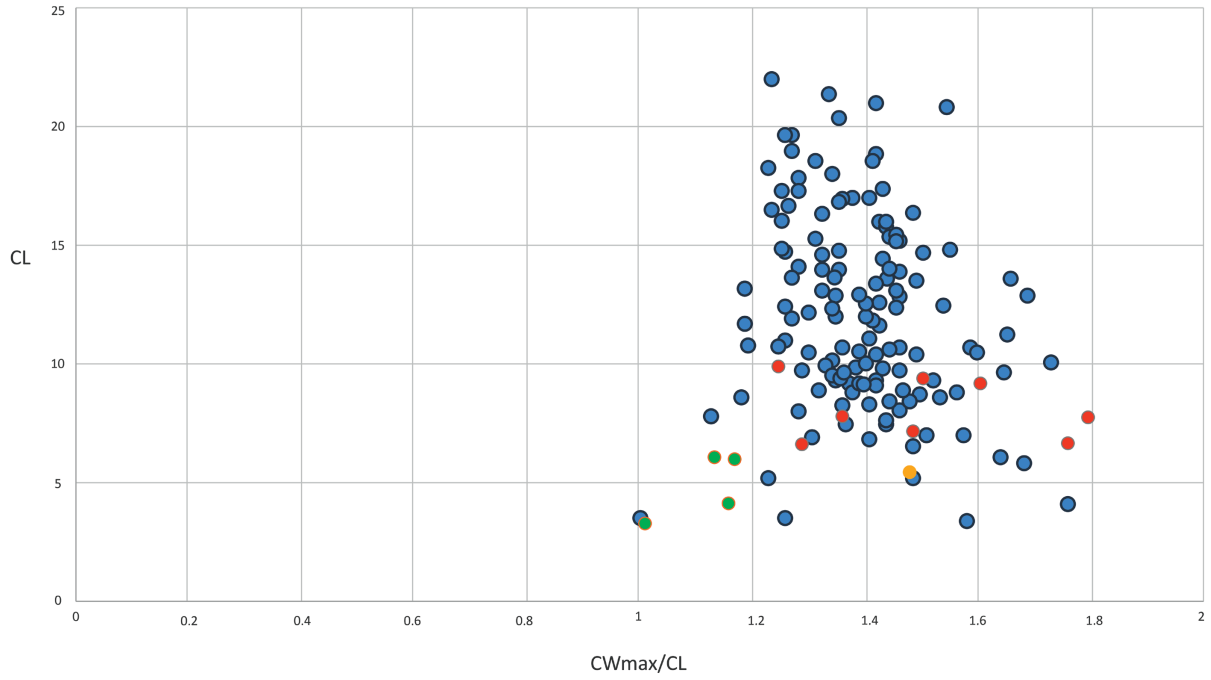


Figure 9. Graph of the CL to CWmax/CL ratios in *Acanthopyge haueri* (blue dots), *Huginarges*? *pervasta* (red dots), *Huginarges*? *aigaion* (green dots) and *Huginarges? parva* (yellow dots). See figure 3 for biometric parameters.

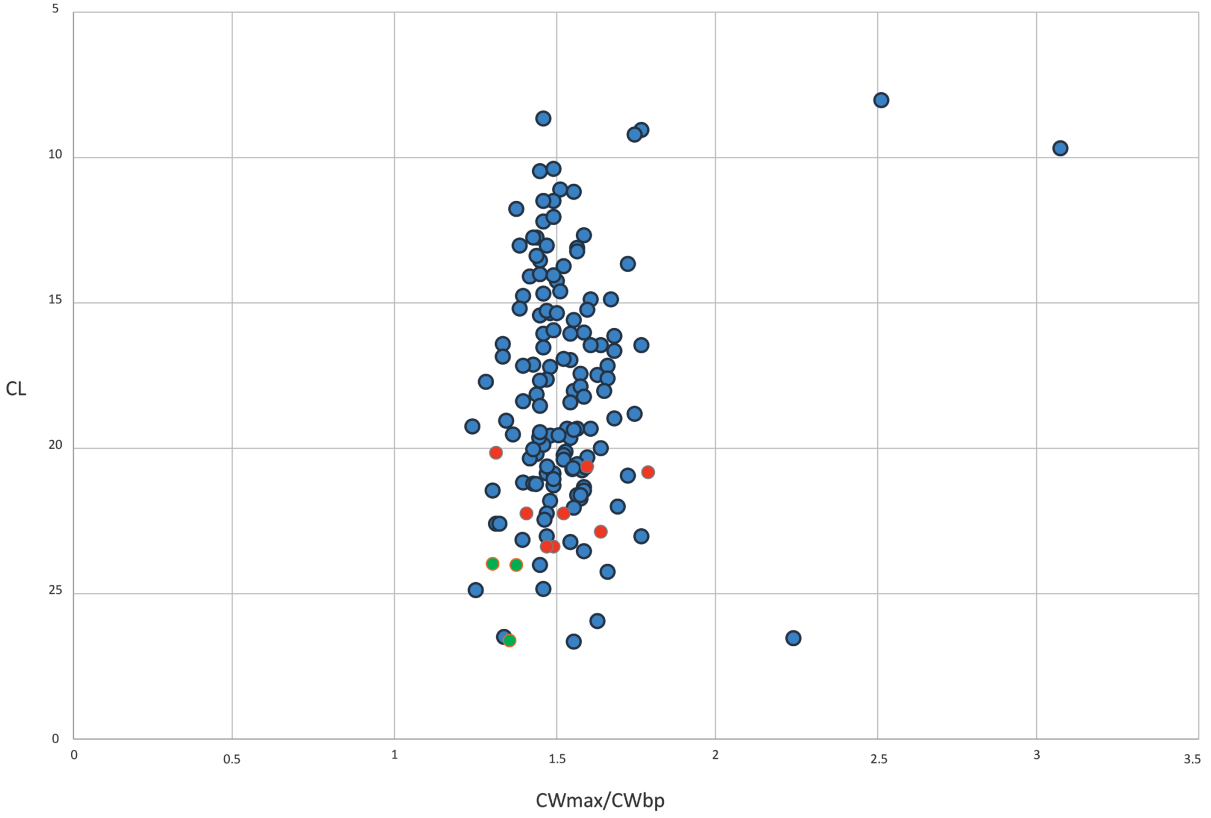


Figure 10. Graph of the CL to CWmax/CWbp ratios in *Acanthopyge haueri* (blue dots) *Huginarges*? *pervasta* (red dots) and *Huginarges*? *aigaion* (green dots). See figure 3 for biometric parameters.

