Dev Genes Evol (2012) 222:253–268
DOI 10.1007/s00427-012-0407-7

ORIGINAL ARTICLE

A holomorph approach to xiphosuran evolution—a case study on the ontogeny of *Euproops*

**Carolin Haug · Peter Van Roy · Angelika Leipner ·
Peter Funch · David M. Rudkin · Lothar Schöllmann ·
Joachim T. Haug**

Received: 1 March 2012 / Accepted: 4 June 2012 / Published online: 10 August 2012

Abstract Specimens of *Euproops* sp. (Xiphosura, Chelicerata) from the Carboniferous Piesberg quarry near Osnabrück, Germany, represent a relatively complete growth series of 10 stages. Based on this growth sequence, morphological changes throughout the ontogeny can be identified. The major change affects the shape of the epimera of the opisthosoma. In earlier stages, they appear very spine-like, whereas in later stages the bases of these spine-like structures become broader; the broadened bases are then successively drawn out distally. In the most mature stage known, the epimera are of trapezoidal shape and approach each other closely to form a complete flange around the thoracetron (=fused tergites of the opisthosoma). These ontogenetic changes question the taxonomic status of different species of *Euproops*, as the latter appear to correspond to different stages of the ontogenetic series reconstructed from the Piesberg specimens. This means that supposed separate species could, in fact, represent different growth stages of a single species. It could alternatively indicate that heterochrony (=evolutionary change of developmental timing) plays an important role in the evolution of Xiphosura. We propose a holomorph approach, i.e., reconstructing ontogenetic sequences for fossil and extant species as a sound basis for a taxonomic, phylogenetic, and evolutionary discussion of Xiphosura.

Keywords *Euproops danae* · *Euproops rotundatus* · Fossilized ontogeny · Tagmatisation · Hapantotype

Communicated by S. Roth

C. Haug (✉) · J. T. Haug
Zoological Institute and Museum, Department of Cytology and Evolutionary Biology, University of Greifswald,
Soldmannstraße 23,
17487 Greifswald, Germany
e-mail: carolin.haug@palaeo-evo-devo.info

P. Van Roy
Department of Geology and Geophysics,
Kline Geology Laboratory, Yale University,
210 Whitney Avenue,
New Haven, CT 06511, USA

P. Van Roy
Research Unit Palaeontology, Department of Geology and Soil Science, Ghent University,
Krijgslaan 281/S8,
9000 Ghent, Belgium

A. Leipner
Museum am Schölerberg,
Klaus-Strick-Weg 10,
49082 Osnabrück, Germany

P. Funch
Department of Bioscience, Aarhus University,
Ny Munkegade 116,
DK-8000 Aarhus C, Denmark

D. M. Rudkin
Department of Natural History (Palaeobiology),
Royal Ontario Museum,
Toronto, ON M5S 2C6, Canada

L. Schöllmann
LWL-Museum für Naturkunde,
Sentruper Straße 285,
48161 Münster, Germany

Introduction

Xiphosura, a monophyletic group within Euchelicerata, is mainly represented by fossil species except for four species of Limulidae, which survived until the present day. Although xiphosurans have many clearly derived and highly specialized characters, they are often treated as "living fossils" with "ancient morphologies". This was probably one of the reasons why many fossil arthropods have been aligned with them, for example, Aglaspidida (e.g., Raasch 1939; Størmer 1944, 1955; Raw

1957; Weygoldt and Paulus 1979a, b). Yet, the latter are clearly no chelicerates, and newer views on arthropod evolution have abandoned many of these older concepts (e.g., Scholtz and Edgecombe 2005; Van Roy 2006). However, the number of fossils that can be ascribed to Xiphosura is still quite high (see for example, Anderson and Selden 1997; Dunlop et al. 2010).

As Xiphosura is supposed to be the sister group to all remaining euchelicerates, it is generally considered to be important for understanding the early evolution of Euchelicerata. Due to the paucity of living xiphosuran species, the study of fossil representatives in comparison with the extant forms is of major importance. Especially interesting are exceptionally preserved fossils that provide not only access to dorsal structures, but also to ventral details such as the limbs.

For understanding the evolutionary history of a taxon in the sense of an evolutionary morphology, i.e., reconstructing the character evolution along an evolutionary lineage, a robust phylogeny is of importance (e.g., Wirkner and Richter 2010; Haug et al. 2010a, b, c). Furthermore, as a basis for phylogenetic systematics (sensu Hennig 1966; see also Ax 2000), a more or less sound species concept is necessary.

Haug et al. (2012b) have considered that with further studies on fossil arthropods (in that case early chelicerates) we might experience a similar effect as in the research on dinosaurs, with earlier developmental stages possibly having been misinterpreted as separate species (Horner and Goodwin 2009; Scannella and Horner 2010). It was also pointed out that this problem can be overcome by aiming at reconstructing ontogenetic sequences (Haug et al. 2012b).

This issue might turn out to be quite important also for investigations on xiphosurans. The taxonomic status of certain fossil xiphosurans has been questioned. For example, Anderson (1994) synonymized most species of *Euproops* with *Euproops danae* (Meek and Worthen, 1865). His argumentation was based on different preservational artifacts that led to the recognition of different “morphotypes”, which have been described as separate species. Yet, we think that for a precise determination of fossil species not only taphonomy, but also ontogeny or other possible factors influencing morphology (such as sexual dimorphism) have to be taken into account.

We reconstruct here parts of the ontogeny of a species of *Euproops* from the Upper Carboniferous, Pennsylvanian, middle to upper Moscovian (corresponding to early Westphalian D) of northwestern Germany, more precisely from the Piesberg quarry near Osnabrück. Very early immature stages of *Euproops* from this quarry have already been described by Schultka (2000). We reconstruct the ontogenetic pattern of selected structures and point out how the observation of these changes influences our view on diagnostic characters for euproopids and Xiphosura as a whole.

Furthermore, we want to emphasize that for progressing with the problem of species determination within *Euproops*, different ontogenetic aspects need to be taken into account: (1) Noncorresponding ontogenetic stages may originally have been compared, so that differential diagnostic characters may become non-informative; (2) supposed separate species might, in fact, represent different instars of a single species; and (3) there may be several species within *Euproops* that evolved through heterochrony.

We use this example for pointing out that a holomorph approach, including the reconstruction of ontogenetic sequences from all available fossil and extant taxa, is the prerequisite for a palaeo-evo-devo approach, which allows a reliable reconstruction of the evolutionary history of Xiphosura. This will be the basis for a sound ground pattern reconstruction of the stem species of Xiphosura and thus again contribute to our understanding of euchelicerate evolution as a whole.

Material and methods

Material

We investigated 37 selected, well-preserved specimens of *Euproops* sp., all from the Piesberg quarry. For a detailed discussion of the geological setting, see Dunlop et al. (2008). The specimens are all part of the collection of the Museum am Schölerberg, Osnabrück (MAS Pal.). An assignment of the investigated specimens to a certain species is currently problematic, as there are different interpretations of the material by different authors. From the nearby locality of Ibbenbüren, the species *Euproops bifidus* Siegfried (1972) has been described. Brauckmann (1982) compared the specimens from the Piesberg quarry with *E. bifidus*. Zawischa (1989) compared specimens from the Piesberg quarry with *Euproops rotundatus* (Prestwich, 1840). Anderson (1994) does not discuss *E. bifidus* in his synonymy discussion, but includes *E. danae* and *E. rotundatus*. Schultka (2000) gives a brief history of the finds of *Euproops* at the Piesberg quarry and describes the taxonomic status of this form, as well as the distinction between *E. danae* and *E. rotundatus*, as currently uncertain.

As we question below the taxonomic status of different *Euproops* species, an a priori ascription of the investigated specimens to a described species appears premature. We keep the discussion, therefore, under open nomenclature; the material is nevertheless considered to be conspecific. Comparative xiphosuran material was documented from the collections of the Royal Ontario Museum, Toronto and from the Invertebrate Paleontology collection of the Yale Peabody Museum, New Haven (YPM IP).

Methods

All specimens were documented under crossed-polarized light settings (e.g., Schaarschmidt 1973; Bengtson 2000; Kerp and Bomfleur 2011). Some images were enhanced either in depth of field (CombineZM/ZP) or field of view (Adobe Photoshop CS3 and Microsoft Image Composite Editor; for details see, for example, Haug et al. 2009).

Some specimens that exhibit some autofluorescence were documented under macrofluorescence settings (Haug et al. 2011a). Specimens with sufficient relief were documented as stereo image pairs and processed as red–cyan stereo images. Counterparts with a negative relief were usually depth inverted. Some stereo images were additionally color inverted as this provides a better contrast in certain cases. Stereo images were prepared in Adobe Photoshop CS3 and Gimp 2.6.11.

Opisthosomal and prosomal lengths and widths were measured on the digital photographs (Fig. 1). Measured dimensions were graphed as scatter plots in Microsoft Excel and OpenOffice. Clusters were identified based on these plots. As not all measured lengths were available on all specimens, assignment of the specimens to certain growth stages is not based on a single plot, but on a combination of all plots.

Line drawings from the literature were redrawn using the vector graphic programs Adobe Illustrator CS3 and Inkscape 0.45. Scatter plots were also redrawn in this way.

Results

Ontogenetic sequence

The material can be grouped into 10 growth stages, mainly based on length measurements (Fig. 2), but additionally through specific morphological changes of the thoracetron (see below; for a general overview on the morphology of the investigated specimens see Figs. 1 and 3). The earliest stage most likely corresponds to the early developmental stage described by Schultka (2000), based on the morphology of the thoracetron (see below). Stage 10 is represented by the largest available specimen. Whether this corresponds to the adult phase or still represents an immature stage cannot be clarified.

