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REVIEW
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Pictorial Atlas of Fossil and Extant Horseshoe Crabs, With Focus on Xiphosurida

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Horseshoe crabs are an iconic group of extant chelicerates, with a stunning fossil record that extends to at least the Lower Ordovician (~480 million years ago). As such, the group has retained significant biological and palaeontological interest. The sporadic nature of descriptive and systematic research into fossil horseshoe crabs over the last two centuries has spread information on the group across more than 200 texts dating from the early nineteenth century to the present day. We present the most comprehensive pictorial atlas of horseshoe crabs to date to pool these important data together. This review highlights taxa such as *Bellinurus lacoei* and *Limulus priscus* that have never been documented with photography. Furthermore, key morphological features of the true horseshoe crab (Xiphosurida) families—Austrolimulidae, Belinuridae, Limulidae, Paleolimulidae, and Rolfeiidae—are described. The evolutionary history of horseshoe crabs is reviewed and the current issues facing any possible biogeographic work are presented. Four major future directions that should be adopted by horseshoe crab researchers are outlined. We conclude that this review provides the basis for innovative geographic and geometric morphometric studies needed to uncover facets of horseshoe crab evolution.

Keywords: Xiphosura, Xiphosurida, synziphosurines, horseshoe crab, pictorial atlas, evolution

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INTRODUCTION

Chelicerates, a group that includes arachnids (spiders, scorpions), eurypterids (sea scorpions), and Xiphosura (the so-called horseshoe crabs) have a stunning and extensive fossil spanning the early Palaeozoic to today and an exceptional modern diversity (Dunlop, 2010). Of these taxa, extant horseshoe crabs have been subject to detailed anatomical (van Der Hoeven, 1838; Owen, 1872; Lankester, 1881; Shuster, 1982; Shultz, 2001; Bicknell et al., 2018b,c,d), biochemical (Kaplan et al., 1977; Botton and Ropes, 1987), physiological (Sokoloff, 1978), morphological (Lee and Morton, 2005; Chatterji and Pati, 2014; Jawahir et al., 2017), and population dynamic (Botton, 1984; Brockmann, 1990; Gerhart, 2007) studies over the past two centuries. Furthermore, the impressive fossil record of this group, and apparent morphological conservatism that allowed survival of all five big mass extinctions, have driven extensive palaeontological interest in the group (Babcock et al., 2000; Rudkin and Young, 2009; Sekiguchi and Shuster, 2009; Krzeminski et al., 2010; Briggs et al., 2012; Dunlop et al., 2012; Lamsdell, 2013; Błazejowski, 2015; Lamsdell and Mckenzie, 2015; Bicknell et al., 2018b,c, 2019b; Bicknell, 2019; **Figure 1**). Despite this extensive

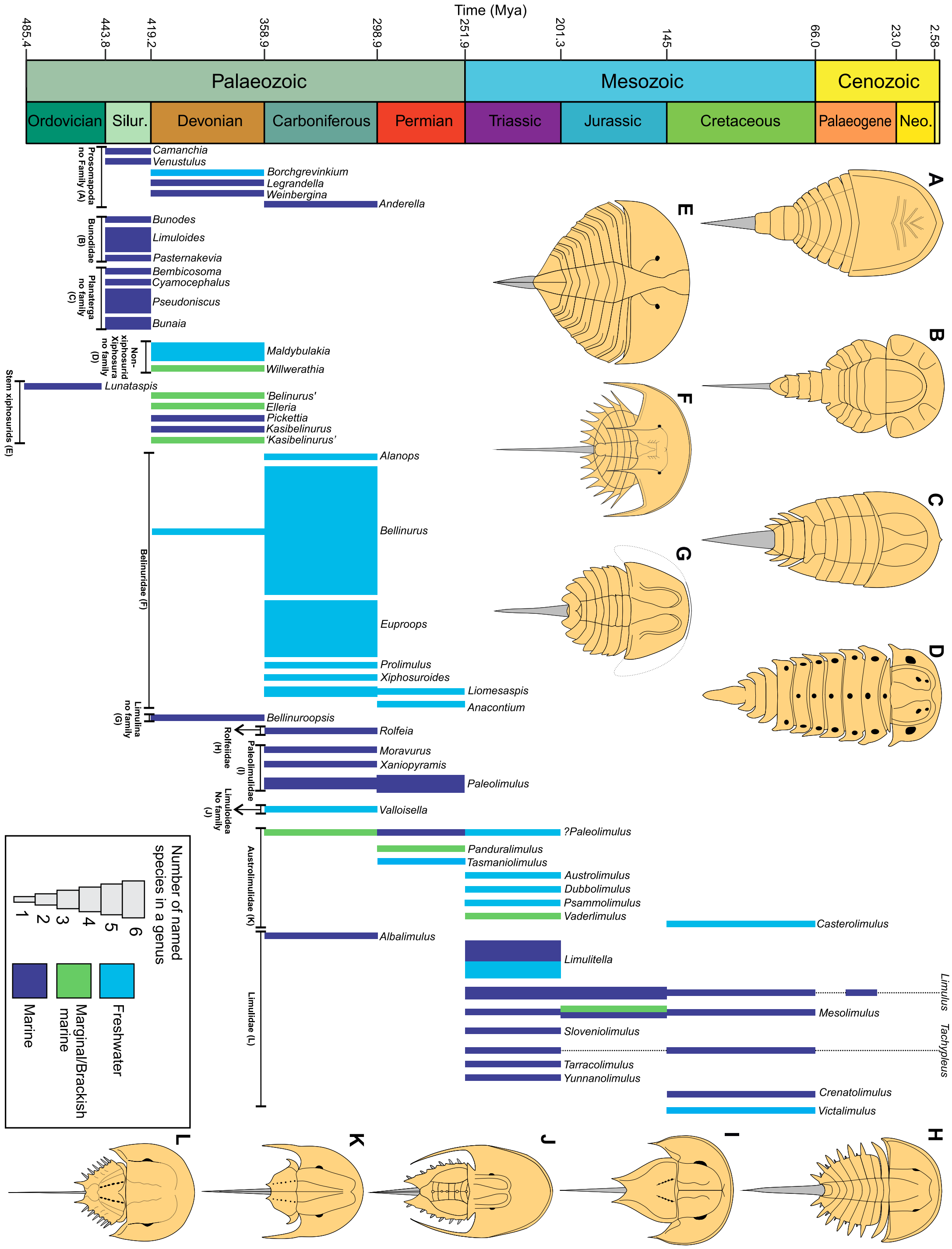

FIGURE 1 | The geological and morphological history of horseshoe crabs across the Phanerozoic. Number of named species is presented as well as suggested palaeoenvironment (**Tables 1**–**7**). A major transition to freshwater conditions occurred between the Devonian and Carboniferous. This was concurrent with a decrease in synziphosurine taxa and an increase in xiphosurids. Limulids had a diversification event in the Triassic and there was a transition back to dominantly marine conditions in the Jurassic. Dashed lines represent ghost lineages.

research, numerous avenues for further research remain for horseshoe crabs, and we highlight three here. Firstly, the evolutionary relationship between synziphosurines (the so-called "Synziphosura") and Xiphosura (Lamsdell, 2013, 2016; Legg et al., 2013; Garwood and Dunlop, 2014). To help clarify this relationship, Lamsdell (2013) removed synziphosurines from Xiphosura and arrayed them within Prosomapoda and Planaterga. Secondly, there are a number of specimens that have been described in open terminology (Haug et al., 2012; Lamsdell et al., 2020) and despite the recent effort to bring taxa into recognized families, and genera, and erect new groups where appropriate (Bicknell, 2019; Bicknell et al., 2019e; Lamsdell et al., 2020), there remain an array of individuals that require taxonomic revision. Lastly, some genera appear to have been extensively over-split (Dunbar, 1923; Størmer, 1972; Fisher, 1984; Anderson, 1994; Haug et al., 2012; Kin and Błazejowski, 2014; Haug and Rötzer, 2018b). We therefore present a pictorial review of horseshoe crabs to aid current and future researchers in (1) the morphology and re-evaluation of taxa, (2) the determination of evolutionary relationships, and (3) the confirmation of species validity (Waterston, 1985; Selden and Siveter, 1987).