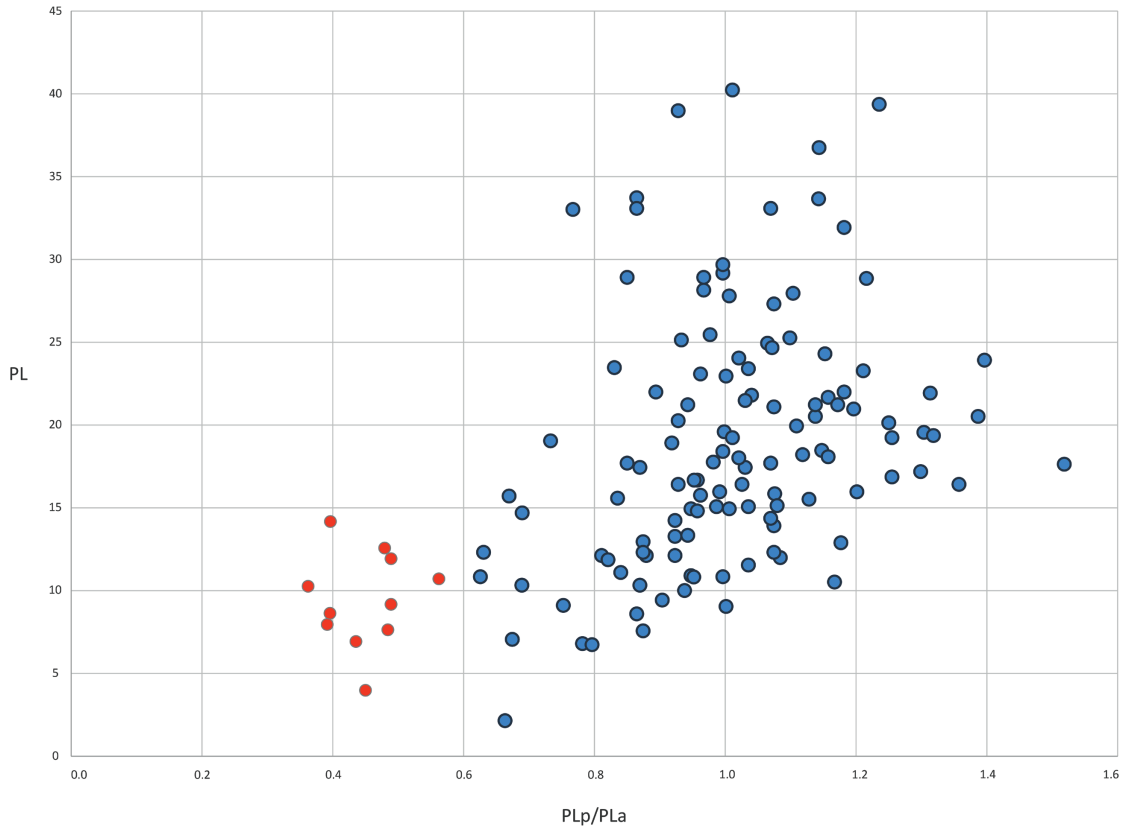


Figure 11. Graph of the PL to PLp/PLa ratios in *Acanthopyge haueri* (blue dots) and *Huginarges*? *pervasta* (red dots). See figure 3 for biometric parameters.

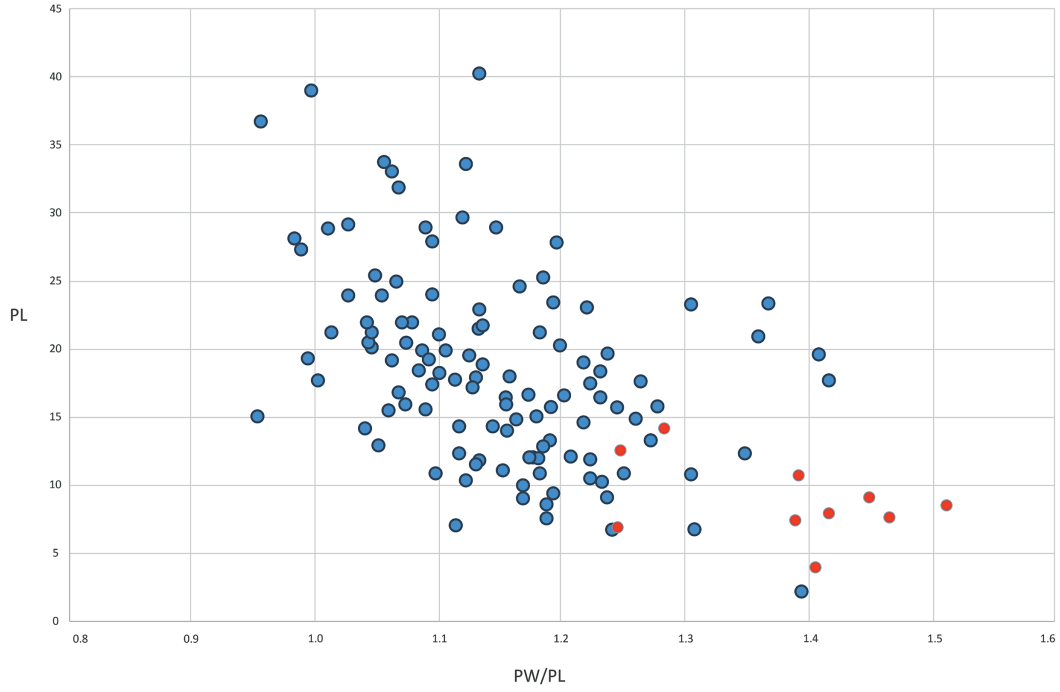


Figure 12. Graph of the PL to PW/PL ratios in *Acanthopyge haueri* (blue dots) and *Huginarges*? *pervasta* (red dots). See figure 3 for biometric parameters.