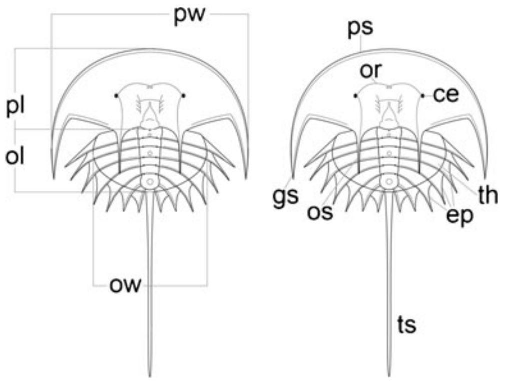

Fig. 1 Scheme of measured lengths (*left*) and explanation of body parts (*right*). *ce* compound eye, *ep* epimera, *gs* genal spine, *ol* opisthosoma length, *or* ophthalmic ridge, *os* ophthalmic spine, *ow* opisthosoma width, *pl* prosoma length, *ps* prosomal shield, *pw* prosoma width, *th* thoracetron

Prosomal shield

The morphology of the prosomal shield is very similar in all observed growth stages. It is broader than long and gently rounded along the anterior margin in dorsal view (Fig. 3a and b). The posterior margin is a very broad triangle with the median tip pointing backwards. The shield is arched, almost dome shaped. The smooth curvature of this dome is only interrupted by the ophthalmic ridges (Figs. 3a–c and 4).

The ophthalmic ridges originate from the posterior rim of the prosomal shield at about one third of the distance between the median ridge and the lateral edge. They continue anteriorly, curving slightly outward (concave) until about three quarters of the total shield length. Here, the ridges turn medially, curving inwards in a gentle convex arc. The ridges from both sides meet at the median ridge, forming a backward pointing angle of about 120°. At the corner at which the ophthalmic ridges change their curvature, a small, more or less circular structure represents the compound eye (Fig. 3c). Individual ommatidia are not preserved.

Five spines originate on the posterior margin, all pointing posteriorly. One pair, the genal spines, arise from the lateral corners. A second pair, the ophthalmic spines, are located where the ophthalmic ridges meet the posterior margin. Right at the median line at the tip of the triangle of the posterior margin, a single short and stout spine arises. Genal spines are known for all ontogenetic stages except for stage 1, which is only represented in our material by one specimen which lacks the prosoma. They are always slightly shorter than the length of the anterior-posterior axis of the prosomal shield (Fig. 4). The ophthalmic spines are only known from later stages (Fig. 4d–f, h), possibly due to preservation, but appear to have more or less the same length as the genal spines. No allometric growth was observed on any of these spines.

Thoracetron

All visible opisthosomal tergites are fused to form an oval-shaped thoracetron in all observed growth stages, with the long axis of the oval oriented transversely (Fig. 3e). Single segmental structures of seven of the opisthosomal tergites can still be recognized through rings on the axial area and ridges on the epimera. The morphology of the epimera of segments 8(?) to 14(?) changes drastically throughout the ontogeny (Figs. 3e and 5).

In the earliest known stage, the epimera are thin, elongate spines, armed with many fine spinules or hairs (Fig. 5a). In the succeeding stage, the bases of the spines are broadened, reaching to the next anterior segment. The bases form a flange surrounding the entire opisthosoma, with the exception of the anterior margin. The length of the proximodistal axis of the bases is about one fifth of the entire epimera length; no

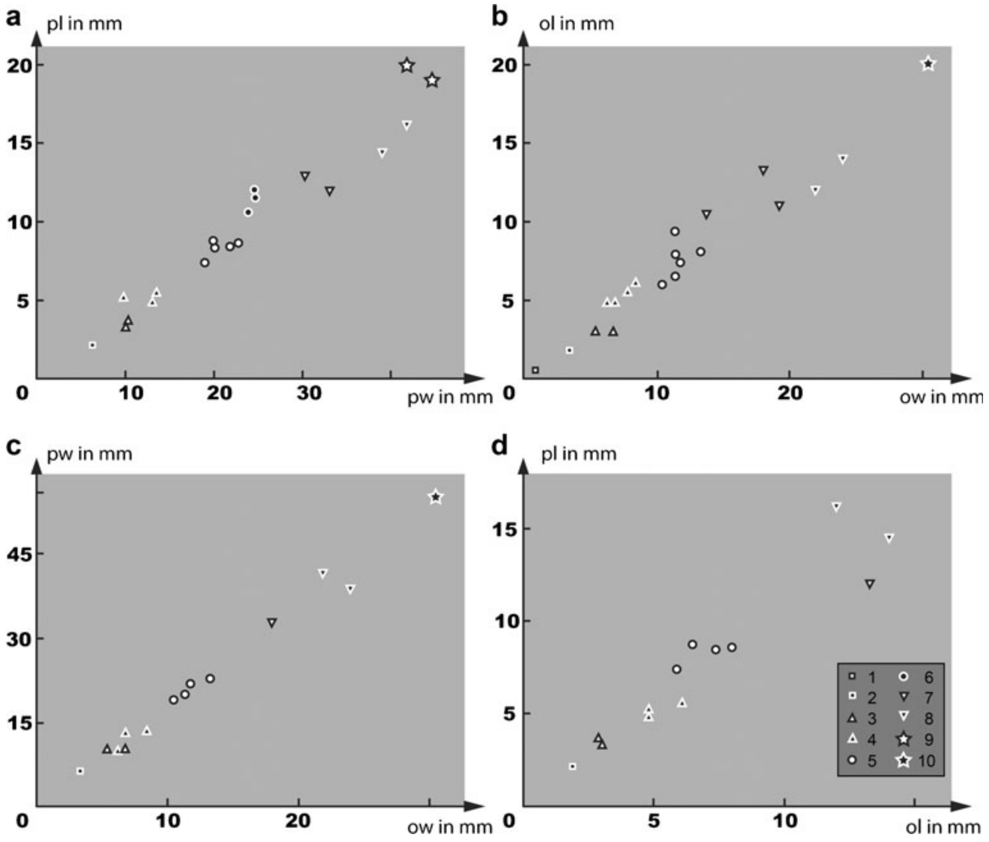

Fig. 2 Scatter plots of measured lengths. **a** Prosoma length versus prosoma width. **b** Opisthosoma length versus opisthosoma width. **c** Prosoma width versus opisthosoma width. **d** Prosoma length versus opisthosoma length. The different symbols represent different growth stages (see key in **d**). When combining all plots, 10 growth stages can be distinguished. *ol* opisthosoma length, *ow* opisthosoma width, *pl* prosoma length, *pw* prosoma width

spinules or hairs can be observed (Fig. 5b). However, this absence may be a taphonomic artifact, as stage 3 appears to have some spinules or hairs (Fig. 5c). The broadened base is extruded further distally throughout the next stages. In stage 3, the flange measures one fourth of the entire epimera length in proximodistal axis (Fig. 5c). It reaches one third in stage 4 (Fig. 5d). Additionally, initial ridges can be observed that separate the bases of the epimera from each other. These ridges are direct continuations of the ridges on the central part of the throracetron demarcating the individual segments. In stage 5, the dimensions of the flange are still about the same, but the ridges separating the epimera are well-developed (Fig. 5e). In stage 6, the flange reaches 50 % of the proximodistal extension of the epimera (Fig. 5f). At stage 7, 75 % proximodistal extension of the flange compared to the epimeral length is reached (Fig. 5g), which appears to be the final condition, retained also in stages 8 (Fig. 5h) to 10 (Fig. 5i). The epimera have lost their spine-like appearance and their shape is almost trapezoidal. All epimera together appear to form an entire flange (in German “Randsaum” of Schultka 2000) as they are directly approaching each other.

Appendages

Details of the appendages are preserved in a number of specimens of different growth stages (see Fig. 6 for details), including walking limbs with their distal chelae (Fig. 6d and e). The appendages appear to be relatively long and can protrude from under the prosomal shield (Fig. 6c), but it cannot be observed whether these are still attached to their basal joints. In the most completely preserved appendage, however, only the distal three elements (of supposedly six or seven based on walking limbs of extant xiphosurans—see below) are visible, so it is possible that the entire limb could have been long enough to extend that far from beneath the shield (Fig. 6).

The third last element of this walking appendage (not appendage six, probably number five; Fig. 6c) is elongate tube-shaped, at least five times as long as its diameter, yet the more proximal part of it is covered by the prosomal shield. The subterminal element is also elongate tube-shaped, about 4.5 times as long as wide and longer than the visible part of the third last element (distal part of subterminal element not preserved in Fig. 6c, but in counterpart in Fig. 6d). Additionally, the subterminal element is distally drawn out into the fixed finger of the chela (digitus fixus), which is about twice as long as the main part of the subterminal element is wide and about one third as wide as the latter. The distal element is shorter than the subterminal element, spine-like in shape, and arises from the distal end of the subterminal element. It represents the movable finger of the chela (digitus mobilis) and is slightly longer and wider than the fixed finger.

Details of the proximal arrangement of the basal elements of the chelicerae and the basipods (“coxae”) of appendages