The palaeontological and evolutionary histories, broad taxonomy of families (Størmer, 1955; Novozhilov, 1991), and phylogenetic relationships (Lamsdell, 2013, 2016) of horseshoe crabs has often been reviewed (Bergström, 1975; Selden and Siveter, 1987; Anderson and Selden, 1997; Anderson and Shuster, 2003; Rudkin and Young, 2009). However, a document illustrating all horseshoe crab taxa has not been presented since Woodward (1866, 1867, 1879), Dix and Pringle (1929, 1930), Eller (1938b), and Raymond (1944). We have therefore collated images of all species considered horseshoe crabs (see taxa Dunlop et al., 2019), in a vital step toward understanding the true diversity and extent of Xiphosura (Lamsdell, 2013). We also present taxonomic descriptions of the facets that define members of xiphosurid families and consider of lifestyle and diversity of each group. We have focused on Xiphosurida as there are more taxa in this group than stem xiphosurids and synziphosurines. Nonetheless, synziphosurines and non-xiphosurid xiphosurans (previously considered Kasibelinuridae) are also briefly considered. It is vital to note that a thorough taxonomic revision of all species is beyond the intended scope of this review—namely the depiction and discussion of major horseshoe crab groups—but the images and details here represent the basis for such future work. The ultimate goal of this work is to depict all taxa in an open-access environment for future researchers to use as a reference point to continue research into this somewhat enigmatic group of chelicerates.

TERMINOLOGY

The following definitions are provided to clarify terminology used in descriptions. See **Figure 2** for a depiction of these features.

Somite: Fundamental unit or division that construct arthropod bodies (Lamsdell, 2013; Dunlop and Lamsdell, 2017).

Tergite: Physical expression of somites as discrete plates on the dorsal exoskeleton (Lamsdell, 2013; Dunlop and Lamsdell, 2017).

Prosoma: Anterior body section consisting of six somites (Dunlop and Lamsdell, 2017). Prosoma refers to the anterior

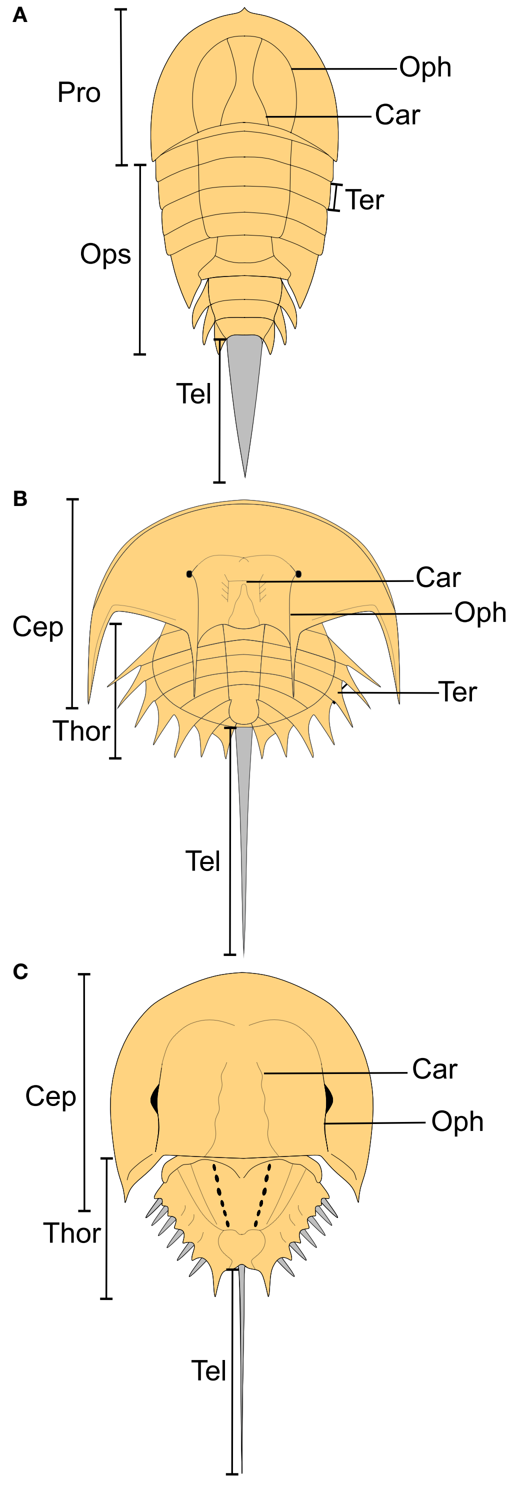

FIGURE 2 | Depiction of horseshoe crab features outlining the key morphological aspects of horseshoe crabs. **(A)** Reconstruction of *Cyamocephalus loganensis* showing main morphological features of synziphosurines. **(B)** Reconstruction of *Euproops danae*, showing main morphological features of belinurids. **(C)** Reconstruction of *Limulus polyphemus*, showing main morphological features of Limulina. Car, cardiac lobe; Cep, cephalothorax; Oph, ophthalmic ridge; Ops, opisthosoma; Pro, prosoma; Tel, telson; Ter, tergite; Thor, thoracetron.

section of synziphosurines and xiphosurans (Dunlop, 2010; Dunlop and Lamsdell, 2017). The prosoma in Xiphosurida is combined with the two most anterior opisthosomal sections to produce the cephalothorax (Dunlop, 2010; Dunlop and Lamsdell, 2017).

Cephalothorax: Anterior body section of Xiphosurida. Combination of two most anterior opisthosomal segments with prosoma (Dunlop, 2010).

Ophthalmic ridge: Ridge above the lateral compound eye that extends anteriorly and posteriorly relative to the compound eye (Størmer, 1955).

Cardiac lobe: Lobe in the center of the prosoma/cephalothorax that extends into opisthosoma/thoracetron (Størmer, 1955).

Opisthosoma: Posterior section of the arthropod body, consisting of up to 13 tergites (Dunlop and Lamsdell, 2017). Used here for synziphosurines and non-xiphosurid xiphosurans as the group lack a fused opisthosoma (=thoracetron) (Lamsdell, 2013).

Thoracetron: Posterior section of Xiphosurida that is a fused solid plate. Shultz (2001) also suggested the termed tergum for this feature. The section may have expressed tergites.

Telson: Most posterior section of the xiphosuran exoskeleton, styliform and highly mobile (Eagles, 1973). Also called a tailspine.

