Abnormal xiphosurids,
with possible application to Cambrian trilobites

Russell D.C. Bicknell, Stephen Pates, and Mark L. Botton

ABSTRACT

Xiphosurida comprise an archetypal arthropod group of considerable interest to both biological and palaeontological researchers. This appeal is generated by a combination of unique anatomical features, utility as modern analogues for extinct arthropod groups, and an impressive fossil record. Although xiphosurids have been extensively studied, there are few published examples of abnormal specimens. Abnormalities in xiphosurids have mostly been attributed to injuries (either self-inflicted, from mating, or predation) or teratologies (developmental and genetic malfunctions). Here we summarise all previously recorded extant xiphosurid abnormalities and describe new examples of injuries and teratologies to *Limulus polyphemus* and *Tachypleus tridentatus.* Furthermore, we present the first evidence of injured fossil xiphosurids: *Euproops danae* and *Mesolimulus walchi*. We identify two main groups of telson teratologies and document new 'U' shaped cephalothoracic injuries to the anterior cephalothoracic margins of *L. polyphemus* and *T. tridentatus*. We show 'V' and 'W' shaped injuries to *E. danae* and *M. walchi* cephalothoracic sections. A further specimen of *E. danae* is described, which likely represents plastic deformation of a recently moulted exoskeleton, rather than an abnormality *sensu stricto.* We compare injuries on extant xiphosurids to extinct Cambrian trilobite injuries to suggest that rare cephalic injuries to trilobites were incurred during soft-shelled exoskeletal stages. Reviewing xiphosurid injuries through time is a pivotal step towards understanding how Recent and extinct arthropods responded to injuries.

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INTRODUCTION

Xiphosurids have been studied extensively due to the unique biological and palaeontological features of the clade. The Atlantic horseshoe crab, *Limulus polyphemus* (Linnaeus, 1758), is the best documented extant xiphosurid, and has been the subject of detailed anatomical (Owen, 1872; Lankester, 1881; Shultz, 2001; Battelle, 2006; Bicknell et al., 2018a), biochemical (Kaplan et al., 1977), physiological (Sokoloff, 1978) and population dynamic (e.g., Botton, 1984; Brockmann, 1990; Schaller et al., 2005; Gerhart, 2007) investigations since the 1800s (van der Hoeven, 1838; Walls et al., 2002). Palaeontologists have studied xiphosurids for multiple reasons, including a fossil record that extends as far back as the lower Ordovician, 480 million years ago (Babcock et al., 2000; Van Roy et al., 2010; Briggs et al., 2012; Lamsdell, 2013; Bicknell et al., 2018a, b). Furthermore, paleontologists have been intrigued by the morphological similarities of *L. polyphemus* and fossil xiphosurids like *Yunnanolimulus luopingensis* Zhang et al., 2009 (Guanling Formation, China, Triassic; Hu et al., 2017), *Mesolimulus walchi* (Desmarest, 1822) (Solnhofen Limestone, Germany, Jurassic; Sekiguchi and Sugita, 1980; Smith and Berkson, 2005) and *Limulus darwini* Kin and Błażejowski, 2014 (Sławno Limestone, Kcynia Formation, Poland, Late Jurassic; Błażejowski, 2015). Finally, *L. polyphemus* is a useful modern analogue for exploring how extinct gnathobase-bearing arthropods consumed food, including large eurypterids (Selden, 1981; Poschmann et al., 2016), *Sidneyia inexpectans* Walcott, 1911 (Zacaï et al., 2016; Bicknell et al., 2018b; Bicknell and Paterson, 2018), and *Alacaris mirabilis* Yang et al. 2018.

Abnormalities to extinct and extant xiphosurids are poorly documented despite the extensive research into the group. Those abnormalities to extant xiphosurids that have been documented are mostly telson teratologies (Table 1) (Shuster Jr, 1982, 2009; Botton and Loveland, 1989; Shuster Jr and Sekiguchi, 2004). Injuries to female opisthosomal sections and cephalothoracic appendages have been documented and are records of injuries incurred during mating, burrowing, or other activi-ties (Brockmann, 1990; Schaller et al., 2004, 2005; Duffy et al., 2006; Shuster Jr, 2009). There is also one documented example of *Limulus polyphemus* with a substantially buckled cephalothoracic margin (Jell, 1989). No explicit evidence of abnormal extinct xiphosurids has been documented to date, although possible predatory drag-marks are known from the Karlstadt Formation, Germany (Middle Triassic) (Diedrich, 2011). The general lack of documented abnormalities suggests that either they are rare in extant and extinct xiphosurids [*sensu* Packard (1870) and Bateson (1894)] or that abnormalities are simply not noted. Here, following Gudger (1935), the second option is supported: extant and extinct xiphosurid abnormalities are undocumented, except in extreme cases. We suggest that documenting new abnormalities may extend our knowledge of recovery patterns (Shuster Jr, 1982) and help elucidate how extinct euarthropods, such as trilobites, recuperated from injuries (Bang and Bang, 1982).

Specimens of *Limulus polyphemus* and *Tachypleus tridentatus* (Leach, 1819) with abnormalities are illustrated here to document new examples thereof. Note that only juvenile and adult specimens with abnormalities are presented, as extensive research on developmental embryonic abnormalities has previously been conducted (e.g., Itow, 1985, 1986; Itow et al., 1998b). Injured specimens of *Euproops danae* (Meek and Worthen, 1865) (Francis Creek Shale, Upper Carboniferous), and *Mesolimulus walchi* (Solnhofen Limestone, Jurassic) are documented to show fossil xiphosurid injuries. The possible causes and implications of these injuries are considered. Finally, injuries to xiphosurid cephalothoraces are compared to those affecting selected Cambrian trilobites to explore the possible timing of the injuries (Babcock, 1993; Pates et al., 2017).

Abnormalities defined

To clarify the terminology used here, we highlight the three major types of abnormalities: injuries (predatory, self-inflicted and through mating), teratologies (genetic and developmental causes) and pathologies (the result of disease or parasites) (Owen, 1985). Although applied originally to trilobites, these same terms are applied here to xipho-

TABLE 1. Summary of documented Recent xiphosurids with abnormalities.