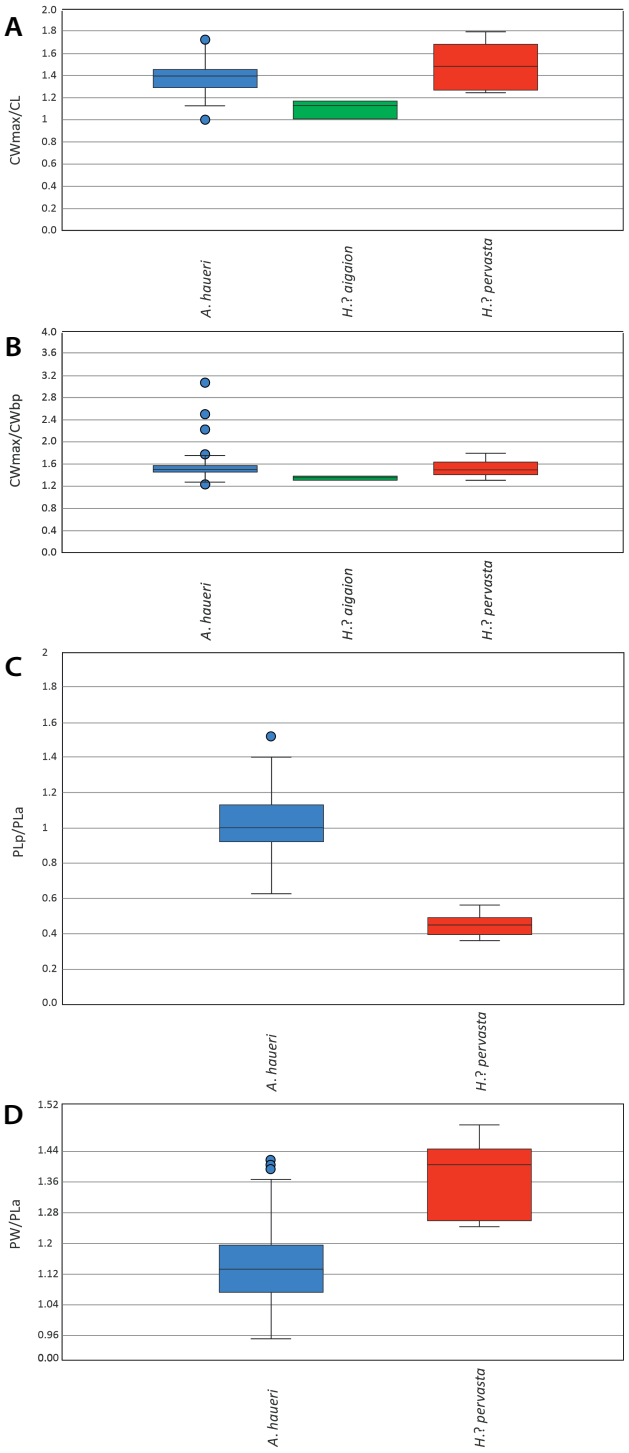


Figure 13. A – boxplot diagram showing the range of CWmax/CL ratios in *A. haueri* (blue), *H.*? *aigaion* (green) and *H.*? *pervasta* (red). See figure 3 for biometric parameters. B – boxplot graph showing the range of CWmax/CWbp ratios in *Acanthopyge haueri* (blue), *Huginarges*? *aigaion* (green) and *Huginarges*? *pervasta* (red). See figure 3 for biometric parameters. C – boxplot graph showing the range of PLp/PLa ratios in *Acanthopyge haueri* (blue) and *Huginarges*? *pervasta* (red). See figure 3 for biometric parameters. D – boxplot graph showing the range of PW/PLa ratios in *Acanthopyge haueri* (blue) and *Huginarges*? *pervasta* (red). See figure 3 for biometric parameters.

relatively shorter spines (Fig. 14). However, this decrease is not uniform for all three pairs of spines. The trend is most pronounced for the PLs2 and the weakest for PLs3 where also the data points are the most scattered. The measurements are influenced in part by taphonomy and the preparation of fragile spines. Nevertheless, this trend confirms previous qualitative observations based on extreme cases (small pygidia with long spines *vs*. large pygidia with relatively shorter spines).

Discussion of biometrics

Data from linear measurements confirm the difficulty of classifying and distinguishing *A. haueri* based solely on cranidial measurements. The variability of cranidium morphology in this species is so high that it is not possible to reliably distinguish *A. haueri* from the related *H.*? *pervasta* and *H.*? *aigaion*, or even from the morphologically more distinct *H.*? *parva*, based solely on these measurements. The situation is different for pygidial measurements. The measured values for *A. haueri* form distinct and clearly defined clusters. These clusters only partially overlap with those of other trochurids, especially in young holaspid individuals of *A. haueri*. Although comparison is complicated by insufficient documentation of some species, the results are nevertheless informative.

Landmark analysis

Cranidia

For cranidia, PCA yielded 22 principal components. The first three PCs account for the most interpretable shape variation, though the patterns are quite complex. PC1 explains 30.46% of variation and reflects the relative reduction of the bullar lobe accompanied by the broadening of the frontal part of the glabella (Fig. 15). Specimens with low PC1 scores have a glabella narrowing anteriorly, whereas those with high PC1 scores show broadening anteriorly (Fig. 15). This change is accompanied by the expansion of the posterolateral lobe posteriorly behind the occipital ring and inward into the cranidium. PC2 explains 21.08% of variation and represents the lateral expansion of the posterolateral cranidial and bullar lobes, producing a more longitudinally flattened cranidium in specimens with high-PC2 scores (Fig. 15). PC3 explains 15.29% of variation and mainly corresponds to differences in the position of the posterolateral cranidial lobes. Specimens with high PC3 scores have the lateral edge of posterolateral lobes positioned more anteriorly (Fig. 16). The remaining PCs each account for less than 10% of the variation.