INSTITUTIONAL ACRONYMS

AM F: Australian Museum, Sydney, NSW, Australia. *AMNH*: American Museum of Natural History, New York, USA. *B*: Geomuseum der WWU Münster, Germany. *BGS.GSE*: British Geological Survey, Keyworth, England, UK. *BMSC*: Buffalo Museum, Buffalo, NY, USA. *CM*: Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA. *CCMGE*: Chernyshev Central Research Geological Exploration Museum, St. Petersburg, Russia. *GIN*: Geological Institute of the Russian Academy of Sciences, Moscow, Russia. *GIUS*: Faculty of Earth Sciences, Silesian University, Sosnowiec, Czech Republic. *GSC*: Geological Survey of Canada, Ottawa, Canada. *GZG INV*: Geowissenschaftliches Zentrum der Georg-August-Universität Geowissenschaftliches Museum, Göttingen, Germany. *ISEA*: Museum of the Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Warsaw, Poland. *L*, *LL*: Manchester Museum, University of Manchester, Manchester, England, UK. *LPI*: Chengdu Geological Center, Chengdu, China. *MAN*: Muséum-Aquarium de Nancy, Lorraine, France. *MAS Pal*: Museum am Schölerberg, Osnabrück, Germany. *MB.A*.: Museum für Naturkunde Leibniz-Insitut, Berlin, Germany. *MCZ*: Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA. *MGSB*: Museo Geológico del Seminario de Barcelona, Barcelona, Spain. Specimens ending in *MLU*, *HAU-WIL*: Institut für Geologische Wissenschaften und Geiseltalmuseum Martin Luther University Halle-Wittenberg, Halle, Saale, Germany. *MM*: Manitoba Museum, Winnipeg, Canada. *MMF*: Geological Survey of New South Wales, Londonderry, NSW, Australia. *MMO B*: Municipal Museum of Ostrava, Ostrava, Czech Republic. *MNHN*: Museum National d'Histoire Naturelle of Paris, Paris, France. *MNHP*: Národní muzeum, Prague, Czech Republic. *MSNM*: Museo Civico di Storia Naturale di Milano, Milan, Italy. *NHMUK PI*: Natural History Museum, London, UK. *NME*: Geologisch-Paläontologischen Sammlung des Naturkundemuseums Erfurt, Germany. *NMK D*: Wolfgang Munk collection in Naturkundemuseum Kassel, Ottoneum in Kassel, Germany. *NMS*: National Museums of Scotland, Edinburgh, Scotland. *NMW*: National Museum of Wales, Cardiff, United Kingdom. *NSM:* Nova Scotia Museum, Halifax, NS, Canada. *NYSM*: New York State Museum, Albany, NY, USA. *OUMNH*: Oxford University Museum of Natural History, Oxford, England, UK. *NMV P:* Museums Victoria, Carlton, Victoria, Australia. *PIN*: Paleontological Museum of Yu A Orlov, Moscow, Russia. *NHM-UIO*: Natural History Museum, University of Oslo, Oslo, Norway. *PMSL:* Natural History Museum of Slovenia, Ljubljana, Slovenia. *SLK*: Leunissen private collection. *SMF:* Forschungsinstitut Senckenberg, Frankfurt am Main, Germany. *SMNH:* Swedish Museum of Natural History, Stockholm, Sweden. *SMNS*: State Museum of Natural History Stuttgart, Stuttgart, Germany. *SNSB-BSPG*: Staatliche Naturwissenschaftliche Sammlungen Bayern – Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany. *SPW*: Poschmann private collection. *TMP*: The Royal Tyrrell Museum, Drumheller, AB, Canada. *TsNIGR*: Chernyshev Central Research Geological Museum, St. Petersburg, Russia. *UCM*: University of Colorado Museum of Natural History, Boulder, CO, USA. *UM:* Paleontology Center of University of Montana, MT, USA. *UMUT PA:* The University Museum of the University of Tokyo, Tokyo, Japan. *USNM*: United States National Museum, Washington, DC, USA. *USTL*: Laboratoire de paléontologie de l'université de Lille-1, Poitiers, France. *UTGD*: Geology Department, University of Tasmania, Tasmania, Australia. *U.W*.: University of Wisconsin Geology Museum, Madison, WI, USA. *W.U*.: Wichita State University, Wichita, KS, USA. *YPM IP*: Division of Invertebrate Paleontology in the Yale Peabody Museum, New Haven, CT, USA. *YPM IZ*: Division of Invertebrate Zoology in the Yale Peabody Museum, New Haven, CT, USA. *ZIK*: Ukrainian Academy of Sciences, 252.150 Kiev, Ukraine. *ZPAL:* Institute of Paleobiology, Polish Academy of Science, Warsaw, Poland.

DIVISIONS OF HORSESHOE CRABS

Synziphosurines

First appearing in at least the early Ordovician of Morocco, synziphosurines went extinct in the Mississippian (**Tables 1**–**4**, **Figures 3**–**9**) (Anderson and Selden, 1997; Moore et al., 2005b, 2007; Krzeminski et al., 2010; Van Roy et al., 2010; Briggs et al., 2012). There are 13 synziphosurine genera and 20 species. *Anderella, Borchgrevinkium, Camanchia, Legrandella, Venustulus*, and *Weinbergina* are currently considered to belong to the clade Prosomapoda (the group that also contains Xiphosura, **Figures 4**, **5**), while *Bembicosoma, Bunaia, Bunodes,*

TABLE 1 | Horseshoe crabs with currently uncertain suprageneric affinities.

Taxon	Family	Geological information (where detailed) and country	Time period	Environment	Citation for figured specimens	Figured here
Drabovaspis complexa Chlupáč, 1963	Unspecified	Letná Formation, Czech Republic	Ordovician	Marine	Chlupáč, 1963, 1965, 1999; Bergström, 1968; Ortega Hernández et al., 2010	**Figure 3D**
Unnamed synziphosurine	Unspecified	Lower Fezouata Formation, Morocco	Ordovician	Marine	Van Roy et al., 2010; Martin et al., 2016	**Figure 3C**
Unnamed xiphosuran	Unspecified	Upper Fezouata Formation, Morocco	Ordovician	Marine	Van Roy et al., 2010; 2015; Lefebvre et al., 2016	**Figure 3E**
Dibasterium durgae Briggs et al., 2012	Unspecified	Herefordshire *Konservat-Lagerstätte*, England, UK	Silurian	Marine	Briggs et al., 2012; Sutton et al., 2014	**Figures 3A,B**

Ordered time period and alphabetically by genus.

TABLE 2 | Taxa in Prosomapoda that are potentially related to Xiphosura.

Taxon	Family	Geological information (where detailed) and country	Time period	Environment	Citation for figured specimens	Figured here
Camanchia grovensis Moore et al., 2011	Unspecified	Wenlock Scotch Grove Formation, Iowa, USA	Silurian	Marine	Moore et al., 2011	**Figure 4F**
Venustulus waukeshaensis Moore et al. 2005	Unspecified	Waukesha *Konservat-Lagerstätte*, Brandon Bridge Formation, Wisconsin, USA	Silurian	Marine (*sensu* Wendruff, 2016)	Moore et al., 2005b	**Figure 4C**
Borchgrevinkium taimyrensis Novojilov, 1959	Unspecified	Sheshenkarinskoy Suite, Kazakhstan	Devonian	Freshwater	Novojilov, 1959	**Figure 4D**
Legrandella lombardii Eldredge, 1974	Unspecified	Icla Formation, Bolivia	Devonian	Marine	Eldredge, 1974; Shuster, 2001; Shuster and Anderson, 2003; Bicknell et al., 2019a	**Figure 5**
Anderella parva Moore et al. 2007	Unspecified	Bear Gulch Limestone, Montana, USA	Carboniferous	Marine	Moore et al., 2007	**Figures 4B,E**
Weinbergina opitzi Richter and Richter, 1929	Weinberginidae	Hunsrück Slate, Germany	Devonian	Marine	Richter and Richter, 1929; Størmer, 1955; Lehmann, 1956; Eldredge, 1974; Stürmer and Bergström, 1981; Novozhilov, 1991; Shuster, 2001; Shuster and Anderson, 2003; Jansen and Türkay, 2010; Rust et al., 2016	**Figure 4A**

Ordered by family, time period and alphabetically by genus.