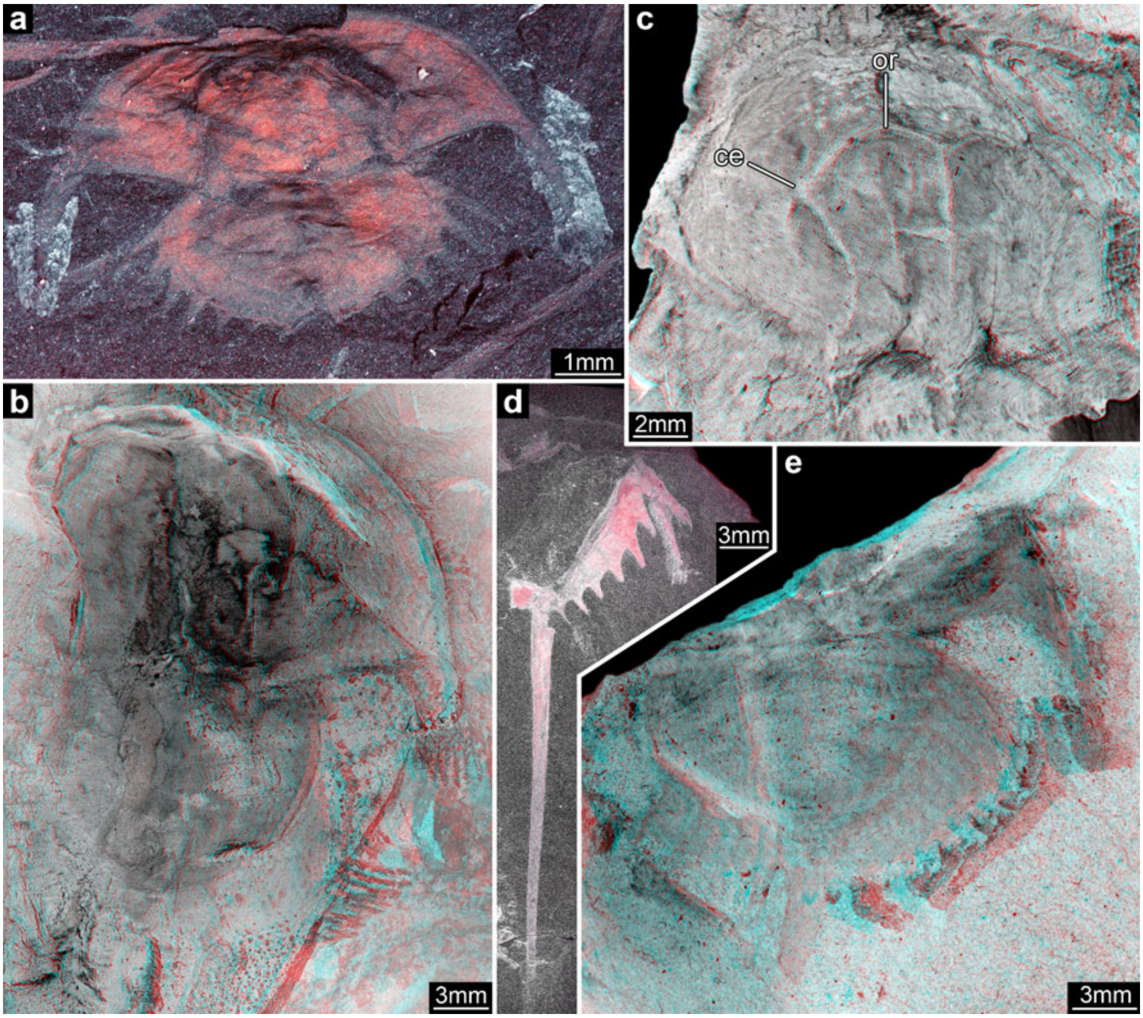

Fig. 3 General habitus of *Euproops* sp. from the Piesberg quarry. **a**, **d** Fluorescence images. **b**, **c**, **e** Color inverted red–cyan stereo images (please use stereo glasses). **a** MAS Pal. 470; stage 4, specimen showing general body outline. **b** MAS Pal. 229; stage 7, specimen showing relief of prosoma and opisthosoma; image depth-inverted to replicate original body shape. **c** MAS Pal. 517; stage 6, details of the prosomal shield; ophthalmic ridges and eyes well preserved. **d** MAS Pal. 533; stage 5, fragmentary opisthosoma with long telson spine; image flipped horizontally. **e** MAS Pal. 523–19; stage 7, opisthosoma with well-preserved epimera forming an entire flange ("Randsaum"). *ce* compound eye, *or* ophthalmic ridge

2–7 around the presumed mouth opening are also preserved (Fig. 6a and b). The position of the chelicerae can be clearly seen anteriorly. Between the basipods of the succeeding limbs there are obvious infillings of sediment, and the distinction between these infillings and the true appendage structures becomes apparent only under stereo view (Fig. 6a) and by strict tracing and counting of alternating structures (Fig. 6b). The exact position of the chilaria (seventh appendages) is also readily apparent. These appendages appear to be functionally fully integrated into the feeding apparatus here, as in extant species.

The basipods of appendages five and six each bear two stout triangular spines (Fig. 6b). Although the shape and the arrangement is unusual compared to corresponding structures in extant xiphosurans, most likely the actual morphology is represented here as this pattern is present on two successive appendages. No movable endites, as seen in extant species, have been preserved. The same specimen also has a deep invagination separating the basipods (Fig. 6a and b), which could indicate that the mouth opening was located between the limb bases, just like in extant xiphosurans. Opisthosomal appendages are not preserved in the material, and it is unclear if ontogenetic changes occur in the prosomal limbs.

Discussion

Newly observed morphological features

The new features observed on the described material enhance our knowledge of the morphology of

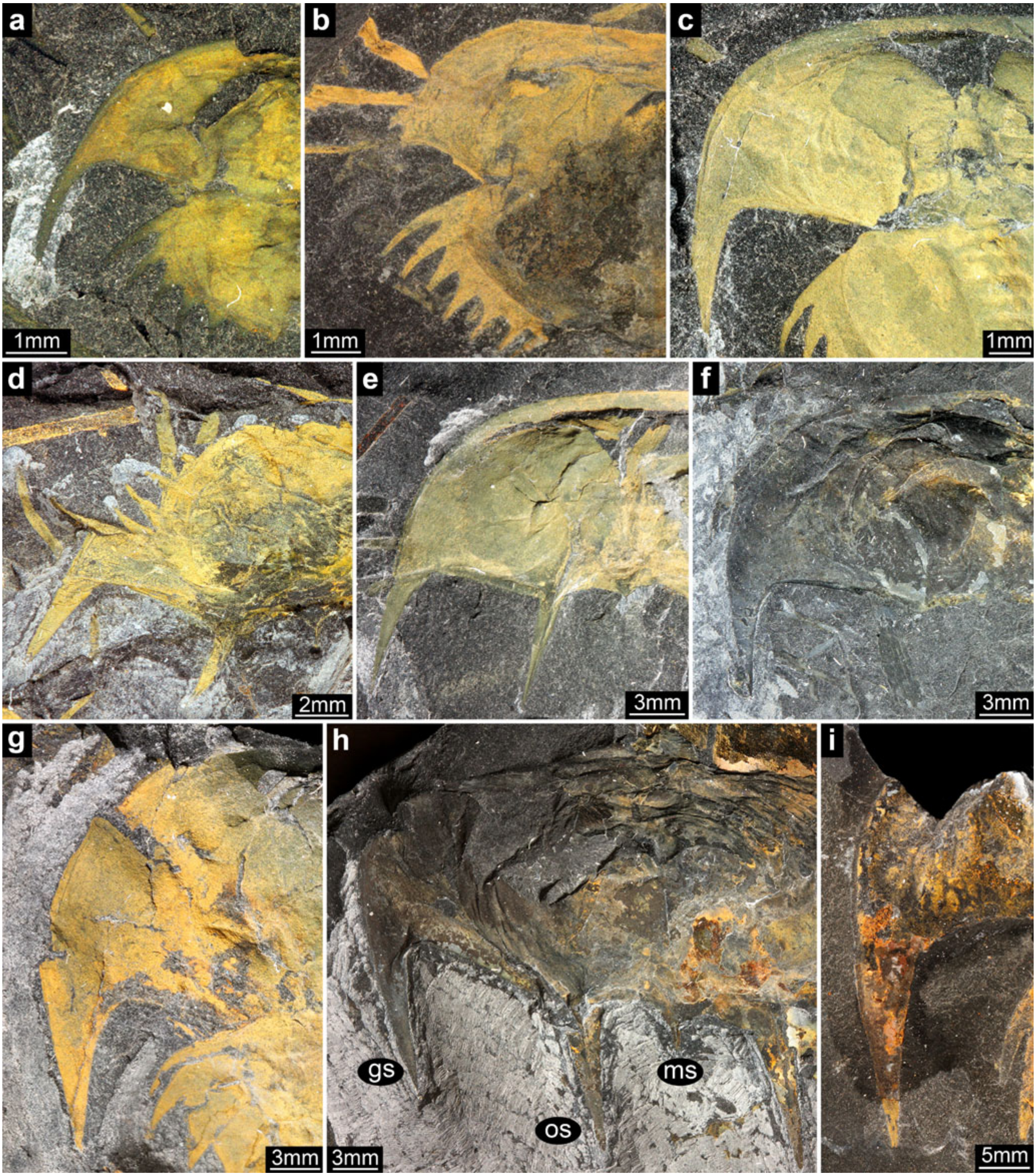

Fig. 4 Spines on the posterior end of the prosomal shield in different growth stages. All images under polarized light. **a**, **d**, **g** flipped horizontally. **a** MAS Pal. 334; stage 2. **b** MAS Pal. 534; stage 3. **c** MAS Pal. 470; stage 4. **d** MAS Pal. 510; stage 5. **e** MAS Pal. 482; stage 6. **f** MAS Pal. 402; stage 7. **g** MAS Pal. 484; stage 8. **h** MAS Pal. 337; stage 9; with full set of spines (genal, ophthalmic, median). **i** MAS Pal. 304; stage 10. *gs* genal spine, *os* ophthalmic spine, *ms* median spine

representatives of *Euproops*. We have found some new morphological details, which do not contain ontogenetic information as they were only preserved on few specimens; these aspects will be discussed here. Other aspects changing during development will be discussed further below.