Reference and figure number (where given)	Abnormality	Species	Possible Cause
Packard (1870, figure 36). Refigured in Bateson (1894, figure 143), and Gudger (1935, no figure number)	Forked telson bifurcating at the last third of the sagittal length	*Limulus polyphemus*	Not stated
Osburn (1911, no figure number). Refigured in Gudger (1935, no figure number)	Double telson bifurcating at opisthosomal joint	*Limulus polyphemus*	Moulting
Gravier (1930, figure 1)	Forked telson bifurcating halfway sagittal length	*Tachypleus* sp.	Mechanical damaged during early development
Gudger (1935, no figure number)	Forked telson bifurcating in the last fifth of the sagittal length	*Limulus polyphemus*	Moulting
van der Meer Mohr (1935, figures 2—4)	Shortened processes, pretarsus and apotele of pushing legs	*Tachypleus gigas* (Müller, 1785)	Not stated
van der Meer Mohr (1935, figure 1)	Slit-like injury to posterior cephalothorax	*Tachypleus gigas*	Not stated
van der Meer Mohr (1941) (not figured)	Shortened processes, pretarsus and apotele of pushing legs	*Tachypleus gigas*	Predation or mating
van der Meer Mohr (1941) (not figured)	Curved telson	*Tachypleus gigas*	Predation or mating
van der Meer Mohr (1941) (not figured)	Removal and recovery of moveable spines	*Tachypleus gigas*	Predation or mating
Bursey (1977) (not figured)	Amputated legs (specific leg not stated) with thickened endocuticle	*Limulus polyphemus*	Not stated
Shuster Jr (1982, figure 14. A)	Double telson bifurcating at the opisthosomal joint	*Limulus polyphemus*	Mechanical injury
Shuster Jr (1982, figure 14. B—D)	Forked telsons. B and C bifurcate halfway along the sagittal length. D bifurcates at the distal section	*Limulus polyphemus*	Mechanical injury
Shuster Jr (1982, figure 14. E)	Enlarged axial spine	*Limulus polyphemus*	Mechanical injury
Shuster Jr (1982, figure 14. F)	Kink halfway along the telson with enlarged axial spine	*Limulus polyphemus*	Mechanical injury
Botton and Loveland (1989) (not figured)	Injured book gills, missing or short telsons	*Limulus polyphemus*	Predation by gulls, mechanical injury
Jell (1989, figure 1)	Left anterior cephalothoracic margin buckled. Left opisthosomal section with two fewer moveable spines than the right	*Limulus polyphemus*	Mechanical deformation post-moult. Rocks or waves
Brockmann (1990, figure 3)	Injured female posterior opisthosoma	*Limulus polyphemus*	Injuries from mating
Schaller et al. (2004) and Schaller et al. (2005) (not figured)	Loss of male pedipalp	*Limulus polyphemus*	Injuries from mating
Schaller et al. (2004) (not figured)	Hole through the dorsal cephalothoracic section	*Limulus polyphemus*	Predation by gulls
Duffy et al. (2006) (not figured)	Decayed lateral eyes, missing or damaged prosomal appendages	*Limulus polyphemus*	Disease, ageing, mechanical injury
Shuster Jr (2009, figure 1)	Butterfly spawning scars on female opisthosoma	*Limulus polyphemus*	Injuries from mating

surids. The cause of an abnormality cannot always be determined with complete certainty. This is especially the case for smaller examples, or injuries that have undergone many stages of recovery and therefore do not reflect the original, potentially diagnostic, shape.

Injuries. Unsuccessful predation, complications during burrowing, mating or moulting can produce injuries. Injuries are identified by cicatrisation (healing through scar formation), repair and/or substantial exoskeletal deformity. Mechanical damage (predation, burrowing, mating) produces 'V', 'W', or 'L' shapes, while injuries incurred during moulting are more often 'U' shaped, indicating a tearing of the soft-shelled exoskeleton. Injuries may undergo partial regeneration during subsequent ecdysial events. This partial regeneration can change the injury shape from 'V', 'W' or 'L' shapes to 'U' shapes, obscuring the distinction between the mechanical or moulting injuries.

Teratologies. Genetic or developmental malfunctions result in the growth of additional or unusual spines, and missing or additional segments, without evidence for cicatrisation or healing. Additional spines have also been reported from the location of a healed injury in trilobites (e.g., Pates et al., 2017, figure 4) blurring the distinction between teratologies and injuries.

Pathologies. Disease causes locally expressed atrophy and parasites force abnormal growth around the infested exoskeleton. The shape of the growth can diagnose parasites. Leibovitz and Lewbart (2003) should be considered for examples of xiphosurid pathologies, as the focuses here are injuries and teratologies.

METHODS

Two *Limulus polyphemus* specimens with injured cephalothoracic margins were collected from the Great Bay area, New Hampshire. These specimens were photographed with a Canon PowerShot SX60 HS. Additional live adult specimens with abnormalities were photographed by M. L. Botton using a Pentax K camera, during the 1980-1990 field seasons in Delaware Bay, New Jersey. The live juvenile specimen was photographed by M. L. Botton with a Fujifilm Finepix camera during the 2015 field season in Jamaica Bay, New York. The specimens from Great Bay, Delaware Bay and Jamaica Bay were not accessioned into collections as they were originally documented as points of interest, not the focus of a specific study. The collections of extant xiphosurids in the Zoological Collection of the Oxford Museum of Natural History

(OUMNH.ZC), and palaeontological collections of the Museum of Comparative Zoology (MCZ), Harvard, Field Museum (FMNH), Chicago and Royal Ontario Museum Invertebrate Palaeontology (ROMIP), Toronto, were examined for abnormalities. These fossil specimens were photographed with a Canon 500D Digital SLR camera and macro lens controlled for remote shooting with EOS Utility 2 or with a Canon PowerShot SX60 HS. Injured trilobite specimens from the South Australian Museum (SAM), Adelaide and National Museum of Natural History (USNM), Washington, DC were photographed with a Canon EOS 5D digital camera with a Canon MP-E 65 mm 1-5x macro lens and Canon EOS 6D Mark II, respectively.