Cyamocephalus, Limuloides, Pasternakevia, and *Pseudoniscus* have been placed into Planaterga (**Figures 6–9**; Lamsdell, 2013). Synziphosurines are characterized by large prosomal shields, unfused opisthosoma with nine to 11 segmented and expressed tergites (Størmer, 1934, 1955; Rudkin et al., 2008; Lamsdell, 2013; Selden et al., 2015). In extreme cases, the three most posterior tergites form a narrow postabdominal (pretelson) section leading to a styliform telson. Lateral compound eyes are known from *Legrandella lombardii* and *Pseudoniscus roosevelti* (Eldredge, 1974; Bergström, 1975; Bicknell et al., 2019a). Furthermore, *Pasternakevia podolica* (Krzeminski et al., 2010) and *Weinbergina opitzi* (Lehmann, 1956; Stürmer and Bergström, 1981) show evidence for putative ocular features. The remaining taxa lack such ocular features and were possibly blind (Bicknell et al., 2019a). Appendages are known from at least *Anderella parva*, *Venustulus waukeshaensis,* and *Weinbergina opitzi* (Richter and Richter, 1929; Størmer, 1934; Stürmer and Bergström, 1981; Moore et al., 2005a,b, 2007). Synziphosurines inhabited marine to marginal marine environments, and the general lack of thick prosomal margin suggests that the group may not have burrowed, and instead potentially moved above the substrate (Størmer, 1952; Bergström, 1975; Stürmer and Bergström, 1981; Lamsdell et al., 2013). Affinities of synziphosurines are actively debated due to the few useful synapomorphies that have been identified to date (Anderson et al., 1998), which has resulted in an unnatural grouping of assorted stem euchelicerates (Krzeminski et al., 2010; Lamsdell, 2013, 2016; Lamsdell and Mckenzie, 2015; Selden et al., 2015). To build on the phylogenetic work presented in Lamsdell (2013), in which Lamsdell highlighted that

TABLE 3 | Taxa in clade Planaterga, excluding the group Dekatriata, *sensu* Lamsdell (2013) that traditionally represent synziphosurine groups.

Taxon	Family	Geological information (where detailed) and country	Time period	Environment	Citation for figured specimens	Figured here
Bunodes lunula Eichwald, 1854	Bunodidae	Oesel Group, Saaremaa Island, Estonia	Silurian	Marine	Eichwald, 1854; Woodward, 1866, 1867; Zittel, 1881; Vogdes, 1917; Eldredge, 1974; Bergström, 1975; Novozhilov, 1991; Bicknell et al., 2019a	**Figure 6**
Limuloides horridus (Woodward, 1872)	Bunodidae	Leintwardine Formation, England, UK	Silurian	Marine (*sensu* Gladwell, 2018)	Woodward, 1872	**Figure 7H**
Limuloides limuloides (Woodward, 1865)	Bunodidae	Leintwardine Formation, England, UK	Silurian	Marine (*sensu* Gladwell, 2018)	Woodward, 1865, 1866, 1867; Zittel, 1881; Gaskell, 1908; Vogdes, 1917; Størmer, 1955; Bergström, 1975; Novozhilov, 1991; Bicknell et al., 2019a	**Figures 7A–C**
Limuloides salweyi (Woodward, 1872)	Bunodidae	Leintwardine Formation, England, UK	Silurian	Marine (*sensu* Gladwell, 2018)	Woodward, 1872	**Figure 7D**
Limuloides speratus Woodward, 1872	Bunodidae	Leintwardine Formation, England, UK	Silurian	Marine (*sensu* Gladwell, 2018)	Woodward, 1872	**Figure 7G**
Pasternakevia podolica Selden and Drygant, 1987	Bunodidae	Ustye Suite Series, Russia	Silurian	Marine	Selden and Drygant, 1987; Krzeminski et al., 2010	**Figures 7E,F**
Bembicosoma pomphicus Laurie, 1899	Unspecified	Reservoir Formation, Scotland, UK	Silurian	Marine	Laurie, 1899; Anderson and Moore, 2003	**Figure 8F**
"*Bunaia*" *heintzi* Størmer, 1934a	Unspecified	Ringerike Sandstone, Norway	Silurian	Marine	Størmer, 1934, 1955; Novozhilov, 1991	**Figure 8E**
Bunaia woodwardi Clarke, 1919	Unspecified	Vernon Formation, New York, USA	Silurian	Marine	Clarke, 1919; Eldredge, 1974; Selden and Nudds, 2008; Rudkin and Young, 2009	**Figures 8B,D**
Cyamocephalus loganensis Currie, 1927	Unspecified	Patrick Burn Formation, Scotland, UK; Wenlock Limestone (?), Shropshire, England, UK	Silurian	Marine	Currie, 1927; Eldredge and Plotnick, 1974; Anderson, 1999; Bicknell et al., 2019a	**Figure 8A**
Pseudoniscus aculeatus Nieszkowski, 1859	Unspecified	Oesel Group, Saaremaa Island, Estonia	Silurian	Marine	Nieszkowski, 1858; Woodward, 1866, 1867; Vogdes, 1917; Eldredge, 1974; Bergström, 1975	**Figure 9B**
Pseudoniscus clarkei Ruedemann, 1916	Unspecified	Vernon Formation, New York, USA	Silurian	Marine	Ruedemann, 1916; Selden and Nudds, 2008; Bicknell et al., 2019a	**Figure 9E**
Pseudoniscus falcatus (Woodward, 1868)	Unspecified	Patrick Burn Formation, Scotland, UK	Silurian	Marine	Woodward, 1868; Ruedemann, 1916; Størmer, 1952, 1955; Bergström, 1975; Novozhilov, 1991; Bicknell et al., 2019a	**Figure 9A**
Pseudoniscus roosevelti Clarke, 1902	Unspecified	Vernon Formation, New York, USA	Silurian	Marine	Clarke, 1902; Størmer, 1955; Eldredge, 1974; Novozhilov, 1991; Bicknell et al., 2019a	**Figures 9C,D**
Indeterminate synziphosurine	Unspecified	Ardenno- Rhenish Massif, Germany	Devonian	Marginal marine	Poschmann and Franke, 2006	**Figure 8C**

Ordered by family, time period, and then genus. Synonyms mentioned in Dunlop et al. (2019): Pseudoniscus = Neolimulus*.* Bunodes = Exapinurus*.* Limuloides = Hemiaspis*. ? denote uncertain formation assignment.*

synziphosurines comprise both possible stem-horseshoe crabs and stem arachnids, images of all accepted synziphosurines are presented here (**Figures 3–9**).

Non-xiphosurid Xiphosura

First appearing in at least the Upper Ordovician of Canada and potentially the Lower Ordovician of Morocco the group contains taxa that have been considered stem-xiphosurids (**Tables 1**, **4**, **Figures 10–12**; Rudkin and Young, 2009). There are eight genera and 10 species in this group. Two genera—*Maldybulakia* and *Willwerathia*—lack a family and the remaining six genera are considered stem-xiphosurids (formerly Kasibelinuridae, although this family was considered unhelpful by Bicknell et al., 2019c as it is a paraphyletic group). Non-xiphosurid xiphosurans are defined as chelicerates with a cardiac lobe extending to the anterior prosomal shield (Lamsdell, 2013). Species of this group

TABLE 4 | Taxa considered non-xiphosurid Xiphosura and stem xiphosurids.