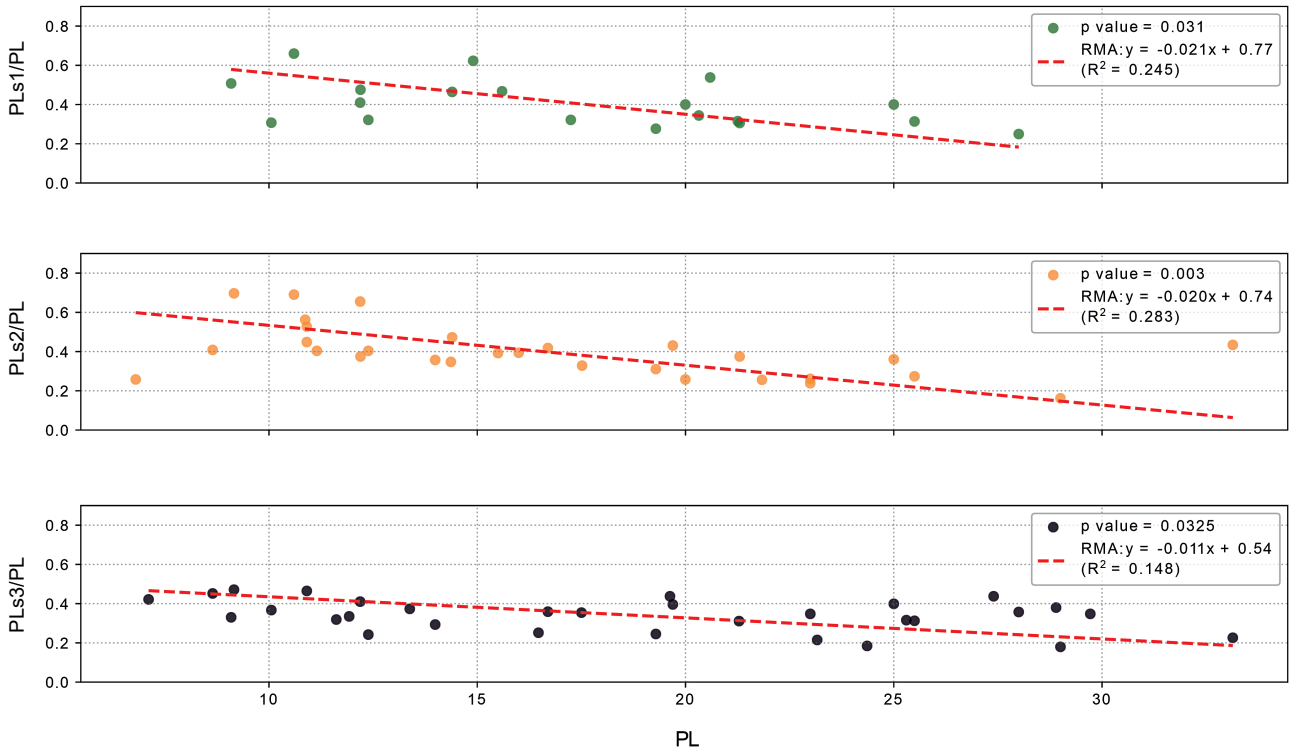


Figure 14. Graphs of the PL to PLs1–3/PL ratios in *Acanthopyge haueri*. Green dots = PLs1/PL (n = 14); Yellow dots = PLs2/PL (n = 30); Dark gray dots = PLs3/PL (n = 29). Dotted lines show reduced major axis (RMA) trend lines together with parameters of the fit (p-value, R^2 and linear fit coefficients). The trends are statistically significant (p-value < 0.05) but still relatively scattered (small R^2) and weak (small negative slope) for all the investigated spines. See figure 3 for biometric parameters.

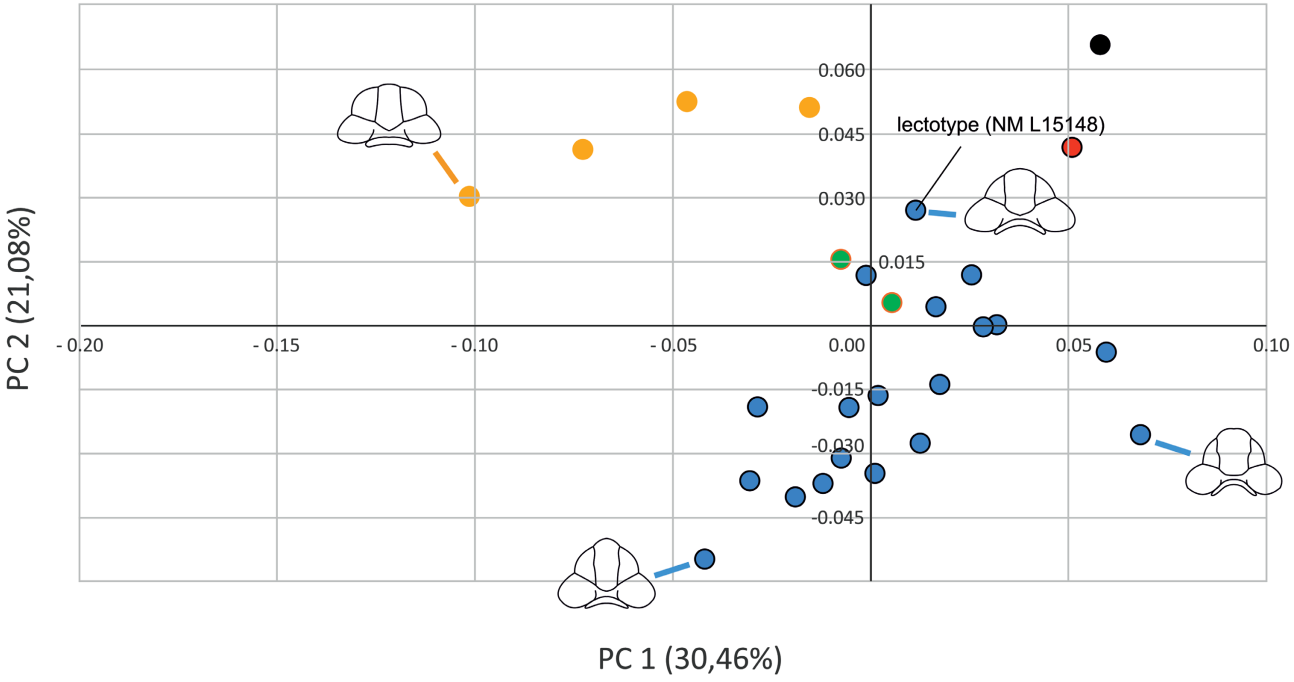


Figure 15. Graph showing the locations of studied cranidia in a morphospace defined by the two first principal components. Blue dots = *Acanthopyge haueri*; red dots = *Huginarges*? *pervasta*; yellow dots = *Huginarges*? *parva*; green dots = *Huginarges? aigaion*; black dot = *Trochurus speciosus.*