RESULTS

Abnormal extant taxa

Telson teratologies. The most often reported *Limulus polyphemus* abnormalities are to the telson: 5% of males and 3% of females in the Delaware Bay spawning population have abnormal telsons (Botton and Loveland, 1989). Excluding short or missing telsons, two types of potential teratologies are described here: (1) forked telsons (the most often observed teratologies) and (2) double telsons (Table 1). These teratologies range between symmetrically bifurcated telsons, as noted by Gudger (1935), to asymmetrical (Figure 1.2, 1.4). The forked telson is characterised by a telson bifurcation at least half way along the spine (Schuster Jr, 1982; Figure 1.2; Table 1). The forked telson can also result in an overdeveloped axial spine (Figure 1.4). Double telsons have full-length telson spines that bifurcate at the opisthosomal base (Gudger, 1935, Figure 1.1, 1.3). Other telson teratologies include the extension of the posterior opisthosoma parallel with a damaged telson (Figure 1.5) and telson spines that curve in side-on view (van der Meer Mohr, 1941).

Cephalothoracic abnormalities. Injuries along the *Limulus polyphemus* cephalothoracic margin are rarer than telson teratologies. The cephalothoracic injuries consist of at least one 'U' shaped embayment in the dorsal margin, with rare examples of multiple embayments (Figure 2.1-7). One extreme cephalothoracic injury to the *Tachypleus tridentatus* specimen was noted (OUMNH.ZC.25121): a large 'U' shaped injury to the right cephalothorax producing a sharply buckled border (Figure 3.1-5). This specimen is similar to the *L. polyphemus* specimen in Jell (1989, figure 1). However, the Jell (1989) specimen has buckling
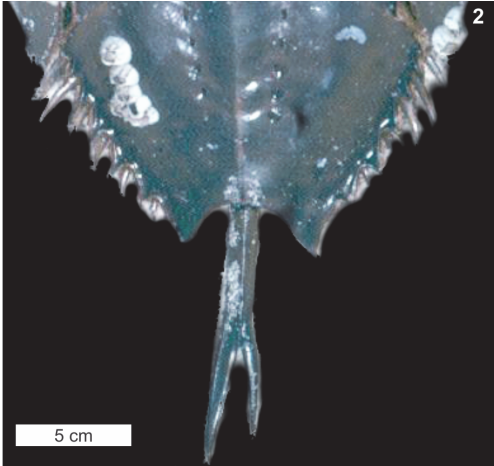
that forced the cephalothoracic margin to extend out laterally from the original margin, a feature not noted here. Other cephalothoracic abnormalities include a slit-like embayment to the left posterior cephalothorax (van der Meer Mohr, 1944, figure 2) and a hole in the dorsal cephalothorax (Schaller et al., 2004).

Opisthosomal injuries. Only one example of an opisthosomal injury was documented here: a 'V' shaped embayment on the left side of the *Tachypleus tridentatus* specimen (OUMNH.ZC.25121). A moveable spine has been removed and the two most posterior spines are shorter than those on the right side (Figure 3.1, 3.3-5). This injury is potentially similar to the opisthosomal injuries described, but not figured, in van der Meer Mohr (1941). The documented injury is more extreme than the Jell (1989, figure 1) specimen, as the Jell specimen did not have an embayment. The other previously documented opisthosomal injuries are broken posterior opisthosomal process on female *Limulus polyphemus* (Table 1) from mating (Brockmann, 1990; Shuster Jr, 2009).

Appendage injuries. No examples of abnormal appendages were illustrated here. However, injured cephalothoracic and thoracetronic appendages have been documented in previous studies (Table 1). Damaged pretarsus, apotele sections and processes of pushing legs are the most documented appendage injuries (van der Meer Mohr, 1935, 1941). Damaged and amputated walking legs and the loss of male pedipalps have also been noted (Bursey, 1977; Schaller et al., 2004, 2005; Duffy et al., 2006). Such injuries can persist through multiple moulting events (Itow et al., 1998a). Only one type of injured thoracetronic appendage is noted: injured book gills (Botton and Loveland, 1989). The examples noted here are detailed further in Table 1.

Injuries to Fossil Taxa

Exceptionally, three dimensionally (3D) preserved fossils assessed here allowed injuries (and potentially teratologies) to be identified, especially as healed injuries are easily distinguished from breaks created during fossilisation. The majority of specimens consisted only of the cephalothorax. As such, no telson and appendage abnormalities were documented, and only one opisthosomal injury was identified.

Mesolimulus walchi is superbly preserved in 3D in the Solnhofen Limestone (Jurassic) (Barthel et al., 1990). Two injured specimens from this deposit are documented (MCZ 106500 and MCZ 106372). One specimen had a 'W' shaped embayment on the left anterior cephalothorax, extending slightly into the most-anterior opisthosoma (Figure 4.1, 4.3). The injury is cicatrised (has raised relief) and is therefore distinct from the breaks in the fossil. The other specimen had an asymmetric 'V' shaped embayment on the left anterior cephalothorax (Figure 4.2, 4.4).

Euproops danae specimens are most famously preserved in 3D within Mazon Creek fossil bed nodules (Upper Carboniferous) (Anderson, 1994; Babcock and Merriam, 2000). Among 430 specimens, three injured specimens were identified. Two had embayments that are considered injuries (FMNH.P 29193 and FMNH.PE 21972): a 'V' shaped embayment in the right anterior cephalothorax (Figure 5.5) and a 'W' shaped embayment in the anterior right cephalothorax (Figure 5.3-4). The third specimen (MCZ 4674) is unique: a series of parallel lineations or folds run across the entire left side, from the lateral ridge to the cephalothoracic margin (Figure 5.1-2). The lineations are closely spaced and follow the cephalothoracic shape. For comparison, consider the uninjured specimen (ROMIP 5827) illustrated in Figure 5.6.