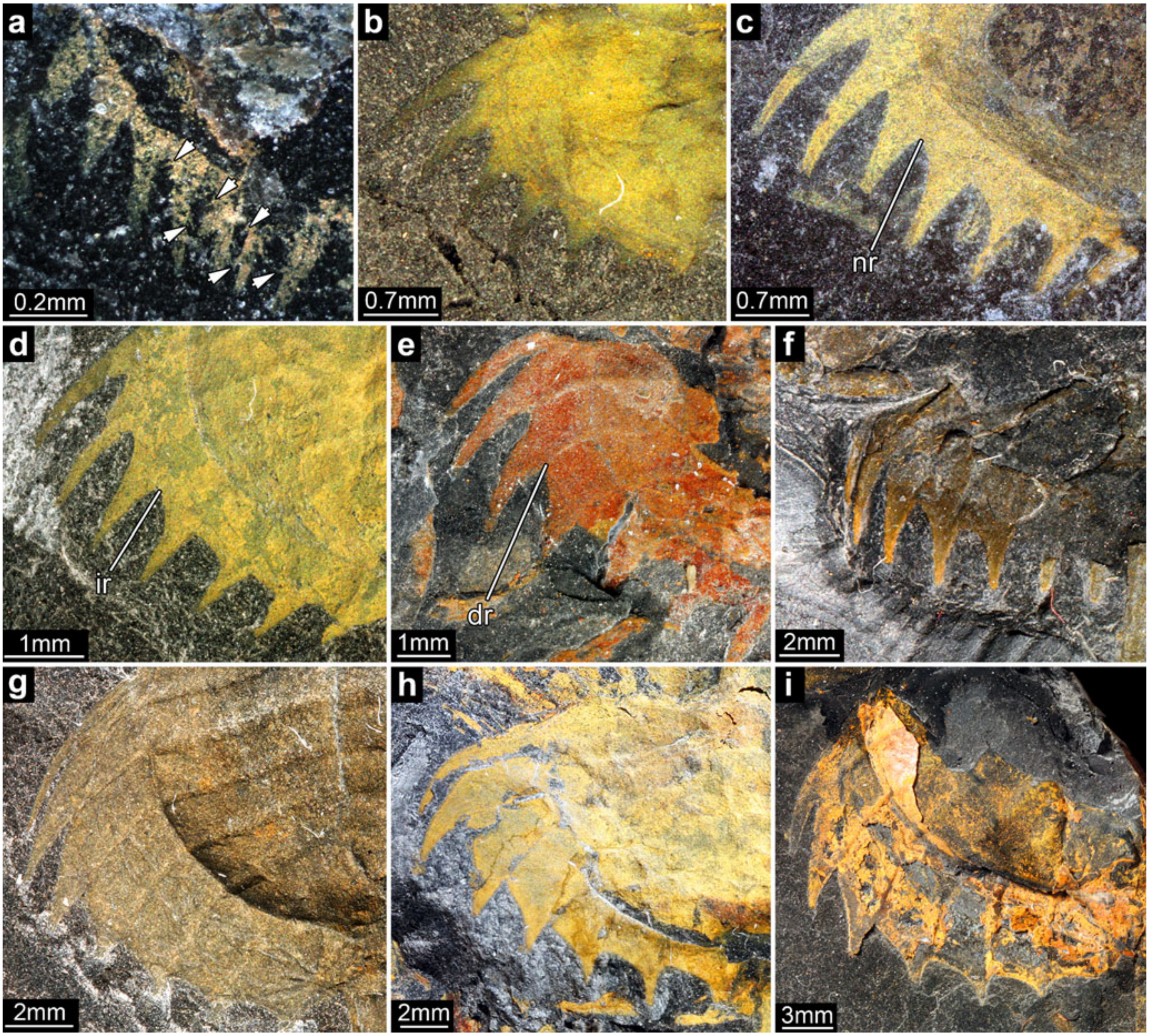

Fig. 5 Ontogenetic change of epimera. All images under polarized light. **a**, **b**, **d**, **g**, **h** flipped horizontally. **a** MAS Pal. 482B; stage 1, epimera spine-like, equipped with spinules (*arrows*). **b** MAS Pal. 334; stage 2. **c** MAS Pal. 534; stage 3, no ridges separate the epimera. **d** MAS Pal. 470; stage 4, initial ridges developed, separating the epimera. **e** MAS Pal. 225; stage 5, epimera separated by well-developed ridges. **f** MAS Pal. 231; stage 6. **g** MAS Pal. 523–19; stage 7. **h** MAS Pal. 484; stage 8. **i** MAS Pal. 304; stage 10. *dr* developed ridges, *ir* initial ridges, *nr* no ridges

The material from the Piesberg quarry is exceptionally preserved, as it includes appendage parts. Schultka (2000) has already shown that distal parts of appendages are preserved in the xiphosurans from the Piesberg, and we also have found similar structures in our material, which we could describe to a certain degree of detail (Fig. 6c–e). However, as no proximal elements are preserved of those appendages of which the distal parts are present, we cannot state with certainty of how many elements these limbs are composed. Fisher (1977) indicated that the appendages of *E. danae* comprise seven elements while extant xiphosurans have only six.

Proximal limb parts have not been described from any other Carboniferous xiphosuran before (besides a short mention of Fisher (1979), but without illustration). We found a very complete set of the proximal parts of the prosomal appendages on one specimen in the material from the Piesberg quarry (Fig. 6a and b). While Fisher (1979) claimed the arrangement of limb bases in *E. danae* to be

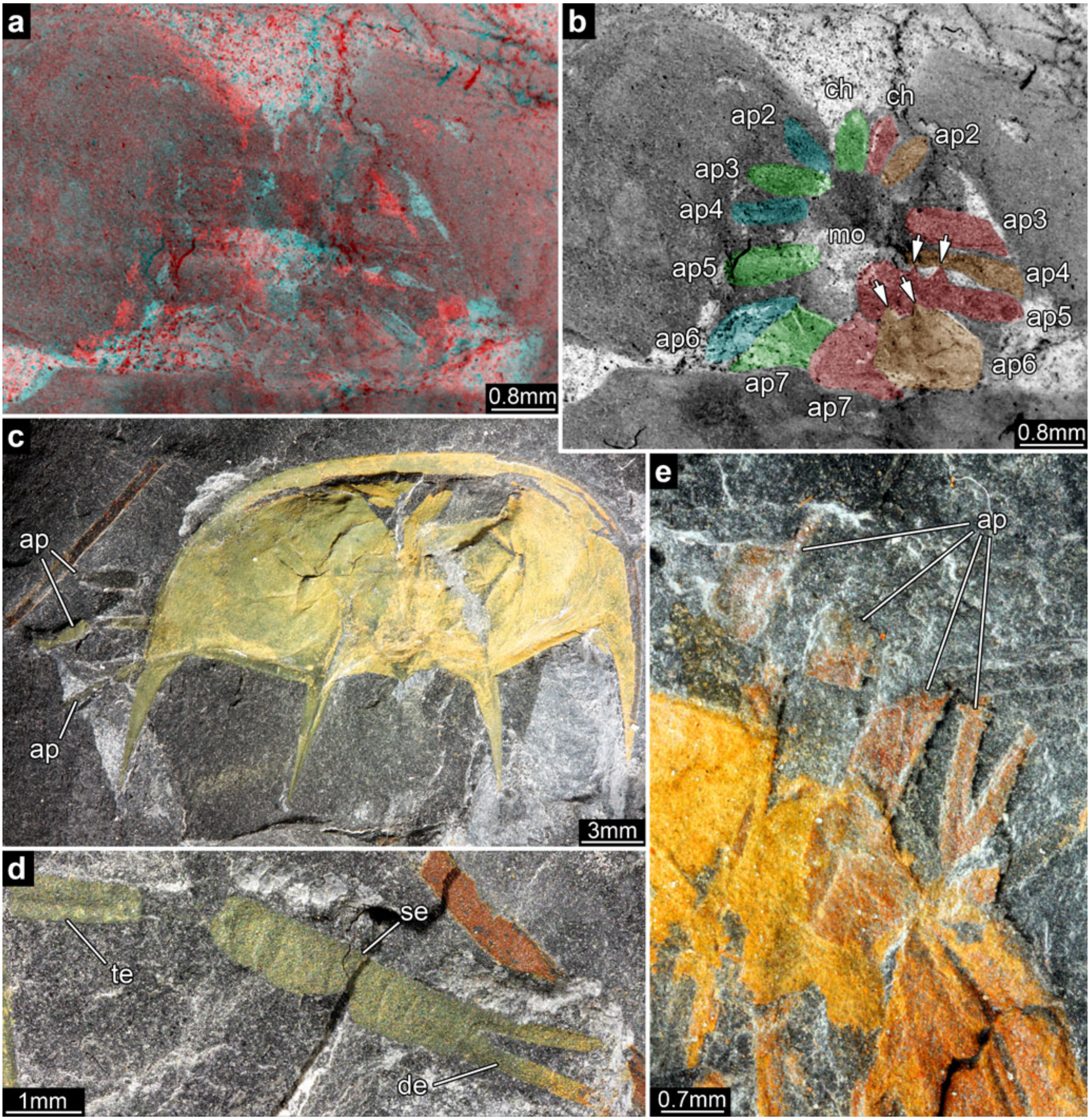

Fig. 6 Details of the appendages. **a**–**b** MAS Pal. 470; stage 4. **a** Stereo image of the ventral antero-median area. The proximal elements of all prosomal appendages are preserved (see explanation in **b**). **b** Explanatory image of **a**. Appendages of the *left series* marked in *green* and *cyan*, appendages of the *right series* marked in *red* and *orange*. *Arrows* mark preserved spines on the basipods ("coxae"). **c**–**d** MAS Pal. 482A; stage 6. **c** Overview. Three appendages protruding from under the prosomal shield. **d** Close up on the second appendage from **c**, but on the counterpart. Three elements are apparent: the third last element, the subterminal element which is drawn out into the fixed finger of a chela (digitus fixus), and the distal element forming the movable finger of the chela (digitus mobilis). **e** MAS Pal. 225; stage 5. Four appendages protruding from under the prosomal shield. Most anterior one (right) preserved with chela. *ap* appendage, *ch* chelicera, *de* distal element, *mo* mouth, *se* sub-terminal element, *te* third last element

different to that of limulids, with legs inserting in a more circular pattern to allow the animal to grip around fern branches more easily, the arrangement revealed in this material is very similar to that of extant xiphosurans (cf. Fig. 10c); even astonishing details like basipodal spines and the mouth opening are preserved and clearly visible three dimensionally (Fig. 6a and b). Surprisingly, xiphosuran fossils of this kind, in which proximal limb parts are preserved, may not be that unusual. For example, a specimen of “*Paleolimulus*” *longispinus* Schram, 1979 (apostrophes due to uncertain assignment) from the Carboniferous Bear Gulch Limestone of North America yields even greater detail, as some appendages appear to be preserved along the entire length, including the distal chelae (cf. Fig. 10a and b).

Enrollment

It is generally assumed that representatives of *Euproops* were able to enroll by folding the opisthosoma under the prosoma, in a manner partly comparable to trilobites (Fisher 1977; Waterston 1985; Anderson 1994). Fisher (1977) reported that about 20 % of the specimens he studied were partly or entirely enrolled. Among our material are three specimens preserved in a way that can be interpreted as more or less fully enrolled (Fig. 7a–c), and one as partly enrolled (Fig. 7d). Yet, Racheboeuf et al. (2002) stated that enrollment is poorly studied in *Euproops* and several biomechanical problems remain with this assumed behavior.