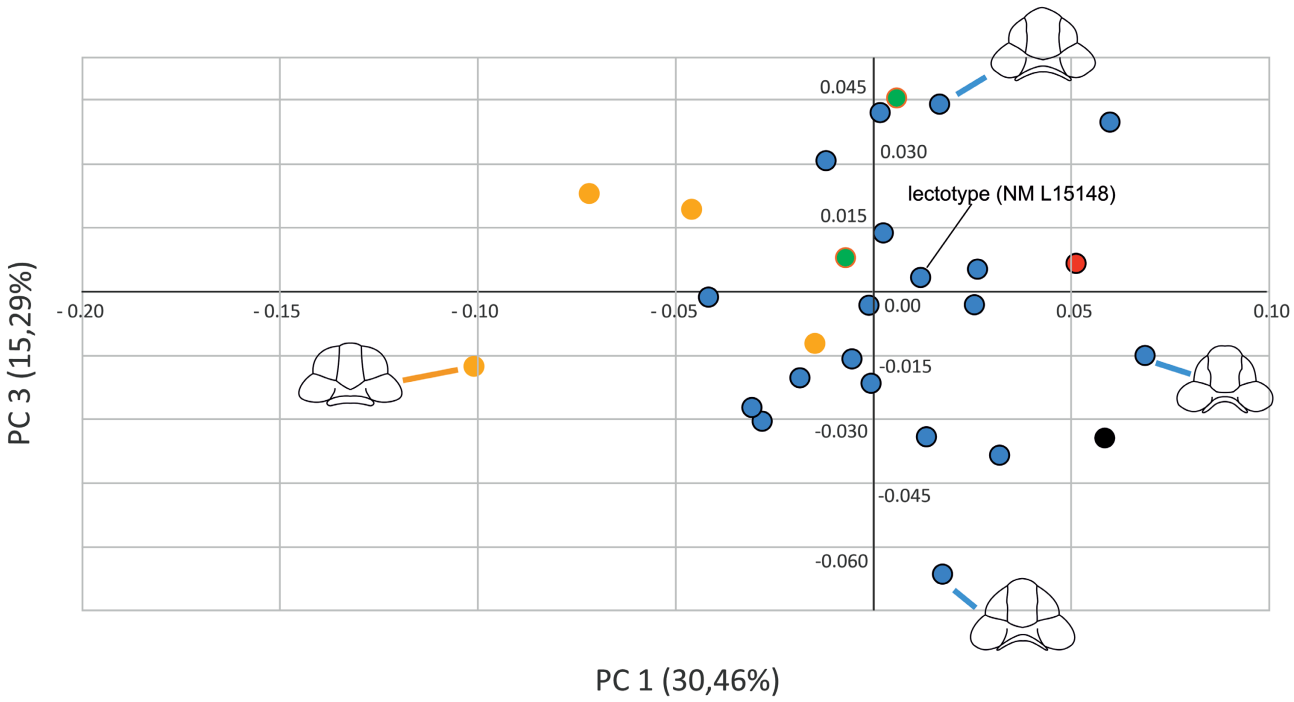


Figure 16. Graph showing the locations of studied cranidia in a morphospace defined by the first and third principal component. Blue dots = *Acanthopyge haueri*; red dots = *Huginarges*? *pervasta*; yellow dots = *Huginarges*? *parva*; green dots = *Huginarges? aigaion*; black dot = *Trochurus speciosus.*

In the morphospace defined by PC1 and PC2 (Fig. 15), most specimens of *A. haueri* form a consistent cluster with few exceptions. The positions of outgroup specimens are less clear. *Huginarges*? *aigaion* falls within the cluster of *A. haueri*, whereas *H.*? *pervasta*, *T. speciosus* and *H.*? *parva* are outside, although *H.*? *pervasta* is relatively close (Fig. 15). *Huginarges*? *parva* shows relatively high variability along PC1 but low along PC2 (Fig. 15).

Plotting PC1 against centroid size shows a trend of lower PC1 values in larger *A. haueri* individuals (Fig. 17), although this correlation is not significant due to the small number of usable specimens. No observable correlations were observed with PC2 or PC3.

Pygidia

For pygidia, PCA yielded 20 principal components. PC1 accounts for 74.51% of variation and depicts the elongation of the postaxial part of the pygidium. PC2 and PC3 explain 8.35% and 5.47% respectively, mainly corresponding to the relative position of lateral spines. Remaining PCs account for 11.67% of variation.

In the morphospace defined by PC1 and PC2 (Fig. 18), pygidia of *A. haueri* form a well-defined cluster that is separated from *H.*? *pervasta* and other outgroups via much lower values on PC1 (Fig. 18). The only exception is specimen ČGS ICh 7300, the smallest pygidium, that occupies an intermediate position between the *A. haueri* and *H.*? *pervasta* clusters (Fig. 18). *Acanthopyge haueri* has noticeably smaller dispersion along the PC2 axis compared to *H.*? *pervasta*, suggesting that relative position of spines plays a minor role in variability of this species. Specimens of *H. branikensis* and *T. speciosus* have very similar PC1 scores to *H.*? *pervasta* but differ in PC2 scores. *Huginarges docekali*, represented by a single specimen, is then separated from other species by a much higher PC1 score.

Plotting PC1 against centroid size shows that the pygidial shape variability in *A. haueri* is partially size-dependent and that smaller individuals have generally higher PC1 scores than larger individuals (Fig. 19). This association between small size and high PC1 score can be observed also with the position of other species, as all the specimens of *H.*? *pervasta* and other species are comparable in size to the smallest specimens of *A. haueri*.

Discussion of landmark analysis

Landmark analysis shows significant shape variability in both cranidia and pygidia of *A. haueri*. Cranidial morphology displays high morphological variability, overshadowing clear interspecific and ontogenetic trends, although size-related shape trends can be observed, such as expansion of bullar lobes in relation to the glabella and