DISCUSSION

Telson teratologies are among the most frequently recorded extant xiphosurid abnormalities (Figure 1 and Table 1). The long, slender morphology means that any abnormalities are obvious and as telsons conduct the high strain activity of overturning individuals, the telson spines are more commonly injured (Eagles, 1973; Shuster Jr and Sekiguchi, 2004). Botton and Loveland (1989) found that abnormal, missing, or damaged telsons were found among 19% of females and 32% of males in a sample of stranded *Limulus polyphemus* during the Delaware Bay spawning season. Shortened ("stubby") telsons were the most

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FIGURE 1 (previous page). Examples of live *Limulus polyphemus* specimens with telson teratologies. (1, 3) Double telson—divided at the opisthosomal joint. (2) Forked telson asymmetrically bifurcated. (4) Forked telson and an overdeveloped axial spine. (5) Damaged telson spine and spine-like overdevelopment of the posterior opisthosomal margin. (1, 2, 4, 5) Images in dorsal view. (3) Image in ventral view. No specimens were accessioned into collections.
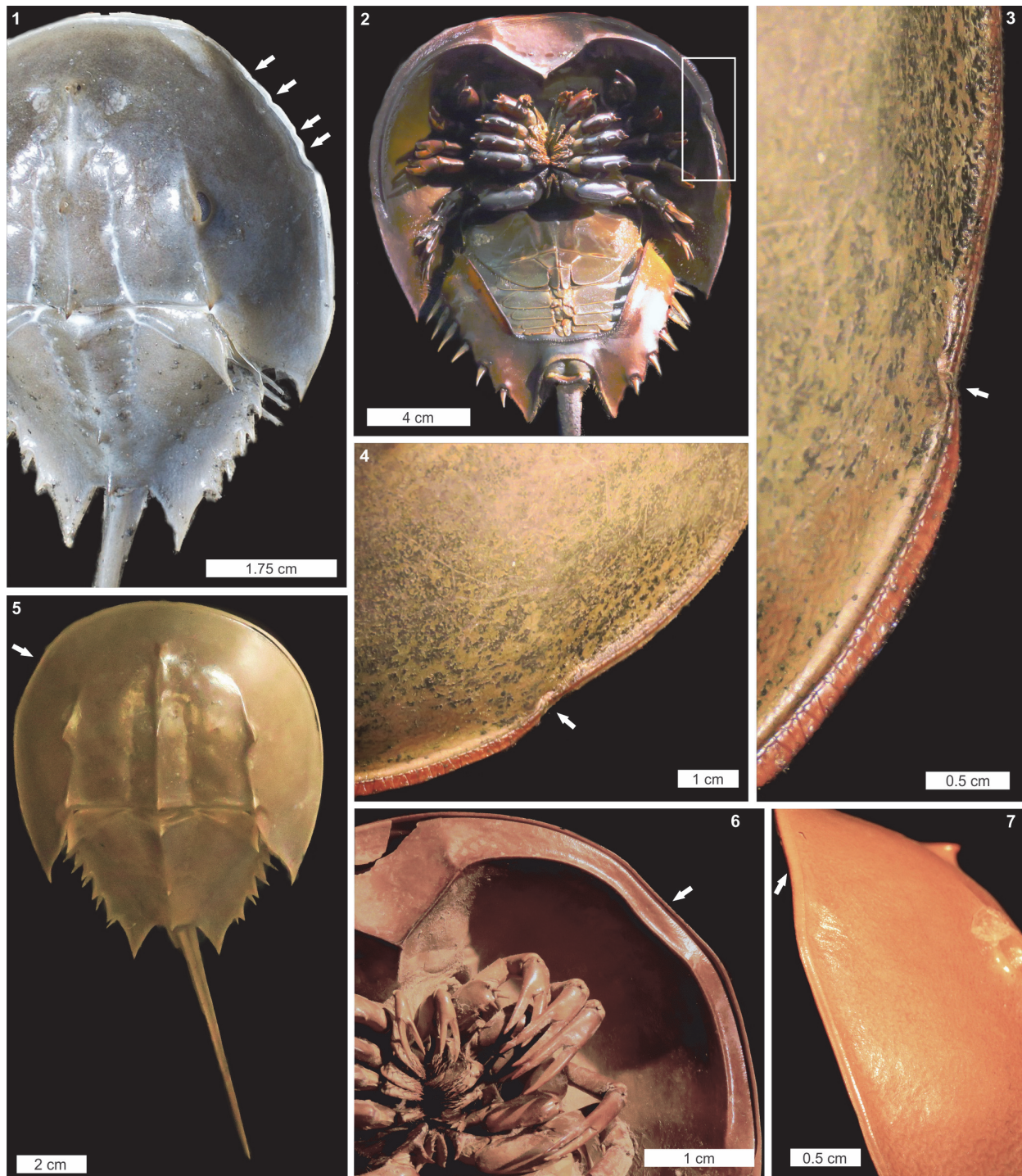
FIGURE 2. Examples of *Limulus polyphemus* with cephalothoracic injuries. (1) Four 'U' shaped embayments on right anterior cephalothorax (white arrows). (2–4) Small 'U' shaped embayment on left anterior cephalothorax. (2) Entire specimen. (3, 4) Close-ups of cephalothoracic buckling (white arrows). (5–7) Injury to left anterior cephalothorax (white arrows). (1, 4–5) images in dorsal view. (2, 5) Images in ventral view. (3, 7) Images in lateral view. No specimens were accessioned into collections.
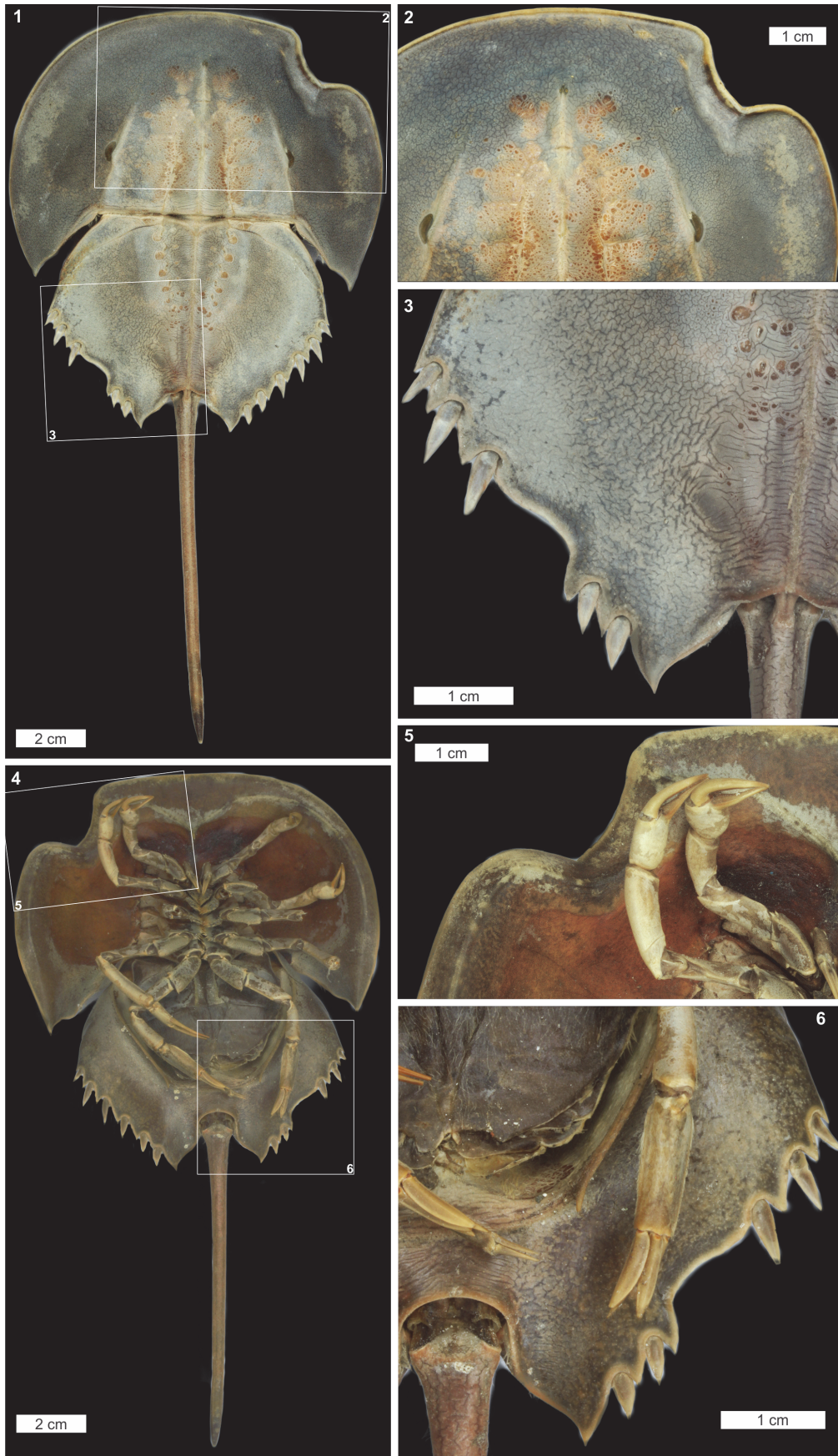
common (15% of stranded females, 23% of stranded males), followed by missing, disarticulated, and curved telsons. Telson abnormalities were less abundant among non-stranded adult horseshoe crabs, suggesting that such abnormalities increased the risk of beach stranding during spawning. Gudger (1935) suggested that telson abnormalities probably occur during moulting and subsequent moult stages propagate spine abnormalities. We agree and therefore suggest that recently moulted individuals that are overturned may damage the telson righting themselves resulting in the development of teratologies. However, long-term studies using live specimens are needed to confirm this suggestion.