Results of the present study suggest a major functional challenge to achieving complete enrollment, namely the “storage” of the appendages. The prosomal limbs are relatively long and do not appear to be extremely thin (Fig. 6). During enrollment, these have to be folded and accommodated within the space enclosed by the prosoma and opisthosoma. Models for the exact mode of enrollment differ between Fisher (1977) and Anderson (1994). According to Fisher, the opisthosoma nests into the prosomal shield, i.e., the epimera do not protrude beyond the margin. The preservation of one of our specimens can be explained by this model (Fig. 7a). In Anderson’s reconstruction, the opisthosoma folds under the prosoma with the epimera extending around the margin. The posture of two of our specimens could be explained by this model (Fig. 7b and c). There appears to be more space inside the enrolled animal in Anderson’s model than in Fisher’s, but it is still questionable whether there is sufficient volume to accommodate all appendages folded into it. Another question is why our specimens show two different types of enrollment. A possible factor may be the growth stages of the specimens. The specimen enrolled according to Fisher’s model is the largest one, corresponding to stage 9 (Fig. 7a), while the two specimens enrolled as in Anderson’s model represent growth

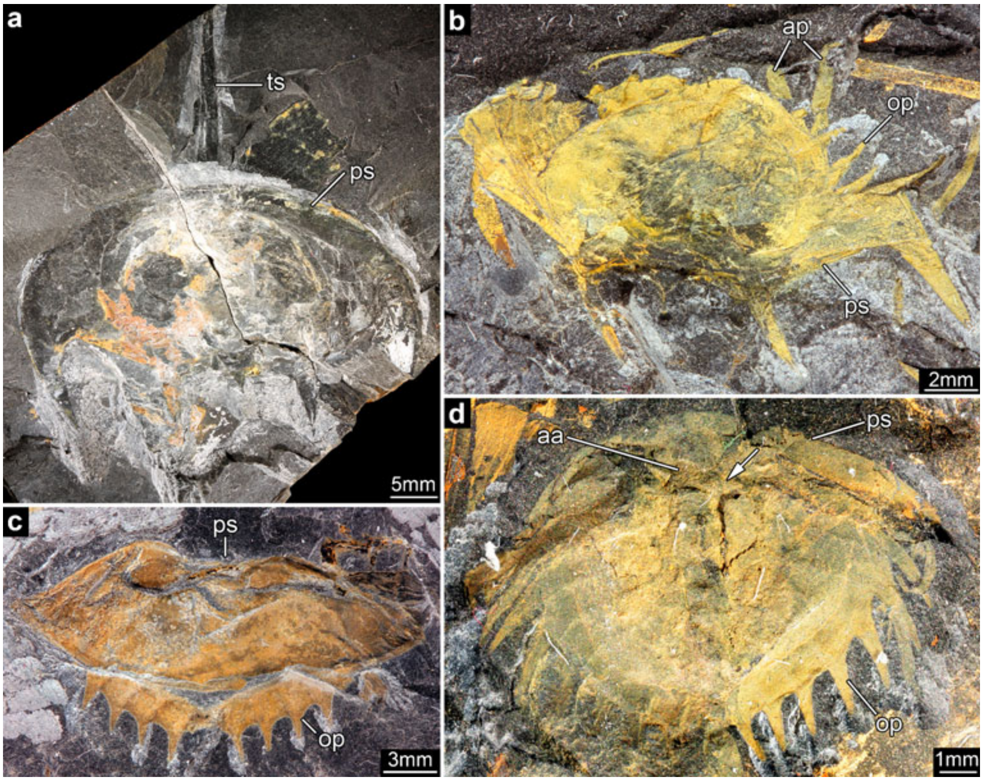

Fig. 7 Enrolled specimens. **a** MAS Pal. 523–24. Fully enrolled specimen of stage 9 preserved from dorsally. Mainly the prosomal shield is visible, but also the anteriorly deflected telson spine. **b** MAS Pal. 510A. Almost fully enrolled specimen of stage 5, also from the dorsal side. The opisthosoma can be identified based on the epimera. Also two appendages are preserved protruding from under the shield. **c** MAS Pal. 343. Almost fully enrolled specimen of stage 5 or 6 from anteriorly. **d** MAS Pal. 503A. Partly enrolled specimen of stage 4, posterior view on the prosoma, dorsal view on the opisthosoma. A structure that might be mistaken as the micro-tergite is the anterior axis of the thoracetron. It is continuous to the most anterior tergite (*arrow*) and epimeron of the thoracetron. No further structure that could represent the microtergite is apparent. *aa* anterior axis, *ap* appendage, *op* opisthosoma, *ps* prosomal shield, *ts* telson spine

stages 5, and 5 or 6, respectively (Fig. 7b and c). An assumed allometric growth resulting in a comparatively larger prosoma in more mature stages could explain this effect. However, the scatter plots (especially Fig. 2c and d) point to a rather isometric growth within our material.

A fossil xiphosuran for which enrollment has been quite convincingly demonstrated is *Alanops magnificus* Racheboeuf et al. (2002) from the Carboniferous Montceau-les-Mines Lagerstätte of France (Racheboeuf et al. 2002). The specimens are three-dimensionally preserved and retain their prosomal appendages. Compared to those of the *Euproops* material presented here, the appendages of *A. magnificus* are rather similar in principal length and diameter. The major difference between the two taxa lies in the dorso-ventral dimensions of both the prosomal shield and the thoracetron. In *A. magnificus*, both shields are highly arched and significantly more dome-shaped than the corresponding structures in our specimens of *Euproops* (our material is taphonomically more or less flattened, but still the three-dimensionality of *Euproops* can be obtained from certain Piesberg specimens as well as, e.g., from those of Mazon Creek). This creates sufficient internal volume to allow all the prosomal appendages to be folded and fully withdrawn when the opisthosoma is closed against the prosoma.

One of our specimens showing nearly complete enrollment demonstrates that the limbs can protrude from under the prosomal shield in this position (Fig. 7b). Whether this means that the two shields have to gape, or that this specimen was in the process of enrolling, remains unclear at present.

Trilobite appendages are only rarely preserved, and as a consequence, very little is known of the positioning of limbs during enrollment. Notable exceptions include enrolled specimens of *Ceraurus* and *Flexicalymene*, which were sectioned and studied by Walcott (1881; see also Whittington 1993, his Fig. 9). We do have a clear picture of limb deployment in the agnostine *Agnostus pisiformis* (Wahlenberg, 1818), a trilobite-like close relative of crustaceans (e.g., Haug et al. 2010b). In early growth stages, this species is also more closely comparable with xiphosurans than are trilobites, as enrollment involves only the head shield and the large shield on the trunk (pygidium); later in ontogeny, two intermediate tergites (those of the trunk segments) are incorporated into the process (Müller and Walossek 1987; Bruton and Nakrem 2005). In *A. pisiformis*, the limbs fit well between the highly arched shields, possibly additionally aided by the fact that the appendages are relatively shorter than those of xiphosurans. It is necessary to fold just the anterior three appendage pairs, as only these are long enough to protrude from under the head shield when extended.

Another problem concerns the region where the body needs to fold drastically during enrollment. All modern arthropods that enroll do not flex around a single joint, but at several joints of a series of consecutive segments (as most trilobites did). Each segment and hinge joint has to accommodate only a fraction of the total rotation, which is easier to achieve for the body. It is difficult to see how *A. magnificus*, with just one hinge joint, could enroll without severely compressing parts of its internal anatomy. In early developmental stages of *A. pisiformis* (lacking free trunk segments), a larger membraneous area between the two shields was definitely involved in the enrollment process (Müller and Walossek 1987). Additionally, the body of agnostines appears to have been specialized for enrollment, and it has been suggested that many, if not all, could not fully extend (Müller and Walossek 1987; Bruton and Nakrem 2005).

If enrollment was not a true behavior of living *Euproops*, how can we explain enrolled fossil specimens? First, enrolled individuals appear to be much rarer in our material than it has been proposed by Fisher (1977) for representatives from the Carboniferous Mazon Creek deposits of North America. Furthermore, enrolled specimens could represent exuviae that became folded during subsequent transport. One specimen appears slightly soft and might be interpreted as a molt (Fig. 7c), but other specimens appear much more robust and more likely represent carcasses (Fig. 7a and b). Still, they could also represent partly decayed carcasses, from which the appendages had already become detached.

Solving the issue of enrollment will demand a focused investigation and more information about the appendages. Furthermore, it is crucial to find out whether a microtergite (see below) between the prosomal shield and the thoracetron might have provided additional accommodation space for limbs.

The microtergite

The presence of a microtergite between the prosomal shield and the thoracetron seems to be widely accepted (also among most co-authors of this study), but is here questioned by some of the co-authors. A difficulty for the discussion is that possible conditions presented below might be developed only in some xiphosurans, while in others the condition could be different. In *A. magnificus*, for example, the presence of a small articulating half ring, possibly the microtergite, has been shown quite convincingly (Racheboeuf et al. 2002, but see below). Similar structures on *Euproops* are more difficult to interpret and are not present in the material at hand. A single specimen in our material is preserved in a partly enrolled position, resulting in a posterior view of the prosoma and a dorsal view of the opisthosoma (Fig. 7d). This posture should be the perfect orientation for identifying the microtergite. There is a structure that at first glance might be interpreted as a separate half ring, but it is, in fact, the most anterior part of the axis of the thoracetron. This becomes obvious as it is continuous with the adjacent tergite and epimeron of the thoracetron. Its seemingly isolated appearance is repeated by the next posterior part of the axis, yet both are in fact fused into the thoracetron (Fig. 7d).

Here, we provide an overview of those aspects of the microtergite issue that need to be resolved independently for each taxon. Arguments presented below are general in nature; they do not necessarily disprove any of the given assumptions, but point out which requirements must be fulfilled in order to show that the assumptions are correct.

Our starting point is the following assumption: The micro-tergite is often considered to be the reduced tergite of the chilarial segment, with the latter as the first opisthosomal segment (see discussion by Eldredge 1974). Therefore, the discussion of the microtergite is also partly a discussion of the chilaria.

1. *The chilaria are functionally prosomal appendages*. If we look at the ventral expression of the chilaria in both modern representatives of Xiphosura and in our specimens of *Euproops*, they are integrated into the feeding apparatus, closing the food groove posteriorly. Functionally, these appendages should therefore be considered as prosomal. This interpretation is independent of the position of the dorsal part of the chilarial segment, as dorsal and ventral tagmatisation is often decoupled (see "Discussion" section below).
2. *Is the chilarial segment part of the prosoma?* Despite their integration into the feeding apparatus, the chilaria are generally assumed to belong to the opisthosoma (see above), but what is the reason for this assumption? Scholl (1977) described the chilarial segment as being of opisthosomal origin based on his studies of the embryology of extant xiphosurans. It is widely accepted for xiphosurans that the developmental origin of a segment is of paramount importance, but this is a strictly in-group view. In crustaceans, segments can be transferred from one tagma into another throughout ontogeny, but always the affiliation of a segment to a tagma in the specific ontogenetic stage is regarded as relevant, not its developmental origin; for example, the fifth appendage pair may not be included in the head during early growth, but this limb-bearing segment clearly becomes part of the head tagma in later stages (e.g., Walossek 1993; Casanova et al. 2002). In trilobites, newly emerging segments are generated at the posterior growth zone as part of the pygidium; during ontogeny, they "move" anteriorly, become articulated and part of the thorax (Chatterton and Speyer 1997). In both examples, the fate of these segments is known, yet they are assigned to the tagma which they are currently functionally part of and not to the tagma which they have previously been part of during ontogeny. The chilaria should, for this reason, clearly be considered as part of the prosoma.