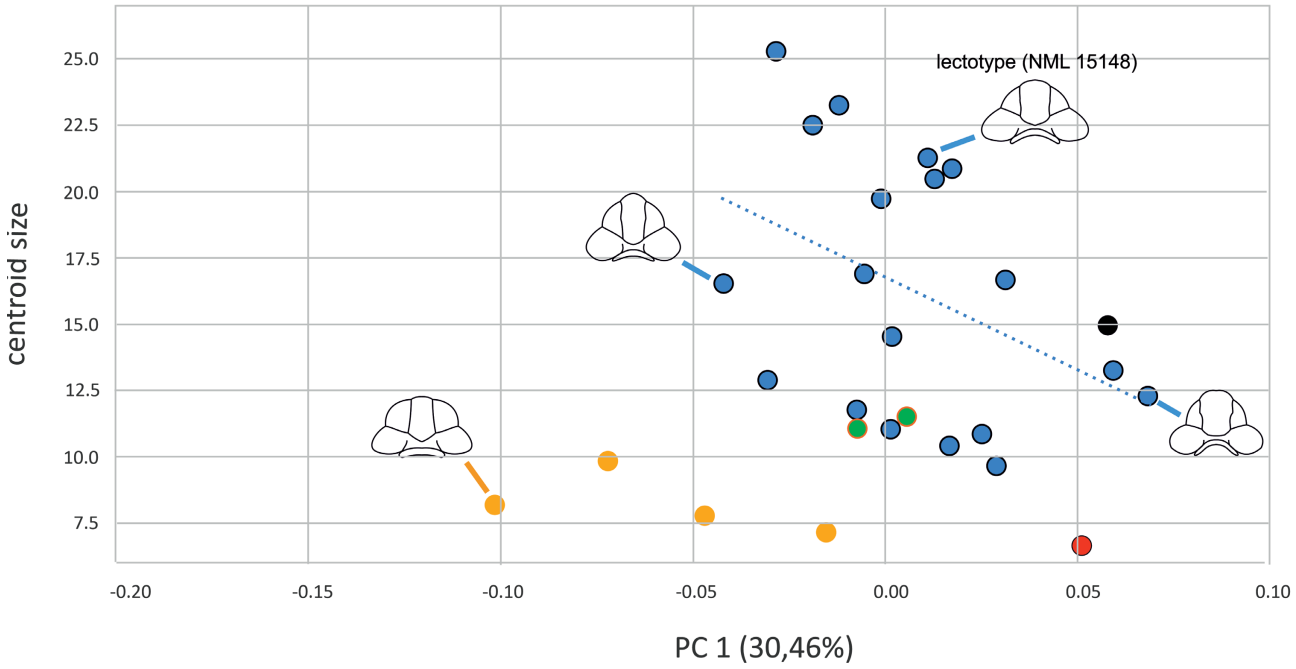


Figure 17. Graph showing the positions of studied cranidia according to the first principal component (X axis) plotted against centroid size (Y axis). Blue dots = *Acanthopyge haueri* (n = 19); red dots = *Huginarges*? *pervasta* (n = 1); yellow dots = *Huginarges*? *parva* (n = 4); green dots = *Huginarges? aigaion* (n = 2); black dot = *Trochurus speciosus* (n = 1). The dotted line shows the linear dependence between PC1 scores and size in specimens of *A. haueri* (y = −69.83x + 16.80, r^2 = 0.1638, r = 0.4047).

overall broadening of the cephalon in larger specimens. This variation could be partially explained by vaulting of the frontal part of the glabella.

In contrast, pygidial shape variability could be mostly explained by a single PC and its scores show reliable differences between studied species and clear ontogenic changes in the elongation and broadening of the postaxial part with increasing size in *A. haueri*. This association also can be observed in the other studied species, which generally reach smaller sizes than *A. haueri* and possess a much shorter and narrower postaxial pygidial region (as exemplified by their higher PC1 scores in our graphs).

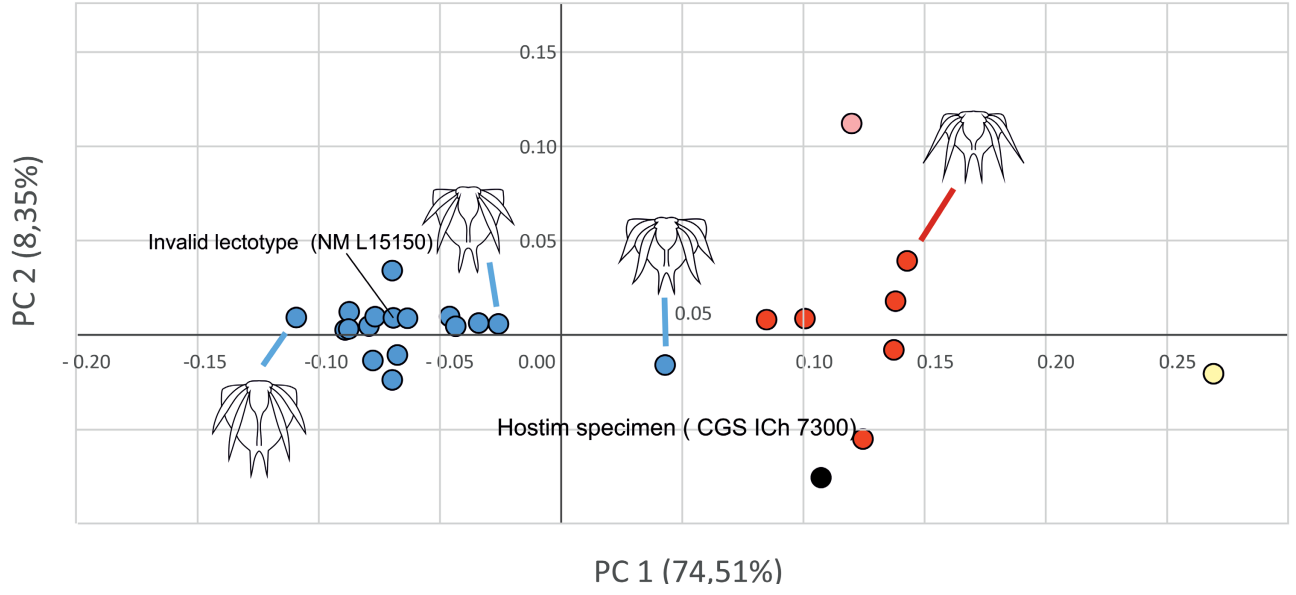


Figure 18. Graph showing the locations of studied pygidia in a morphospace defined by the two first principal components. Blue dots = *Acanthopyge haueri*; red dots = *Huginarges*? *pervasta*; yellow dot = *Huginarges*? *docekali*; pink dot = *Huginarges branikensis*; black dot = *Trochurus speciosus.*