Possible Source of Non-telson Abnormalities

Extensive injuries to the *Tachypleus tridentatus* (Figure 3) and *Limulus polyphemus* (Jell 1989, figure 1) cephalothoracic and opisthosomal sections likely reflect predation. Jell (1989) suggested that such injuries reflect damage from rocks or storms. However, the likelihood that similar injuries are documented on different taxa challenges this idea. We suggest instead that a single predatory attack produced these extreme injuries.

Predatory attacks on *Limulus polyphemus* by large gulls frequently occur when the animals become stranded on intertidal beaches during spawning. Gulls usually target the ventral surface, especially the book gills (Botton and Loveland, 1989), but individuals can survive these attacks if they right themselves. Adult *L. polyphemus* are also preyed upon by American alligators (*Alligator mississippiensis* (Daudin, 1802)) and loggerhead turtles (*Caretta caretta* (Linnaeus, 1758)) (Reid and Bonde, 1990; Keinath, 2003); both can produce significant injuries on the cephalothorax and opisthosoma during unsuccessful predation events. Today, many carapace injuries in adult *L. polyphemus* are man-made mechanical injuries resulting from oyster dredges and other mobile fishing gear, motorized vehicles on beaches and intertidal sand flats, etc. (M. L. Botton, pers. observ.).