Taxon	Group	Geological information (where detailed) and country	Time period	Environment	Citation for figured specimens	Figured here
Lunataspis aurora Rudkin et al., 2008	Stem xiphosurid	Churchill River Group, Canada	Ordovician	Marine	Rudkin et al., 2008; Rudkin and Young, 2009; Dunlop, 2010; Young et al., 2013; Bicknell et al., 2019a	**Figure 10B**
"Belinurus" alleghenyensis Eller, 1938b	Stem xiphosurid	Chadakoin Formation, New York State, USA	Devonian	Marginal marine (*sensu* Engelder and Oertel, 1985)	Eller, 1938b; Bicknell et al., 2019c	**Figure 10C**
Elleria morani (Eller, 1938a)	Stem xiphosurid	Venango Formation, Pennsylvania, USA	Devonian	Marginal marine	Eller, 1938a; Størmer, 1955; Babcock et al., 1995	**Figure 10D**
Kasibelinurus amicorum Pickett, 1993	Stem xiphosurid	Mandagery Sandstone, Australia	Devonian	Marine	Pickett, 1993; Itow et al., 2003; Bicknell et al., 2019a,c	**Figure 11A**
"Kasibelinurus" randalli Beecher, 1902	Stem xiphosurid	Chadakoin Formation, Pennsylvania, USA	Devonian	Marginal marine	Beecher, 1902; Babcock et al., 1995; Bicknell et al., 2019c	**Figures 11B–D**
Pickettia carteri (Eller, 1940)	Stem xiphosurid	Cattaraugus Formation, Pennsylvania, USA	Devonian	Marine (*sensu* Wilmarth, 1938)	Eller, 1940; Bicknell et al., 2019c	**Figure 10A**
Maldybulakia angusi Edgecombe, 1998b	Unspecified	Sugarloaf Creek Formation, NSW, Australia	Devonian	Freshwater	Edgecombe, 1998a,b	**Figures 12C,F,G**
Maldybulakia malcomi Edgecombe, 1998b	Unspecified	Boyd Volcanic Complex, NSW, Australia	Devonian	Freshwater	Edgecombe, 1998a,b	**Figures 12B,E**
Maldybulakia mirabilis (Tesakov and Alekseev, 1992)	Unspecified	Sheshenkarinskoy Suite, Kazakhstan	Devonian	Freshwater	Tesakov and Alekseev, 1992	**Figure 12D**
Willwerathia laticeps Størmer, 1936	Unspecified	Köppen quarry, Willwerath, Klerf Formation, Germany	Devonian	Marginal marine	Størmer, 1936; Anderson et al., 1998; Poschmann and Franke, 2006	**Figure 12A**

Taxa order alphabetically by grouping, time period, and then genus. Synonyms mentioned in Dunlop et al. (2019): Maldybulakia = Lophodesmus. *Note "Kasibelinuridae" is not used here as the group is considered paraphyletic (Bicknell et al., 2019b).*

can also have ophthalmic ridges, but this is taxon-specific and may be taphonomically controlled. Select taxa have preserved eyes: *Kasibelinurus amicorum* (Pickett, 1993; Dunlop and Selden, 1998) *Lunataspis aurora* (Rudkin et al., 2008; Rudkin and Young, 2009), and putatively *Willwerathia laticeps* (Anderson et al., 1998). Appendages are not known from this group of horseshoe crabs. Similar to synziphosurines, these taxa are mostly marine. Select non-xiphosurid xiphosurans, such as *Lu. aurora*, show a remarkable morphological similarity to xiphosurids (Rudkin et al., 2008).

Xiphosurida

True horseshoe crabs are an extant order that first appeared in the Devonian (**Figure 1**). Key characteristics of true horseshoe crabs are a large, keeled, crescentic cephalothorax with anteriorly located lateral compound eyes, a thoracetron of fused tergites containing one or two sections, and a styliform telson (Anderson and Selden, 1997; Rudkin et al., 2008; Briggs et al., 2012; Lamsdell, 2016). There are 30 genera and at least 82 species in Xiphosurida that are arrayed across the two suborders Belinurina and Limulina (**Tables 5–7**). Belinurina comprises only the family Belinuridae. Limulina comprises the superfamily Limuloidea, which includes Austrolimulidae, Limulidae, Paleolimulidae, and Rolfeiidae, and the genera *Bellinuroopsis* and *Valloisella* (*sensu* Lamsdell, 2016).

Belinurina

All taxa within this sub-order are members of the family Belinuridae. The fossil record of Belinuridae spans possibly from latest Devonian, with the example of *Bellinurus kiltorkensis* (Eller, 1938b), through to the Carboniferous and the Permian (**Figure 1**) and this family has the second largest generic diversity in Xiphosurida, with seven genera *Alanops*, *Anacontium*, *Bellinurus, Euproops, Liomesaspis, Prolimulus*, and *Xiphosuroides*, and 37 named species (**Table 5**, **Figures 13–21**). Belinurids have domed cephalothoraxes with flattened margins, genal spines that are either flat, posteriorly extending, or vestigial (Størmer, 1955), and ophthalmic ridges that curve posteriorly from the lateral compound eyes (Størmer, 1955; Fisher, 1977; Haug et al., 2012), which sometimes extend into ophthalmic spines (Fisher, 1977). The thoracetron is fused and ranges between round, trapezoidal, or triangular shapes (Størmer, 1955). *Euproops* and *Bellinurus* species have between five and seven articulated and expressed thoracetronic tergites with lateral spines (Størmer, 1955; Bergström, 1975; Fisher, 1977; Haug et al., 2012; Lamsdell, 2016). *Anacontium*, *Liomesaspis*, *Prolimulus,* and *Xiphosuroides* species have no exposed tergites and no marginal spines (Størmer, 1955; Shpinev and Vasilenko, 2018). Where known, the telson is styliform and elongate for all genera (Bergström, 1975). Appendages are known from select belinurids. Chelicerae and prosomal appendages are known from *Euproops danae*