Although the chilaria are clearly positioned in the prosomal area, the dorsal part of the chilarial segment could still be opisthosomal and correspond to the assumed microtergite. This is possible as segments do not always have a straight "downwards" dorsoventral correspondence, i.e., perpendicular to the anterior-posterior axis. Examples for such oblique segment conditions can, for instance, be found in the opisthosomal segments of Opiliones (e.g., Moritz 1957). The same dorsoventral "non-correspondence" could apply to xiphosurans.

Alternatively, the tagmatic identity of dorsal and ventral segmental structures (such as legs or tergites) can be decoupled, i.e., the ventral area of the chilarial segment can be part of the prosoma, while its dorsal part is not. The most widespread case of decoupling involves the head–trunk boundary. An example are cephalocarid crustaceans, in which the fifth limb-bearing segment is included into the head dorsally, yet the appendage resembles the trunk limbs, i.e., it is functionally coupled to the feeding apparatus of the trunk (Olesen et al. 2011). In many fossil arthropods, the head is strictly defined as a tagma dorsally through the head shield, but ventrally certain appendages are not differentiated from the trunk appendages (e.g., Hesselbo 1992; Waloszek 2003; Haug et al. (in press)). Also, decoupling the other way round can be found among crustaceans. In mystacocarids, the first trunk limb is differentiated as a maxilliped being tightly coupled to the head feeding apparatus, yet the limb is not included into the head dorsally (as it is in the closely related Copepoda; e.g., Haug et al. 2011b). Such a case of decoupling could also be the case for (certain?) xiphosurans concerning the chilarial segment.

The supposed microtergite may or may not be the tergite of the chilarium segment. Independent of this aspect, the chilaria themselves are functionally part of the prosoma.
3. *Is there a "need" for an extra tergite?* This seemingly strange question refers to another interesting in-group view for chelicerates, namely a fixed number of prosomal and opisthosomal segments. The prosoma is generally considered to comprise six limb-bearing segments (but see above), while in Xiphosura the opisthosoma should have eleven segments. In most xiphosurans, however, only ten opisthosomal segments can be reliably identified. As a consequence, a reduced segment was "needed" between the prosoma and the opisthosoma corresponding to the microtergite, or the loss of a tergite has to be assumed (Selden and Siveter 1987; Anderson and Selden 1997). In other arthropod taxa, a "missing" tergite in the trunk is usually associated with a segment that remained unreleased from the posterior growth zone. Also plausible is the assumption that the "missing" tergite could be interpreted as either fused to the prosomal shield or the thoracetron.
4. *Is the microtergite necessarily a tergite?* This question is relatively complicated to answer. In fossil xiphosurans, it is

often not easy to differentiate between membraneous and truly sclerotic areas. A good candidate for indeed having a microtergite is *A. magnificus* (see above). Yet, here the supposed microtergite might also represent nonsclerotized arthrodial membrane smoothened due to stretching.

Even if the structure can be shown to be truly sclerotized, it still does not necessarily have to represent a tergite. Membraneous areas of arthropods are capable of forming sclerites secondarily. In this aspect, an assumed microtergite reported in eurypterids (Dunlop and Webster 1999, their Figs. 2 and 3) is of importance. This supposed microtergite, i.e., a sclerotization behind the prosomal shield, lies on a valley fold according to the authors' figures. Tergites, however, usually lie on mountain folds and the eurypterid structure may instead be a sclerotized valley fold. This interpretation could also apply to the supposed microtergite in xiphosurans.

Observed ontogeny and possible consequences for systematics

The described specimens from the Piesberg quarry provide useful insight into developmental patterns of *Euproops* species. The most significant observation is the change in shape of the epimera of the opisthosomal segments (Figs. 5 and 8). Schultka (2000) concluded that early ontogenetic stages do not possess a flange, which is true according to his terminology (although not totally clear from his reconstruction, cf. Fig. 9a). However, we think that it is more precise to state that the epimera at the earlier stages are spine-like and develop a broadened base in later stages.

The observation that the shape of the epimera changes so drastically during ontogeny has a major impact on our understanding of *Euproops* taxonomy and systematics (as already indicated by Schultka 2000). Comparing the epimera of the opisthosoma of other named *Euproops* species reveals that their shape appears to correspond to different ontogenetic stages of the material described herein.

For example, the reconstruction of *Euproops kilmersdonensis* Ambrose and Romano (1972) appears to correspond to a juvenile of the species from the Piesberg quarry, at about growth stage 5–6 (Fig. 9b; Ambrose and Romano 1972). *E. kilmersdonensis* has been synonymised with *E. danae* by Anderson (1994). Interestingly, Anderson's

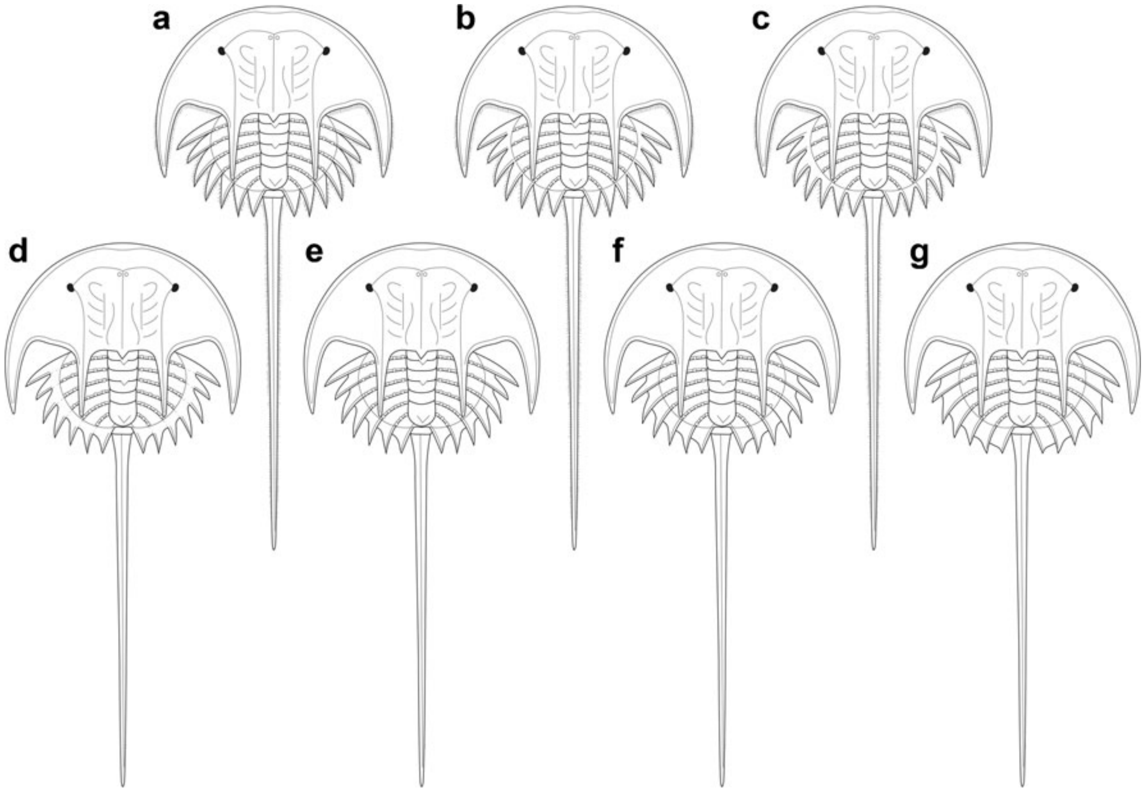

Fig. 8 Schematic drawings of ontogenetic series from growth stage 1 (**a**) to growth stage 7 (**g**) of *Euproops* sp. from the Piesberg quarry. Besides isometric growth, no further morphological changes were observed in stages 8–10. All growth stages depicted to the same size to emphasize the ontogenetic changes. The main changes appear on the opisthosoma, with the first separate epimera forming a continuous, progressively broadening flange with pronounced ridges. Stages 1–3 bear hairs or spinules on the epimera and on the posterior rim of the prosoma (partly based on observations of Schultka 2000)

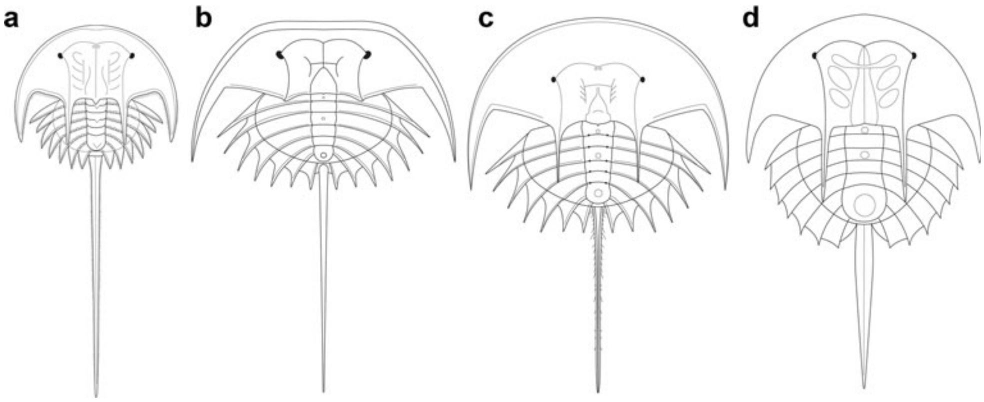

Fig. 9 Different reconstructions of representatives of *Euproops*. Redrawn and modified after Schultka (2000) for **a**, Ambrose and Romano (1972) for **b**, Anderson (1994) for **c**, and Filipiak and Krawczynski (1996) for **d**. **a** *Euproops* sp. from the Piesberg quarry, early ontogenetic stage. **b** *E. kilmersdonensis* Ambrose and Romano (1972). **c** *E. danae* (Meek and Worthen, 1865). **d** *E. rotundatus* (Prestwich, 1840)

reconstructions of *E. danae* also resemble the juvenile morphology of the material described here (Fig. 9c). *E. rotundatus* generally seems to have a very mature epimeral morphology (Fig. 9d; e.g., Filipiak and Krawczynski 1996), and the original specimens of *E. bifidus* appear to correspond to an advanced developmental stage as well (Siegfried 1972).