Comparing Xiphosurid Injuries with Trilobite Injuries

Trilobites are an extinct arthropod group adorned with biomineralised exoskeletons that arose during the early Cambrian (Series 2) (Bicknell and Paterson, 2018). Their exoskeletons were ideal protection against predators and recorded injuries from failed predation (Babcock, 2003; Zamora et al., 2011). As such, the record of potentially predatory injuries to Cambrian trilobites is extensively documented (see examples in Rudkin, 1979; Babcock, 1993, 2007; Pratt, 1998; Nedin, 1999; Fatka et al., 2008; Pates et al., 2017; Vinn, 2017; Bicknell and Paterson, 2018, table 1). Large Cambrian trilobite injuries are typically 'W', 'V', and 'U' shapes, and located on the cephalon, thorax, and pygidium (Babcock, 1993, 2003; Nedin, 1999). Most injuries are to thoracic and pygidial sections (Bicknell and Paterson, 2018) and are therefore not easily compared to the documented xiphosurid injuries. However, rare examples of cephalic injuries, specifically 'U' and 'W' shapes, are somewhat similar to xiphosurid cephalothoracic injuries, suggesting that they may have been incurred at similar developmental stages (Figure 6.1-4). *Limulus polyphemus* cephalothoracic injuries are likely incurred during a moulting event or the subsequent soft-shell stage when the exoskeleton is much softer and easier to damage (Brandt, 2002). Babcock (1993) suggested that injuries to trilobites reflect either predatory attacks on newly moulted or soft-shelled individuals, or moulting complications, as the exoskeleton is similarly easily damaged post-moult (e.g., Owen 1985; Babcock 1993; Brandt 2002; Zong et al. 2016; Bicknell and Paterson 2018). Given the similarity between the Recent xiphosurid cephalothoracic injuries and the cicatrised trilobite cephalic injuries, we suggest that, at least for the extreme examples documented here, cephalic injuries occurred during the soft-shelled stage. In this moult stage the exoskeletal strength of trilobites and xiphosurids would have been comparable and trilobites were "highly vulnerable to predators and accidents of tearing the new exoskeleton" (Brandt, 2002, p. 411). This comparison