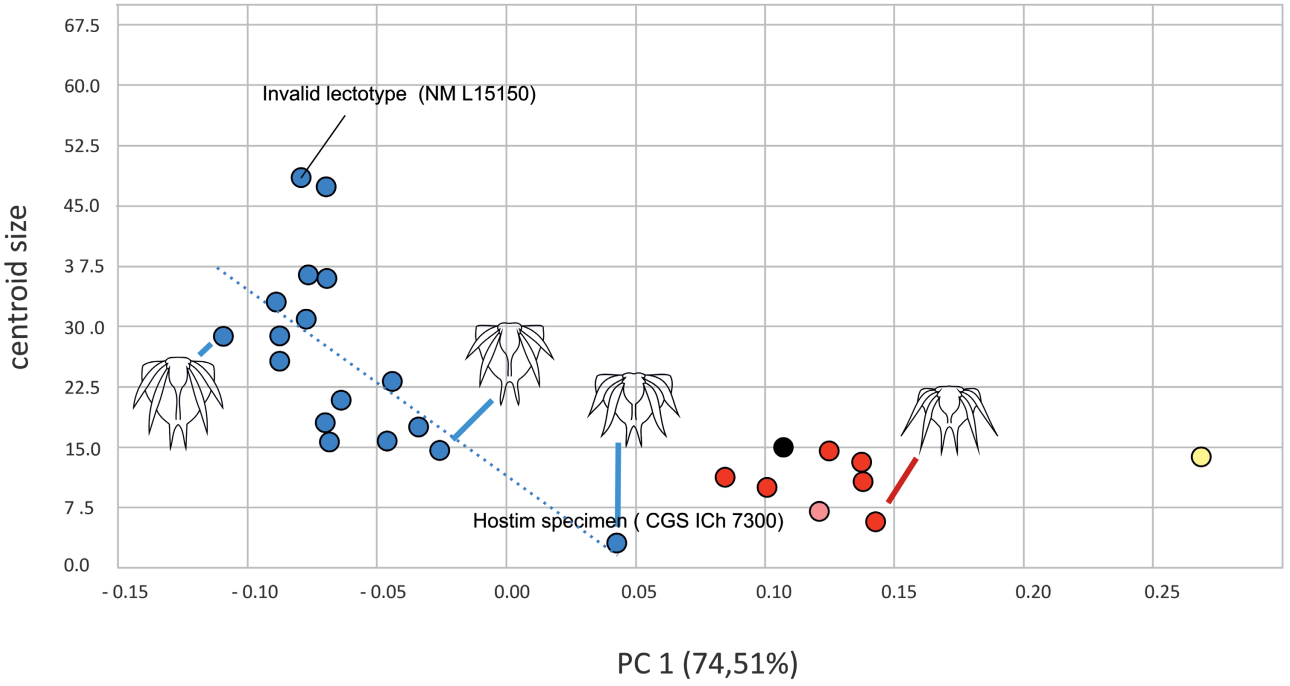


Figure 19. Graph showing the positions of studied pygidia according to the first principal component (X axis) plotted against specimen size (Y axis). Blue dots = *Acanthopyge haueri* (n = 17); red dots = *Huginarges*? *pervasta* (n = 6); yellow dots = *Huginarges*? *docekali* (n = 1); pink dot: *Huginarges branikensis* (n = 1); black dot = *Trochurus speciosus* (n = 1). The dotted line shows the linear dependence between PC1 scores and size in specimens of *A. haueri* (y = −231.48x + 11.82; r^2 = 0.4405, r = 0.6637).

Discussion

All data show notable morphological variability within a supposedly well-defined species *A. haueri*, as well as in other Devonian trochurines of the Prague Basin. All measured parameters (see Fig. 3) are variable; some of them might even be considered of generic importance. A major problem, however, is the uncertain stratigraphic assignment of most of the museum specimens. It is possible that the designation "*Acanthopyge haueri*" actually encompasses multiple species. However, with the data currently available, it is not possible to resolve this issue. The variability is notable especially in the pygidium, which includes differences in overall outline, relative length (sag.) of the pygidial axis and postaxial ridge, and in the length/width ratio of the pygidium (see also previous study of Thomas & Holloway 1988).

In the cephalon, the variability is similarly conspicuous, including differences in the height of the cranidium and its vaulting, the length/width ratio of the cranidium (tr.), the width of the median glabellar lobe, bullar lobes, and posterolateral lobes, among others. The variability of cranidia in Devonian trochurines of the Prague Basin is considerable, often overshadowing many traits useful for species identification in other taxa. This makes species identification difficult and sometimes even impossible.

The hypostome also shows considerable variability, especially in length/width ratios, the prominence of terrace lines and other sculpture which may differ individually (Fig. 7).

Pronounced allometric trends are visible during ontogenetic development – early holaspid specimens obviously have less vaulted cephala with less prominent lobation, pygidia with nearly semicircular outlines and long, straight marginal spines. In contrast, larger specimens are characterized by more strongly vaulted cephala, longer pygidia, often semi-elliptical to elongate sub-triangular in outline, relatively shorter marginal spines, a longer (sag.) post-axial ridge and vaulted lateral lobes of the pygidium (the axis is moderately vaulted in these specimens) – see Fig 18. An increase in the relative length of the pygidium compared with its width during ontogenesis has also been documented in other groups of trilobites: see, for example, Henningsmoen (1960) or Wernette *et al.* (2023).

Acanthopyge haueri uralensis Maksimova, 1979, from the Eifelian of the Western Polar Urals could, based on our study, be considered as a junior subjective synonym of the nominate species, as the distinctive features discussed by Maksimova (1979) fall well within the documented variability of topotypes of *A. haueri*. However, given the practical unavailability of the published material, this

interpretation can only be considered preliminary. Thomas & Holloway (1988) assigned the species *uralensis* to "*Lobopyge*". A figured paratype pygidium of *A. haueri uralensis* however represents a young holaspid specimen, with a morphology similar to that of comparably sized topotypes of *A. haueri* (figured by Barrande 1852 and Vaněk 1959).

New material (32 specimens) has enabled us to supplement the description of the previously poorly known, putatively ancestral *H.*? *pervasta* (Přibyl *et al*., 1986), a species that is rare in the Suchomasty Limestone of Emsian age that underlies the Acanthopyge Limestone, which yielded the type material of *A. haueri*. The general morphology of this species is intermediate between that of *Acanthopyge* and *Huginarges* Basse *in* Basse & Müller, 2004. Notably, early holaspid specimens of *A. haueri* are similar to the minute *H.*? *pervasta* in morphology, including the presence of a shorter postaxial ridge on the pygidium. The length as well as the outline of the pygidium vary in *H.*? *pervasta,* though to a lesser extent than observed in *A. haueri* (this observation may, however, be influenced by the limited material available for *H.*? *pervasta*). The shape of the pleurae and the basic pygidial morphology, however, are similar in both species. Cranidia of *H.*? *pervasta* closely resemble early holaspid cranidia of *A. haueri*. It is possible that *A. haueri* evolved from *H.*? *pervasta* through predominant peramorphosis.

A morphology identical to that of *H.*? *pervasta* is also shared by part of the syntypes of *H.*? *greifensteinensis* Kim, 1997, from the Eifelian of Germany. It is therefore very probable that both species are conspecific.

Taphonomy and paleoecology

A striking feature characterizing the occurrence of *Acanthopyge* representatives in the Devonian of the Koněprusy area is the total absence of complete or articulated specimens. In fact, the only such remnant is the early holaspid cranidium NM L 46864 (Fig. 5A, B) with an articulated free cheek. Apparently, the high-energy, shallow-water carbonate environment with organic buildups was not conducive to the preservation of articulated lichids. Remains of thoracic segments are missing in the studied material – they were probably carried away by currents or wave action, or mechanically damaged to the point that identification is impossible. In such fragmentary preservation, there is also a certain risk of confusion with the thoracic segments of scutellluid trilobites.

The abundance of cranidia and pygidia is nearly equivalent; cranidia slightly predominate (162 *vs*. 132) despite their lower collecting attractiveness, suggesting that their true abundance might be even higher. We suppose that *Acanthopyge* was associated with the seafloor in life. This interpretation is consistent with its functional morphology, as the structure of the trunk probably allowed relatively high flexibility (Whittington 2015) and may have facilitated rapid short-distance swimming or hopping as an escape strategy from predators. The reduced pleural areas may also have affected the mass distribution and inertial properties of the body, although their specific functional significance remains uncertain (for an interpretation of a flat and wide pygidium in scutelluids, see Chatterton 1971). The hypostome of *Acanthopyge* with its distinct terrace lines further suggests benthic lifestyle, and is compatible with shallow infaunal deposit feeding.