These similarities could indicate that some of the specimens used to define new *Euproops* species actually represent juveniles, with the further implication that supposed diagnostic features might be ontogenetic in origin. For most of these species, we have no early growth stages available to compare to the sequence elucidated herein. Fisher (1977) described allometric growth of the spines of the prosomal shield in *E. danae* from Mazon Creek, a pattern that could not be observed in our Piesberg material. Unfortunately, he did not attempt to reconstruct an entire sequence that also highlighted morphological change in other structures, including the epimera (of most interest for our case). However, the recognition of different growth patterns of prosomal shield

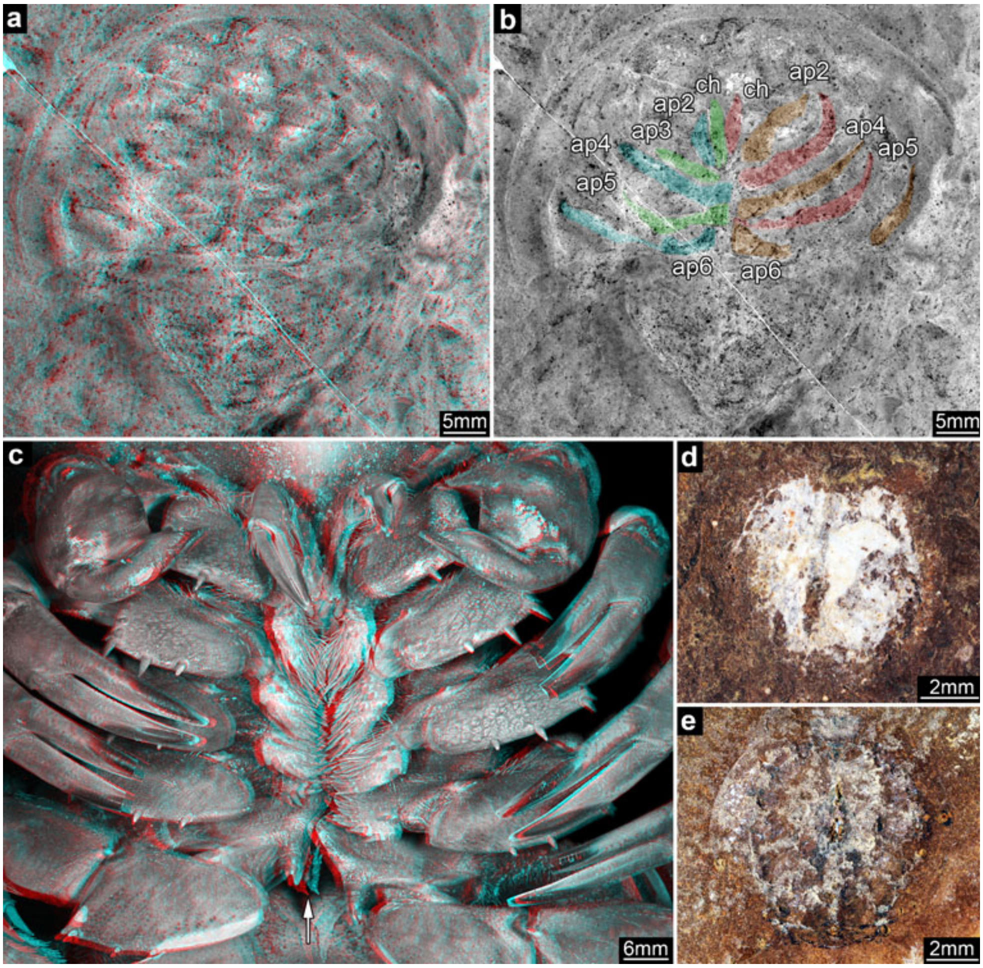

Fig. 10 Comparative xiphosuran material. **a**, **b** ROM 61508. "*Paleolimulus*" *longispinus* Schram, 1979 from the Carboniferous Bear Gulch formation, North America. **a** Red–cyan stereo image (cf. Fig. 6a); for explanations see **b**. **b** Explanatory image for **a** (cf. Fig. 6b). **c** YPM IP 030358. Red–cyan stereo image of *Limulus polyphemus* (Linnaeus, 1758); ventral view on median prosomal area; *arrow* points to one chilarium. **d**, **e** Supposed small specimens of *E. danae* (Meek and Worthen, 1865) from the Carboniferous Mazon Creek deposits of North America. **d** ROM 61554. **e** ROM 61549. *ap* appendage, *ch* chelicera

spines in specimens from the Piesberg and Mazon Creek may on its own provide a well-founded differential diagnostic character supporting their separate species status.

Different growth patterns may also indicate that various species within *Euproops* have evolved through heterochrony. This would in turn require a reexamination of many diagnostic features, as differential diagnoses should then be compared to corresponding juvenile stages of the most closely related species.

This entire issue surely reaches beyond *Euproops*. We can go at least one step further and compare the shape of the epimera of the different stages of *Euproops* sp. presented here with the epimera in representatives of *Bellinurus*. In *Bellinurus* species, different morphologies have been reconstructed, for example, with jointed spine-like epimera (cf. Filipiak and Krawczynski 1996), or with epimera comparable to those in the early stages of *Euproops* sp. (Schultka 1994). This again may be an indication that heterochronic evolution has affected either the one or the other of these lineages.

Ideas on a possible solution: the hapantotype concept

For reliably distinguishing the different species of *Euproops*, it will be necessary to establish ontogenetic series for each, wherever possible. Currently, the general nomenclature is still fixed to the designation of a single holotype specimen. However, as we demonstrate here, these holotypes do not necessarily represent corresponding ontogenetic stages, making it difficult, if not impossible, to utilize differential diagnoses within the taxon.

Yet, there is a taxonomic concept available allowing the treatment of several life stages as a single holotype. The *hapantotype* concept is generally in use for protists (e.g., Evenhuis 2008; Hawksworth 2010), but Williams (1980) has argued for its application to Cnidaria and later expanded his argument to encompass other groups, including arthropods (Williams 1986). Until now, the idea of establishing hapantotypes for fossils has not been discussed in detail (originally, even fossil protists were excluded from the hapantotype concept). Despite the efforts of Williams (1980, 1986), the nomenclatural rules did not change, and the hapantotype can still be only assigned for extant protists. The situation herein presented demonstrates that there is a strong case for reconsidering such a type concept for other taxa, both living and fossil.

Outlook

In summary, the ontogenetic sequence of *Euproops* material we describe here demonstrates the necessity of investigating the growth stages of supposedly different species of *Euproops* before attempting to resolve taxonomy, phylogeny, or evolution of this taxon. Our study has already yielded important results in this context, including a clear documentation of the ontogenetic change of the epimera in the material from the Piesberg.

With this, we declare our intention to provide ontogenetic sequence data similar to those presented here in upcoming studies on different representatives of *Euproops* and other xiphosuran species. The study range will cover early Palaeozoic (e.g., Fezouata biota, Morocco), late Palaeozoic (e.g., Bear Gulch, Fig. 10a and b; Mazon Creek, Fig. 10d and e, and additional Piesberg material), Mesozoic (e.g., Solnhofen limestones, Germany) as well as extant taxa (Fig. 10c), for providing a first framework for a palaeo-evo-devo approach on xiphosuran evolution.

Acknowledgments Our acknowledgement for the permission to search for fossils in the Piesberg quarry goes to CEMEX Kies and Splitt GmbH, Steinbruch Piesberg, Osnabrück, Germany. Many thanks to the private collectors that are active at the Piesberg quarry, providing new specimens to the collection of the Museum am Schölerberg (MAS), Osnabrück. Special thanks to Michael Sowiak (Glandorf, Germany) who drastically increased the number of *Euproops* specimens from the Piesberg quarry by looking systematically for the layers yielding most specimens. He donated many specimens to the MAS. Jean-Bernard Caron, Janet Waddington, Peter Fenton, all Royal Ontario Museum, Toronto, as well as Susan Butts and Jessica Utrup, Yale Peabody Museum, New Haven, kindly provided us access to comparative material. Furthermore, we would like to thank Dieter Waloszek, Ulm, for valuable discussions, especially about image enhancement methods. Two anonymous reviewers made helpful comments to an earlier draft of the manuscript. We also thank all people involved in programming free software that was used during the course of this study, such as GIMP, Inkscape, OpenOffice, and Microsoft Image Composite Editor. JTH is currently kindly funded by the Alexander von Humboldt-Foundation with a Feodor Lynen research fellowship for postdoctoral researchers. PVR was funded by a Special Research Fund (BOF) scholarship from Ghent University. PF was funded by the Forskningsrådet for Natur og Univers (FNU; grant no. 272-06-0534), the EAC Foundation, and Knud Højgaard. CH, PVR and JTH also express their thanks to their host at the Yale University and the Yale Peabody Museum, Derek E. G. Briggs, for his support.