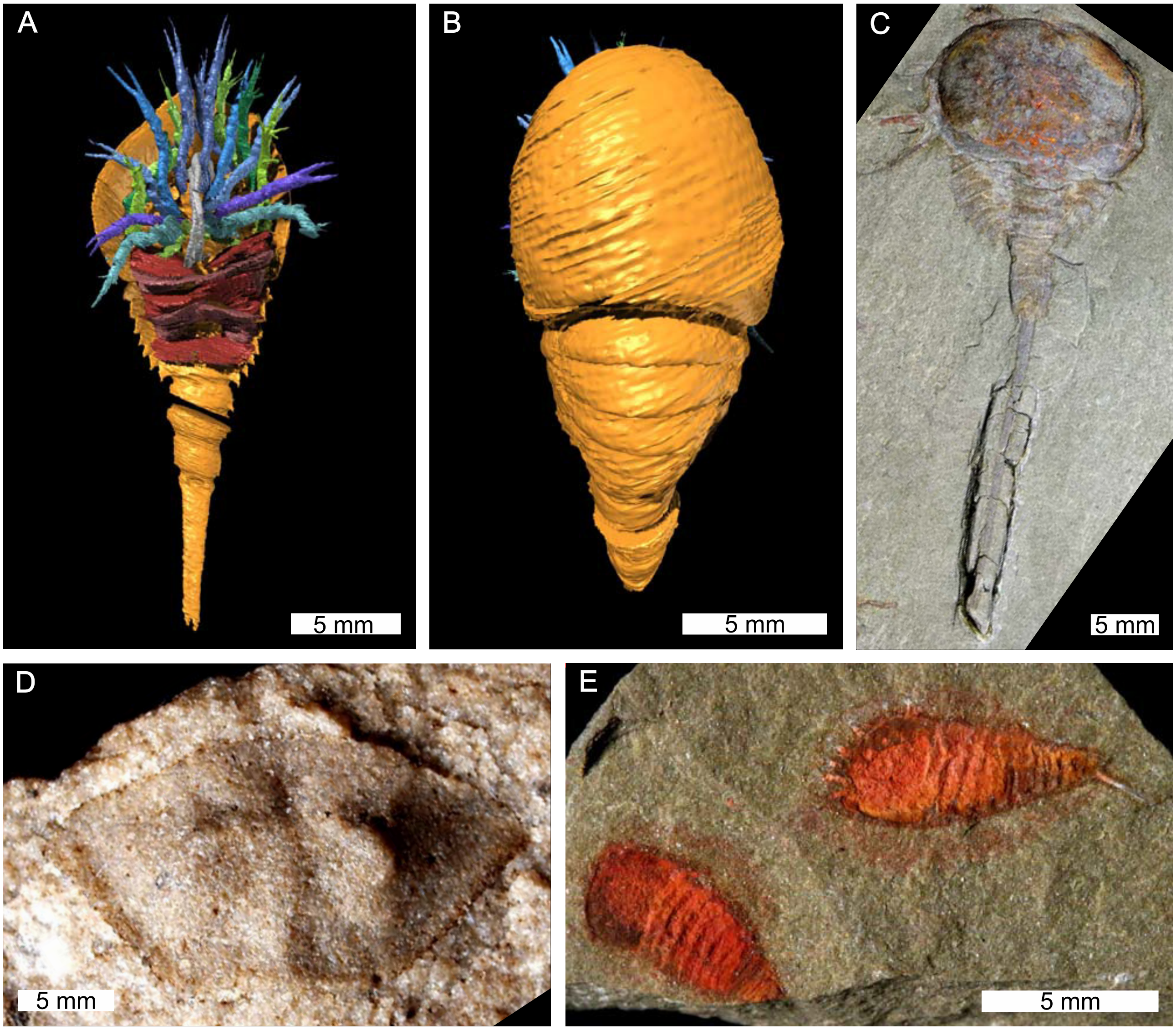

FIGURE 3 | Taxa considered possible horseshoe crabs that currently lack definitive affinities. **(A,B)** *Dibasterium durgae*: reconstructed in 3D from the Silurian-aged Herefordshire *Konservat-Lagerstätte*, England, UK. OUMNH C.29640, holotype **(A)** Ventral view. **(B)** Dorsal view. **(C)** An unnamed xiphosuran from the lower Ordovician-aged Upper Fezouata Formation, Morocco. YPM IP 227586. **(D)** *Drabovaspis complexa* from the Ordovician-aged Letná Formation, Czech Republic. MNHP L23577, holotype. This taxon is also considered to have aglaspidid affinities (Dunlop et al., 2019). **(E)** Two unnamed synziphosurines from the lower Ordovician-aged Lower Fezouata Formation, Morocco. YPM IP 517856. Photo credit: **(A,B)** Russell Garwood (also see Briggs et al., 2012); **(C)** Russell Bicknell; **(D)** Javier Ortega Hernández; **(E)** Jessica Utrup.

(Mazon Creek *Konservat-Lagerstätte*, Carbondale Formation, USA; Schultka, 2000; Haug et al., 2012; Haug and Rötzer, 2018b; Bicknell et al., 2019b) and *Alanops magnificus* (Montceau-les-Mines *Konservat-Lagerstätte*, Great Seams Formation, France; Racheboeuf et al., 2002; Bicknell et al., 2019b).

Belinurids are an extremely well-studied group of xiphosurids reflecting the expansive literature on the life mode, ontogeny and taxonomy of the group (e.g., Fisher, 1977, 1979; Anderson, 1994; Haug et al., 2012; Haug and Rötzer, 2018a,b; Bicknell et al., 2019d). Belinurids were the most successful horseshoe crab group in exploiting freshwater conditions (Fisher, 1984; Lamsdell, 2016). It has been suggested, that select taxa were likely effective at sub-aerial activity (more so than extant taxa) as cephalothoracic appendages were arranged similarly to extant xiphosurids, permitting more on-land exploration than is observed in extant taxa (Racheboeuf et al., 2002; Haug and Rötzer, 2018b). *Euproops danae* specifically had morphological characteristics that may have mimicked co-occurring leaves and arachnids (Dunbar, 1923; Fisher, 1979; Todd, 1991; Filipiak and Krawczynski, 1996),