Acanthopyge haueri and the Basal Choteč Event

The sudden abundance of *Acanthopyge* may reflect the partial vacancy of ecological niches following the extensive extinction of shallow-water scutellluid trilobites during the Basal Choteč Event (Chlupáč 1983a). This interpretation is particularly supported by the body size increase in *Huginarges–Acanthopyge* lineage and especially by prominent changes in pygidial morphology in *Acanthopyge*, associated with extensive enlargement of its ventral surface area. As a result, this morphology somewhat resembles the large, flat pygidium of scutelluids.

The only scutelluid genus that co-occurs locally in abundance with *Acanthopyge* is *Thysanopeltis*, characterized by a distinctive posterior pygidial morphology with marginal spines. It is also possible that the adaptations of the originally small, supposedly actively swimming isopygidial trochurid trilobites (*Huginarges–H.*? *pervasta* group) to a predominantly benthic lifestyle in macropygidial *Acanthopyge* occurred in response to partial eutrophication of the water column during the Basal Choteč Event. This eutrophication likely provided an abundance of small seabed food particles, such as algae and cyanobacteria.

In this context, it is interesting that no occurrence of trochurid trilobites is known from the basinal Choteč Limestone (Eifelian), with the exception of a few records of *Acanthopyge* near Hostim in shallow-water bioclastic limestones (of shallow-water origin, Hostim is not far from the Koněprusy area, see Fig. 1). We correlate the extinction of *Acanthopyge* in the Barrandian area with the onset of the anoxic Kačák Event. It is interesting, that in other areas (mainly the Rhenish Massif, and partially Morocco), records of *Acanthopyge* and *Huginarges*-type trochurid trilobites are known from the "pre-Taghanican Middle Givetian" (see Basse & Müller 2023, pl. 31, fig. 9).

It seems that these regions served as a refuge, allowing the *Acanthopyge* lineage to continue up to the Taghanic Event. For discussion of the Kačák Event and reaction of some Morocco non-trilobite faunas to it, see, for example, Ellwood *et al.* (2011) and Monnet *et al*. (2011).

Notes on paleogeography

When projecting all known confirmed occurrences of *Acanthopyge* onto a paleogeographic map of the Early and Middle Devonian Earth (Fig. 20: 1–4), it becomes apparent that the palaeogeographic range of this genus was restricted to the areas traditionally referred to as Northwest Gondwana and European peri-Gondwana (Budil & Fatka 2022), as well as the Rhenohercynian Basin and Kazakhstania. All these occurrences correspond to the subtropical or tropical climatic zones, indicating a relatively limited latitudinal distribution of this genus, practically confined to the closing Rheic Ocean and its surroundings (Galle *et al.* 1995). The only exception is a highly debated occurrence in present-day Japan (see above); but the possible congenerity of *Nipponarges* and *Acanthopyge* remains uncertain.

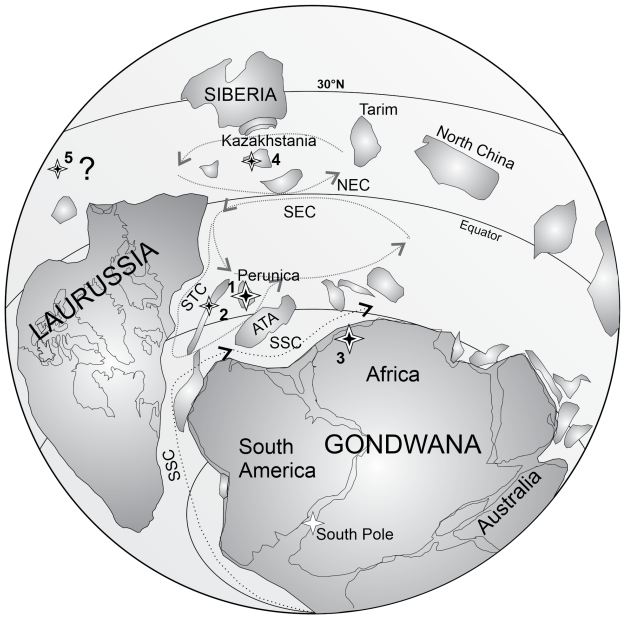


Figure 20. Palaeogeographic map of the Early to Middle Devonian World (after Cocks & Torsvik 2006, modified) showing the position of outcrops yielding *Acanthopyge* in Perunica (1), the Rhenohercynian Basin (2), African West Gondwana (3), and Kazakhstania (4). Occurrence (5) refers to findings of *Niponarges* in present-day Japan; its possible congenerity with *Acanthopyge* remains uncertain. Supposed direction and abbreviations of ocean currents modified after Wilde *et al.* (1991): SEC – South Equatorial Current; STC – South Tropical Current; SSC – South Subpolar Current.

Conclusions

(1) The gathered data show notable morphological variability within the supposedly well-defined species *Acanthopyge haueri*. All measured parameters are variable, and some of these characters, previously considered of generic significance, show substantial variability. This is particularly notable in the pygidium, including differences in overall pygidial outline, relative length (sag.) of the pygidial axis and postaxial ridge, and the length/width ratio of the pygidium. In cranidia, the variability includes the height of the cranidium and its vaulting, the cranidial length/width ratio, and the widths (tr.) of the median glabellar lobe, bullar lobes, and posterolateral lobes. Considerable ontogenetically-related variability is also observed in the hypostomes.

(2) Young holaspid specimens of *A. haueri* are generally less variable, whereas more mature specimens show much greater variability that can partly reflect diagenetic and tectonic deformation. Prominent allometry is observed during development – early holaspid/smaller specimens have less vaulted cephala with less prominent lobation; and such pygidia have an almost sub-circular outline and long, straight marginal spines. In contrast, large specimens have prominent vaulting of the cephalon (sag.), relatively longer pygidia, often semi-elliptic to elongate, subtriangular in outline, relatively shorter marginal spines, a relatively longer (sag.) post-axial ridge, and distinctly vaulted lateral lobes of the pygidium (with the axis only moderately vaulted).

(3) No complete, articulated exoskeleton has been found so far; only one early holaspid cranidium was found with a free cheek or cheeks attached.

(4) The sudden abundance of *Acanthopyge* probably reflects the partial release of niche habitats following the extensive extinction of shallow-water scutellluid trilobites during the early Eifelian Basal Choteč Event. The subsequent disappearance of the genus is related with the early Givetian Kačák anoxic Event.

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