References

Ambrose T, Romano M (1972) New Upper Carboniferous Chelicerata (Arthropoda) from Somerset England. Palaeontology 15:569–578

Anderson LI (1994) Xiphosurans from the Westphalian D of the Radstock Basin, Somerset Coalfield, the South Wales Coalfield and Mazon Creek, Illinois. Proc Geol Assoc 105:265–275

Anderson LI, Selden PA (1997) Opisthosomal fusion and phylogeny of Palaeozoic Xiphosura. Lethaia 30:19–31

Ax P (2000) Multicellular animals: the phylogenetic system of the Metazoa. Springer, Berlin

Bengtson S (2000) Teasing fossils out of shales with cameras and computers. Palaeontol Electron 3(1):14, art. 4

Brauckmann C (1982) Der Schwertschwanz *Euproops* (Xiphosurida, Limulina, Euproopaceae) aus dem Oberkarbon des Piesbergs bei Osnabrück. Osnabr Naturwiss Mitt 9:17–26

Bruton DL, Nakrem HA (2005) Enrolment in a Middle Ordovician agnostoid trilobite. Acta Palaeontol Pol 50:441–448

Casanova B, De Jong L, Moreau X (2002) Carapace and mandibles ontogeny in the Dendrobranchiata (Decapoda), Euphausiacea, and Mysidacea (Crustacea): a phylogenetic interest. Can J Zool 80:296–306

Chatterton BDE, Speyer SE (1997) Ontogeny. In: Moore RC (ed) Treatise on invertebrate paleontology. Part O, revised. Arthropoda 1, Trilobita. Geological Society of America and University of Kansas Press, Boulder, CO, pp 173–247

Dunlop JA, Webster M (1999) Fossil evidence, terrestrialization and arachnid phylogeny. J Arachnol 27:86–93

Dunlop JA, Brauckmann C, Steur H (2008) A Late Carboniferous fossil scorpion from the Piesberg, near Osnabrück, Germany. Fossil Rec 11:25–32

Dunlop JA, Penney D, Jekel D (2010) A summary list of fossil spiders and their relatives. In: Platnick NI (ed) The world spider catalog, version 11.0 American Museum of Natural History. Available online at http://research.amnh.org/entomology/spiders/catalog/index.html. Accessed 01 March 2012.

Eldredge N (1974) Revision of the suborder Synziphosurina (Chelicerata, Merostomata), with remarks on merostome phylogeny. Am Mus Novit 2543:1–41

Evenhuis NL (2008) A compendium of zoological type nomenclature: a reference source. Bish Mus Tech Rep 41:1–23

Filipiak P, Krawczynski W (1996) Westphalian xiphosurans (Chelicerata) from the Upper Silesia Coal Basin of Sosnowiec, Poland. Acta Palaeontol Pol 41:413–425

Fisher DC (1977) Functional significance of spines in the Pennsylvanian horseshoe crab *Euproops danae*. Paleobiology 3:175–195

Fisher DC (1979) Evidence for subaerial activity of *Euproops danae* (Merostomata, Xiphosurida). In: Nitecki MH (ed) Mazon creek fossils. Academic, New York, pp 379–447

Haug JT, Maas A, Haug C, Waloszek D (in press) Chapter 2. Evolution of crustacean appendages. In: Watling L, Thiel M (eds) Vol. 1. Functional morphology and diversity of the Crustacea. The natural history of the Crustacea. Oxford University Press

Haug C, Haug JT, Waloszek D, Maas A, Frattigiani R, Liebau S (2009) New methods to document fossils from lithographic limestones of southern Germany and Lebanon. Palaeontol Electron 12(3):12, 6T

Haug JT, Haug C, Maas A, Kutschera V, Waloszek D (2010a) Evolution of mantis shrimps (Stomatopoda, Malacostraca) in the light of new Mesozoic fossils. BMC Evol Biol 10:17, art. 290

Haug JT, Maas A, Waloszek D (2010b) †*Henningsmoenicaris scutula*, †*Sandtorpia vestrogothiensis* gen. et sp. nov. and heterochronic events in early crustacean evolution. Earth Environ Sci Trans R Soc Edinb 100:311–350

Haug JT, Waloszek D, Haug C, Maas A (2010c) High-level phylogenetic analysis using developmental sequences: the Cambrian †*Martinssonia elongata*, †*Musacaris gerdgeyeri* gen. et sp. nov. and their position in early crustacean evolution. Arthropod Struct Dev 39:154–173

Haug JT, Haug C, Kutschera V, Mayer G, Maas A, Liebau S, Castellani C, Wolfram U, Clarkson ENK, Waloszek D (2011a) Autofluorescence imaging, an excellent tool for comparative morphology. J Microsc 244:259–272

Haug JT, Olesen J, Maas A, Waloszek D (2011b) External morphology and post-embryonic development of *Derocheilocaris remanei* (Mystacocarida) revisited, with a comparison to the Cambrian taxon *Skara*. J Crustac Biol 31:668–692

Haug JT, Waloszek D, Maas A, Liu Y, Haug C (2012b) Functional morphology, ontogeny and evolution of mantis shrimp-like predators in the Cambrian. Palaeontology 55:369–399

Hawksworth DL (2010) Terms used in Bionomenclature. The naming of organisms (and plant communities). Global Biodiversity Information Facility, Copenhagen. Available online at http://links.gbif.org/gbif_terms_nomenclature_guide_en_v1.pdf. Accessed 01 March 2012

Hennig W (1966) Phylogenetic systematics. University of Illinois Press, Urbana

Hesselbo SP (1992) Aglaspidida (Arthropoda) from the Upper Cambrian of Wisconsin. J Paleontol 66:885–923

Horner JR, Goodwin MB (2009) Extreme cranial ontogeny in the Upper Cretaceous dinosaur *Pachycephalosaurus*. PLoS One 4 (10):11, art. e7626

Kerp H, Bomfleur B (2011) Photography of plant fossils—new techniques, old tricks. Rev Palaeobot Palynol 166:117–151

Moritz M (1957) Zur Embryonalentwicklung der Phalangiiden (Opiliones, Palpatores) unter besonderer Berücksichtigung der äußeren Morphologie, der Bildung des Mitteldarmes und der Genitalanlage. Zool Jahrb Abt Anat Ontog Tiere 76:331–370

Müller KJ, Walossek D (1987) Morphology, ontogeny, and life habit of *Agnostus pisiformis* from the Upper Cambrian of Sweden. Fossils Strata 19:1–124

Olesen J, Haug JT, Maas A, Waloszek D (2011) External morphology of *Lightiella monniotae* (Crustacea, Cephalocarida) in the light of Cambrian 'Orsten' crustaceans. Arthropod Struct Dev 40:449–478

Raasch GO (1939) Cambrian Merostomata. Spec Pap Geol Soc Am 19:1–146

Racheboeuf PR, Vannier J, Anderson LI (2002) A new three-dimensionally preserved xiphosuran chelicerate from the Montceau-les-Mines lagerstätte (Carboniferous, France). Palaeontology 45:125–147

Raw F (1957) Origin of chelicerates. J Paleontol 31:139–192

Scannella JB, Horner JR (2010) *Torosaurus* Marsh 1891 is *Triceratops* Marsh 1889 (Ceratopsidae: Chasmosaurinae): synonymy through ontogeny. J Vertebr Paleontol 30:1157–1168

Schaarschmidt F (1973) Pflanzenfossilien in ungewöhnlichem Licht. Nat Mus 103:247–253

Scholl G (1977) Beiträge zur Embryonalentwicklung von *Limulus polyphemus* L. (Chelicerata, Xiphosura). Zoomorphologie 86:99–154

Scholtz G, Edgecombe GD (2005) Heads, Hox and the phylogenetic position of trilobites. In: Koenemann S, Jenner RA (eds) Crustacea and arthropod relationships. Crustacean issues 16. CRC Press, Boca Raton, pp 139–165

Schultka S (1994) *Bellinurus* cf. *truemanii* (Merostomata) aus dem tiefen Oberkarbon (Namur B/C) von Fröndenberg (Nordrhein-Westfalen, Deutschland). Paläontol Z 68:339–349

Schultka S (2000) Zur Palökologie der Euproopiden im Nordwestdeutschen Oberkarbon. Mitt Mus Naturwiss Berl Geowiss R 3:87–98

Selden PA, Siveter DJ (1987) The origin of limuloids. Lethaia 20:383–392

Siegfried P (1972) Ein Schwertschwanz (Merostomata, Xiphosurida) aus dem Oberkarbon von Ibbenbüren/Westf. Paläontol Z 46:180–185

Størmer L (1944) On the relationships and phylogeny of fossil and recent Arachnomorpha. A comparative study on Arachnida, Xiphosura, Eurypterida, Trilobita and other fossil Arthropoda. Skr utg Nor Vidensk-Akad Oslo, I. Mat-Naturvidensk Kl 5:1–158

Størmer L (1955) Merostomata. In: Moore RC (ed) Treatise on invertebrate paleontology. Part P. Arthropoda 2. Geological Society of America and University of Kansas Press, Boulder, CO, pp 4–41

Van Roy P (2006) An aglaspidid arthropod from the Upper Ordovician of Morocco with remarks on the affinities and limitations of Aglaspidida. Trans R Soc Edinb Earth Sci 96:327–350

Walcott CD (1881) The trilobite: new and old evidence relating to its organization. Bull Mus Comp Zool Harv 8:191–224

Walossek D (1993) The Upper Cambrian *Rehbachiella* and the phylogeny of Branchiopoda and Crustacea. Fossils Strata 32:1–202

Waloszek D (2003) Cambrian ‘Orsten’-type preserved arthropods and the phylogeny of Crustacea. In: Legakis A, Sfenthourakis S, Polymeni R, Thessalou-Legaki M (eds) The New panorama of animal evolution. Proceedings of the 18th International Congress of Zoology. Pensoft, Sofia, pp 69–87

Waterston CD (1985) Chelicerata from the Dinantian of Foulden, Berwickshire, Scotland. Trans R Soc Edinb Earth Sci 76:25–33

Weygoldt P, Paulus HF (1979a) Untersuchungen zur Morphologie, Taxonomie und Phylogenie der Chelicerata. I. Morphologische Untersuchungen. Z Zool Syst Evolutionsforsch 17:85–116

Weygoldt P, Paulus HF (1979b) Untersuchungen zur Morphologie. Taxonomie und Phylogenie der Chelicerata. II. Cladogramme und die Entfaltung der Chelicerata. Z Zool Syst Evolutionsforsch 17:177–200

Whittington HB (1993) Anatomy of the Ordovician trilobite *Placoparia*. Philos Trans R Soc Lond B 339:109–118

Williams RB (1980) Comment on report of the committee of typification of species of Protozoa. Bull Zool Nomencl 37:137–140

Williams RB (1986) Hapantotypes: a possible solution to some problems of parasite nomenclature. Parasitol Today 2:314–316

Wirkner CS, Richter S (2010) Evolutionary morphology of the circulatory system in Peracarida (Malacostraca; Crustacea). Cladistics 26:143–167

Zawischa D (1989) *Euproops* aus dem Oberkarbon vom Piesberg bei Osnabrück. Arbeitskr Paläontol Hann 17(3):53–56