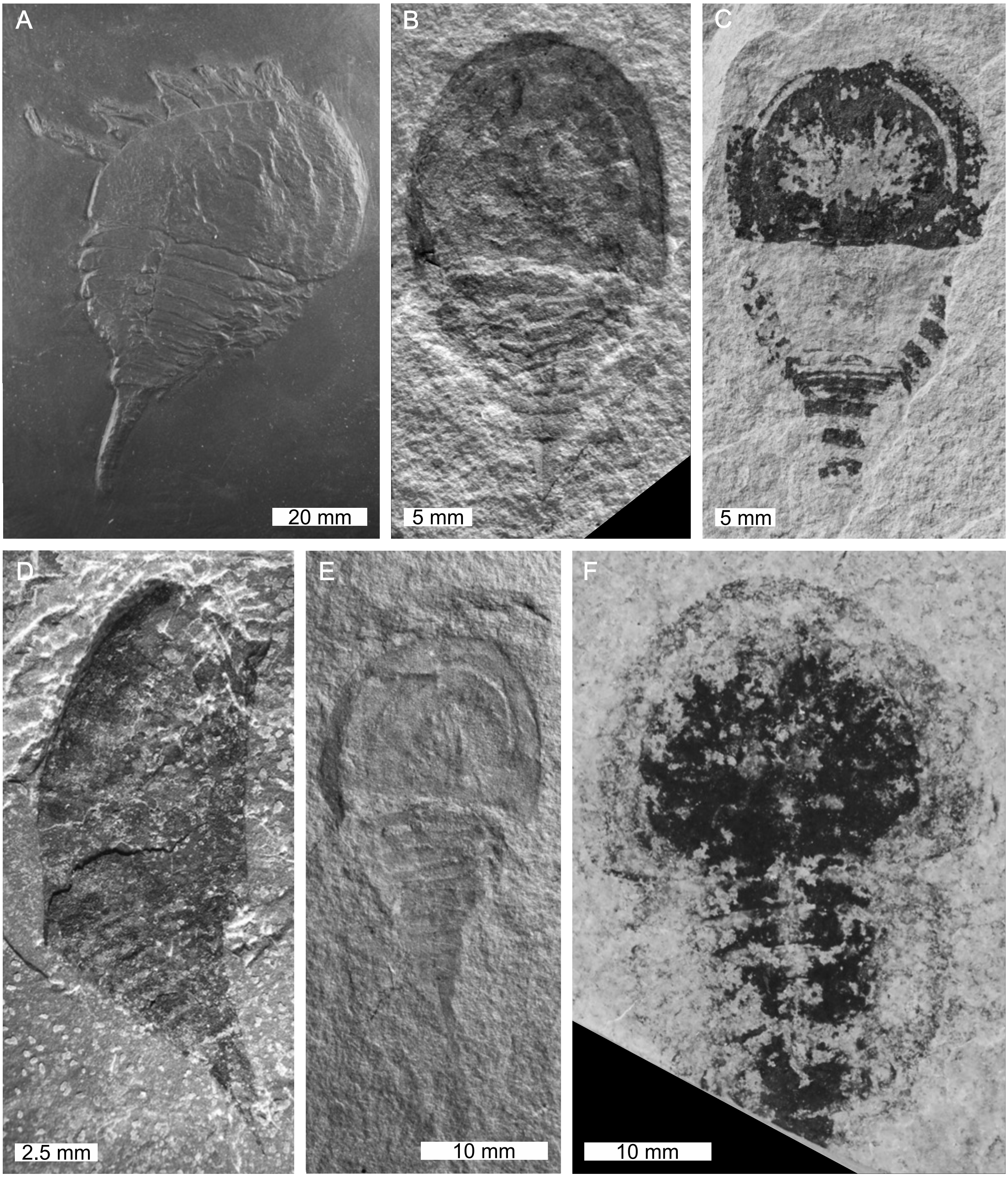

FIGURE 4 | Taxa in Prosomapoda that are not within Planaterga or Xiphosura. **(A)** *Weinbergina opitzi* from the Devonian-aged Hunsrück Slate Rheinland, Germany. MB.A.1987. **(B,E)** *Anderella parva* from the Carboniferous-aged Bear Gulch Limestone, Montana, USA. **(B)** CM 54200, holotype. **(E)** CM 54201, paratype **(C)** *Venustulus waukeshaensis* from the Silurian-aged Waukesha *Lagerstätte*, Wisconsin, USA. YPM IP 204461. **(D)** *Borchgrevinkium taimyrensis* from the Devonian-aged Sheshenkarinskoy Suite, Kazakhstan. PIN 12711, holotype. **(F)** *Camanchia grovensis* from the Silurian-aged Wenlock Scotch Grove Formation, Iowa, USA. U.W.4018/1a, holotype. Photo credit: **(A)** Andreas Abele, **(B,C,E)** Russell Bicknell, **(D)** Dmitry E. Shcherbakov, **(F)** Carrie A. Eaton. All converted to gray scale.

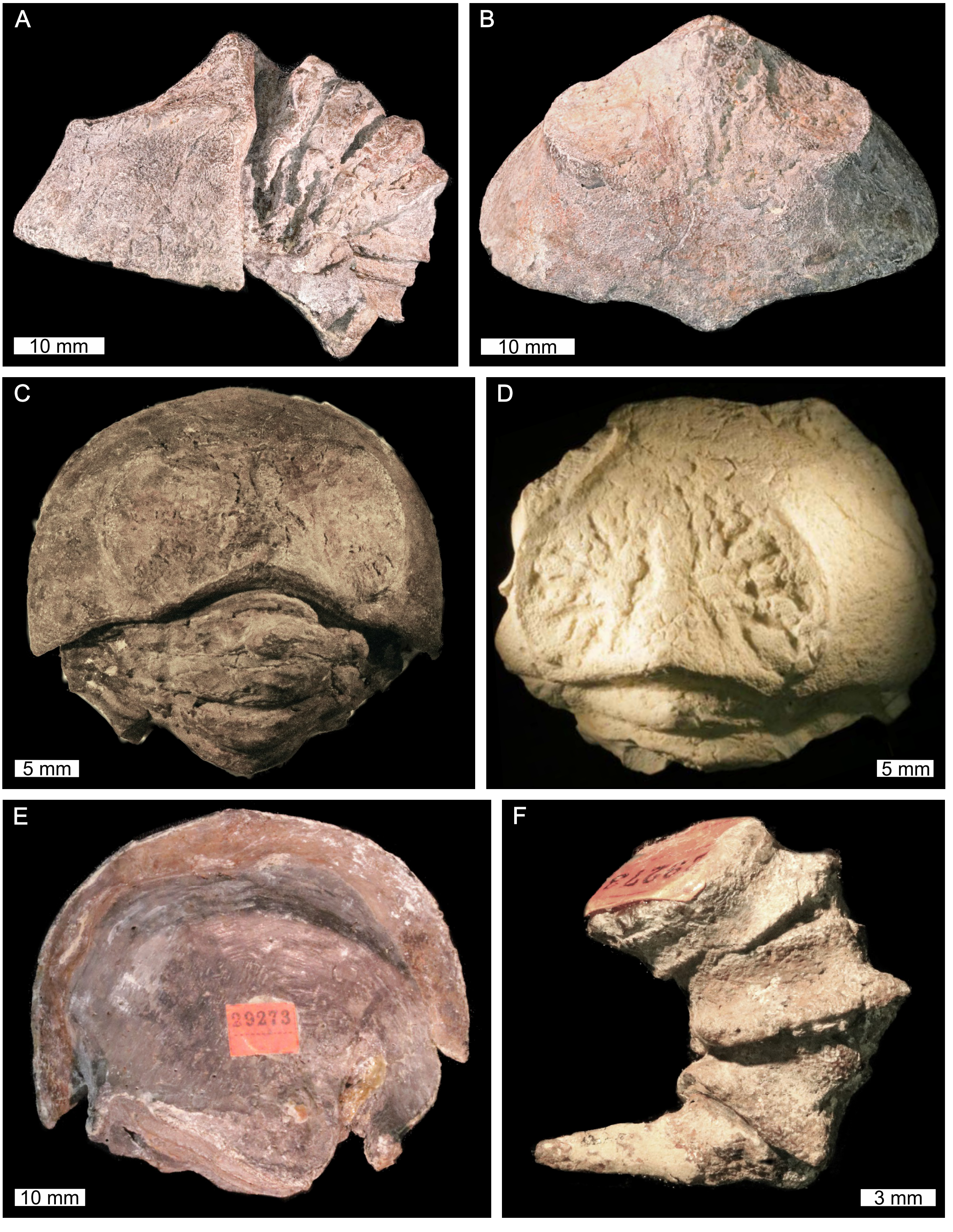

FIGURE 5 | *Legrandella lombardii* from the Devonian-aged Icla Formation, Bolivia. **(A–C,E,F)** AMNH 029273, holotype. **(A)** Lateral view. **(B)** Anterior view of prosoma. **(C)** Dorsal view of prosoma. **(E)** Ventral view of prosoma. **(F)** Lateral view of telson. **(D)** AMNH 029274, plastoparatype. Dorsal view of prosoma. Photo credit: Russell Bicknell.