FIGURE 3 (previous page). A *Tachypleus tridentatus* carcass with a cephalothoracic and opisthosomal injury (OUMNH.ZC.25121). (1, 4) Entire specimen with boxes around the injuries. (2, 5) Close-ups of large, buckled 'U' shaped embayment on anterior right cephalothorax. (3, 5) Close-ups of 'V' shaped injury to posterior left opisthosoma. Note missing fourth moveable spine. (4–5) Images in ventral view. Images courtesy of Oxford Museum of Natural History.
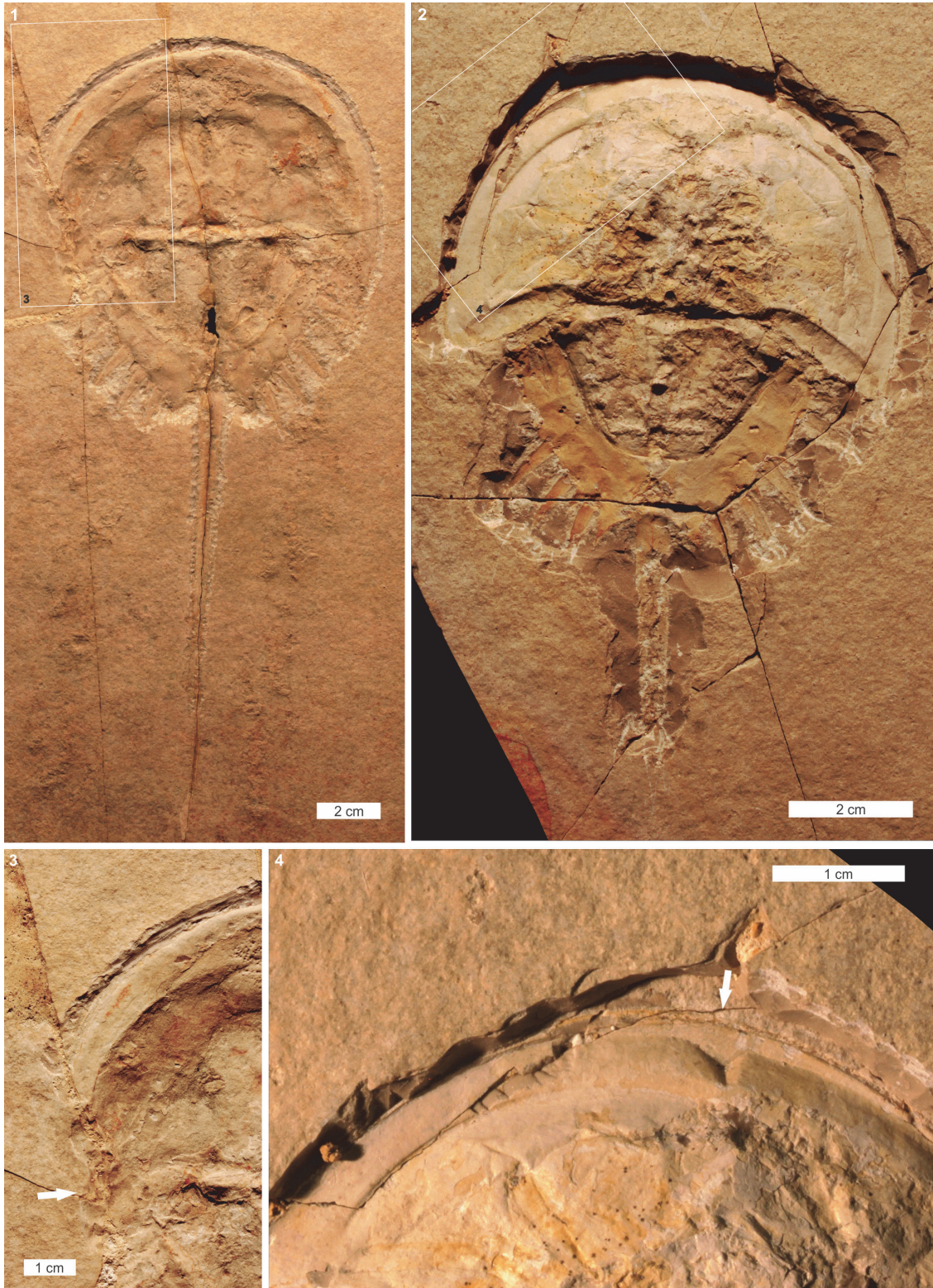
FIGURE 4. Cephalothorax injuries to *Mesolimulus walchi* (Jurassic, Solnhofen Limestone, Bavaria, Germany). (1, 3) MCZ 106372. Large 'W' shaped embayment (white arrow) on left cephalothorax. Injury extends into the opisthosoma. Box in (1) enlarged in (3). (2, 4) MCZ 106382. Prominent 'V' shaped injury (white arrow) to anterior left cephalothorax. Image credit: (1-4) Museum of Comparative Zoology, Harvard University
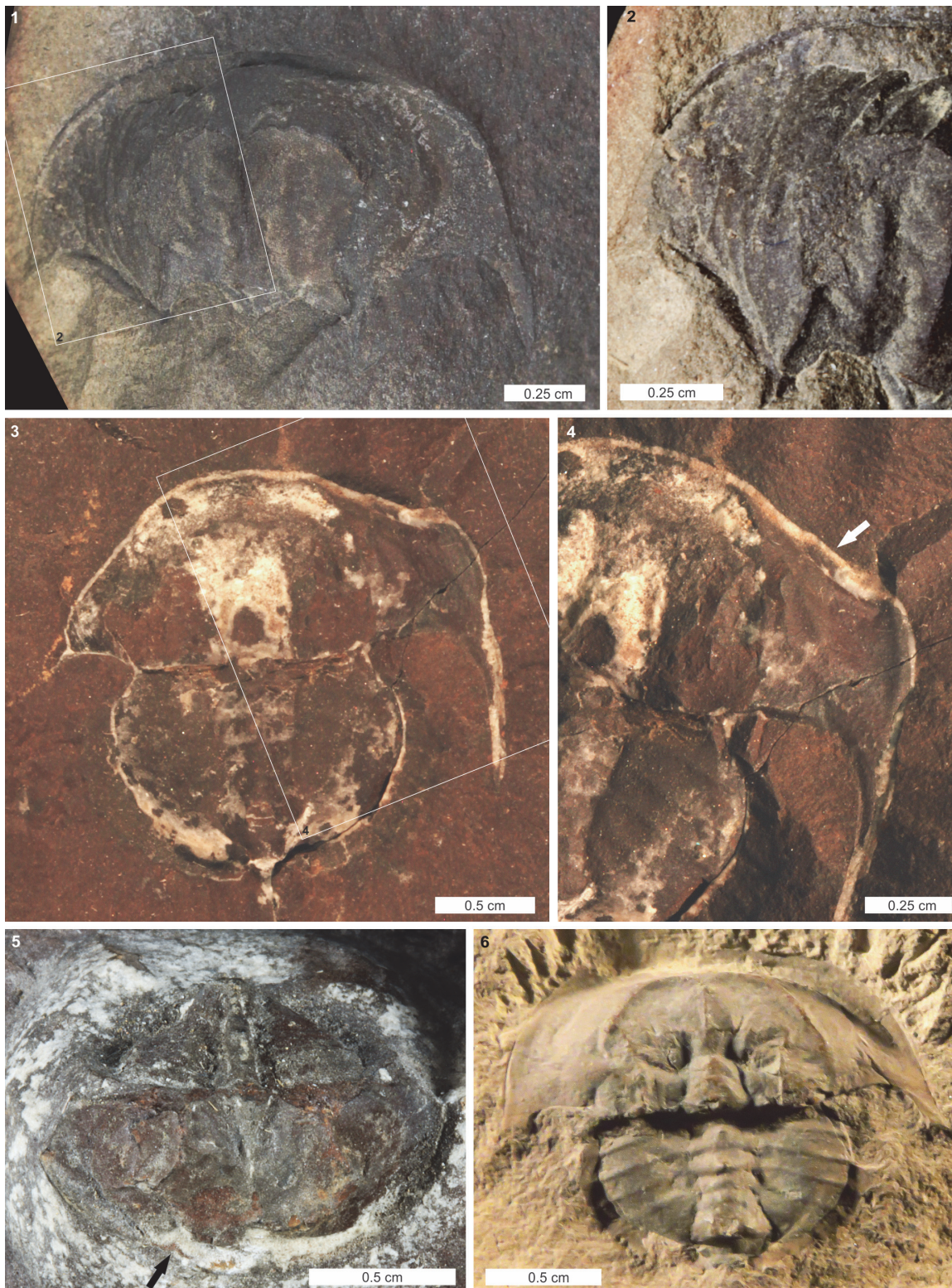
FIGURE 5. Cephalothorax injuries to *Euproops danae* (Francis Creek Shale, Will County, Illinois, USA, upper Carboniferous). (1, 2) FMNH.PE 21972. Parallel linear distortions to anterior left cephalothorax. (3, 4) MCZ 4674. 'W' shaped injury (white arrow) to right cephalothorax. (5) FMNH.P 29193. 'V' shaped injury (black arrow) on anterior right cephalothorax. (6): ROMIP5827. Complete, uninjured specimen for comparison. Image credit: (1) Mane Pritza, (3, 4) Museum of Comparative Zoology, Harvard University.
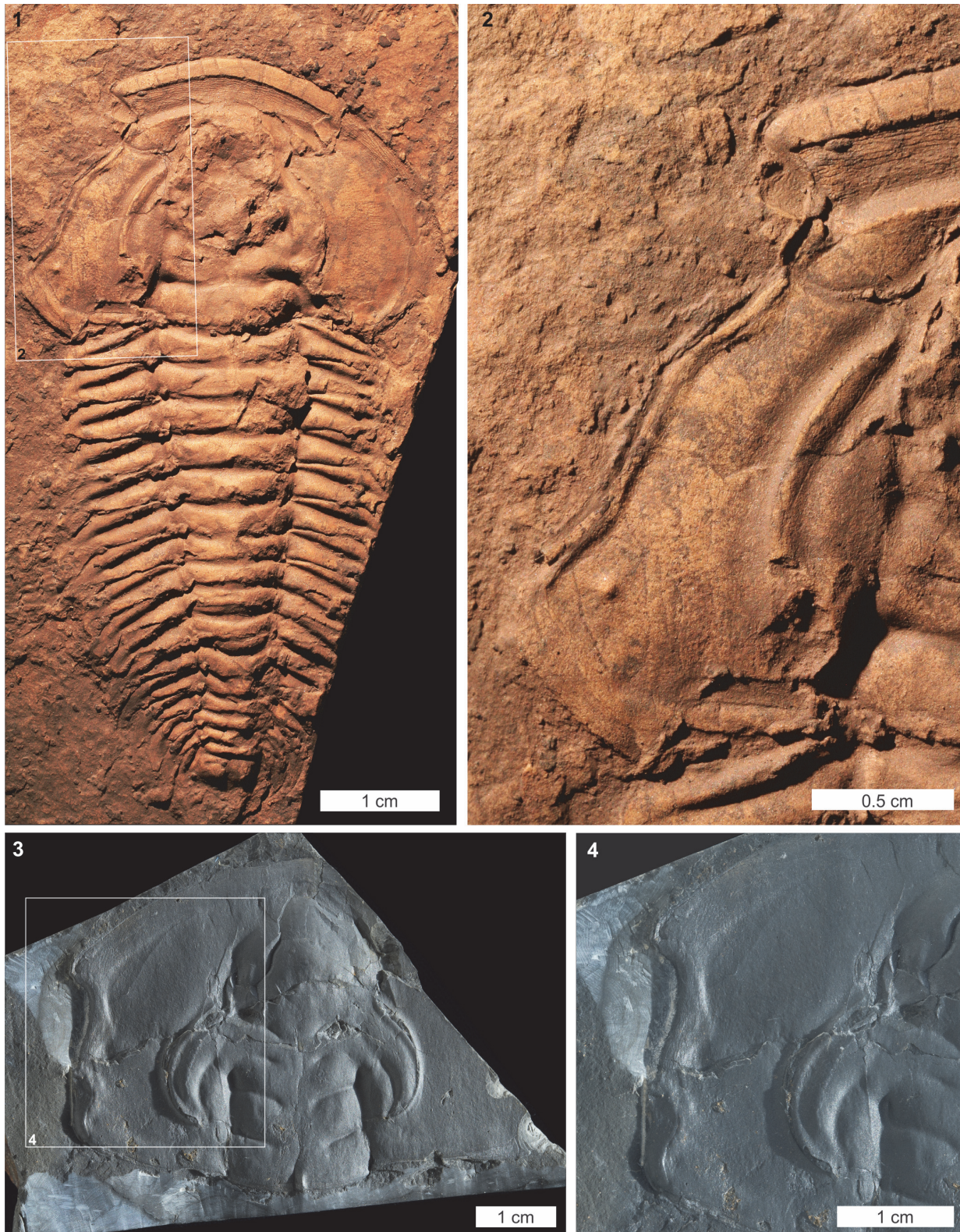
FIGURE 6. Cephalic injuries to Cambrian trilobites. (1, 2) *Redlichia takooensis* Lu, 1950 from the lower Cambrian (Series 2, Stage 4) Emu Bay Shale, Kangaroo Island, South Australia; SAM P48187. Cicatrised 'W' shaped injury to left cephalon. Injury was incurred during a recent moult. (3, 4) *Olenellus thompsoni* (Hall, 1859) from the Cambrian (Series 2, Stage 4) Kinzers Formation, Pennsylvania; USNM PAL 90809. Asymmetric, cicatrised 'U' shaped injury to left cephalon. Image credit: (1, 2) Originally figured in Bicknell and Paterson (2018); (3, 4) Frederick Cochard.

is purely based on injury shape and the likelihood that the illustrated trilobite injuries were incurred during a soft-shelled stage and should not be extended to consider the predators that made the injuries. Although the broad mechanics of predation (e.g., crushing, breaking, striking) were likely similar, the predator groups are very different. Cambrian trilobite predators—Euarthropoda *Sidneyia inexpectans, Wisangocaris barbarahardyae* Jago et al., 2016, a *Fuxianhuia*-like arthropod, and perhaps other trilobites (Bruton 1981; Zhu et al., 2004; Daley et al., 2013; Jago et al., 2016; Zacaï et al., 2016; Bicknell and Paterson, 2018)—were very different to the predators of extant xiphosurids (see Walls et al., 2002). Nonetheless, these preliminary results highlight that such comparative research could be explored further.

Fossil Xiphosurids

Cephalothoracic sections of fossil xiphosurids are occasionally preserved well enough to examine for injuries, which augments the trace fossil evidence of predation noted in Diedrich (2011). The xiphosurids considered here have broadly similar cephalothoracic morphologies, and similar asymmetric 'V' and 'W' shaped injuries (Figures 4.1-4, 5.3-5). Furthermore, the only unusual non-marginal cephalothoracic features recorded here were on *Euproops danae*. The lineations along the cephalothorax suggest deformation immediately after a moulting event, perhaps from scratching. Alternatively, an equally plausible origin would be plastic deformation of a freshly moulted exoskeleton, where the lineations are subparallel folds due to compression. No examples of 'U' shaped injuries were identified on the extinct xiphosurid species, and we suggest that smaller 'U' shaped injuries, like those to *Limulus polyphemus*, may not be identifiable (Figure 2). This is because during healing, injuries become less angular and prominent, and are therefore harder to distinguish from taphonomic distortion.

The comparison of Recent and fossil xiphosurid injuries highlights two areas of future research. (1) The identification of potentially predatory injuries to xiphosurids in the Carboniferous suggests that analyses of injury frequencies through time are possible. Large museum collections of fossil Xiphosurida and spawning events of Recent species could therefore be examined for injury and teratology counts to highlight temporal changes to abnormalities. (2) The identification of Recent moulting abnormalities could inform the identity of fossil moulting complications, as xiphosurids are morphologically conservative (Avise et al., 1994; Rudkin and Young, 2009). If predatory injuries can be differentiated from such moult abnormalities, similar patterns may be identified for extinct groups such as the trilobites.

CONCLUSION

Our study of xiphosurid abnormalities concludes that (1) telson teratologies are the most commonly documented abnormality; (2) cephalothoracic and opisthosomal abnormalities are either seldom incurred or reported; (3) 'V' and 'W' shaped cephalothoracic injuries are preserved on fossil xiphosurids; and (4) cephalothoracic injuries to Recent xiphosurid can be used to explore the timing of cephalic injuries to Cambrian trilobites. The underdocumentation of extant and extinct xiphosurid abnormalities shows how this iconic group requires further attention and exploration, and has much potential for macroevolutionary studies.

ACKNOWLEDGEMENTS

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