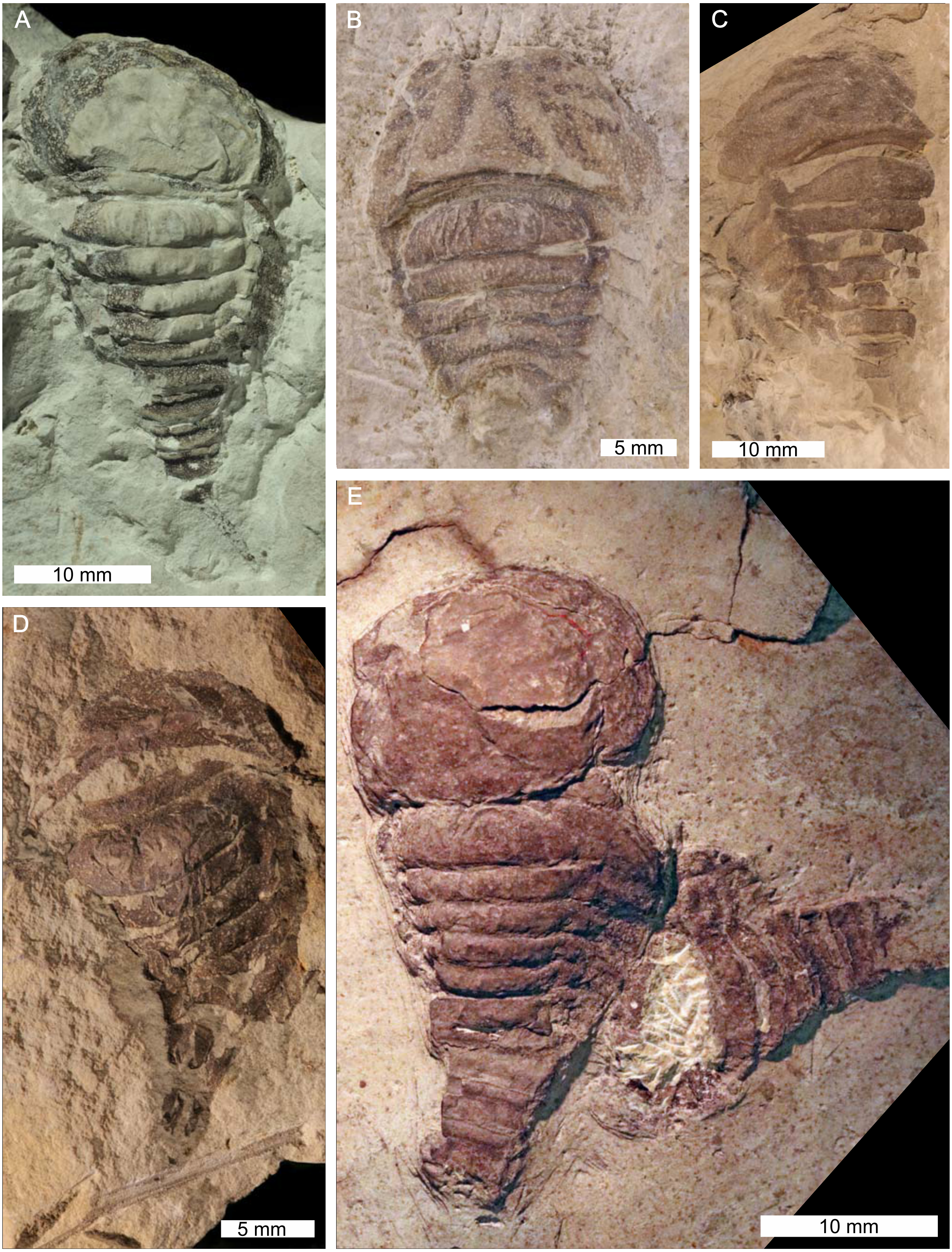

FIGURE 6 | Examples of *Bunodes lunula* from the Silurian-aged Oesel Group, Saaremaa Island, Estonia. **(A)** NMS G.2001.10.1. **(B)** YPM IP 212839. **(C)** NYSM 19113. **(D)** NYSM 19114. **(E)** Slab showing two specimens. AMNH 028734. Photo credit: **(A)** Bill Crighton; **(B–E)** Russell Bicknell.

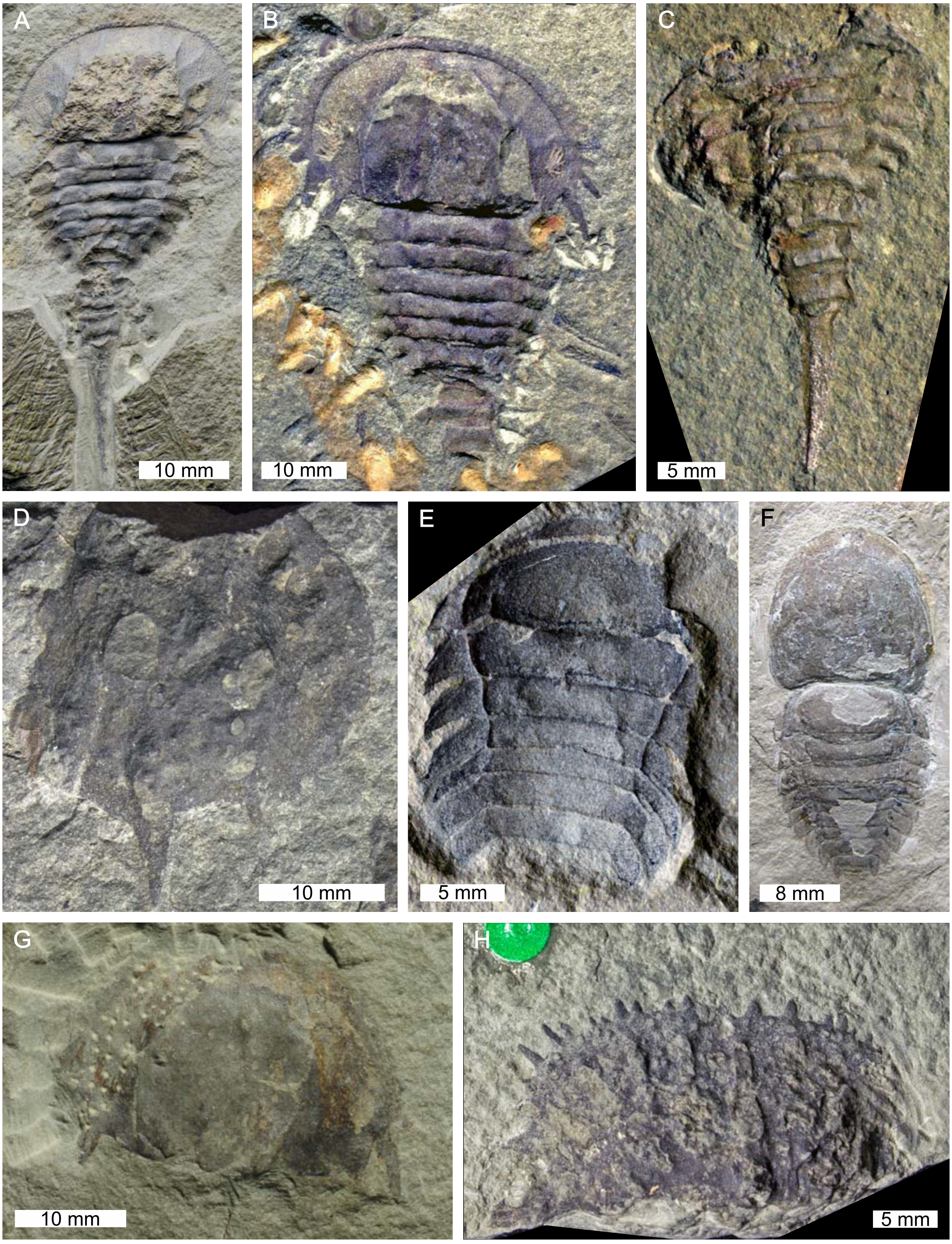

FIGURE 7 | *Limuloides* and *Pasternakevia*. **(A–C)** *Limuloides limuloides* from the Silurian-aged Leintwardine Formation, England, UK. **(A)** BGS.GSE 32393. **(B)** NHMUK PI. In. 60018. **(C)** NHMUK PI. In. 48422. **(D)** *Limuloides salweyi* from the Silurian-aged Leintwardine Formation, England, UK. NHMUK PI. In. 61510, holotype. **(E,F)** *Pasternakevia podolica* from the Silurian-aged Ustye Suite Series, Russia. **(E)** ISEA I–F/MP/3/1499/08. **(F)** ZIK 35611, holotype. **(G)** *Limuloides speratus* from the Silurian-aged Leintwardine Formation. NHMUK PI. I. 1180. **(H)** *Limuloides horridus* from the Silurian-aged Leintwardine Formation, England, UK. NHMUK PI. In. 61509, holotype. Photo credit: **(A)** David Marshall; **(B–D,G,H)** Stephen Pates; **(E)** Błażej Błażejowski; **(F)** Ewa Krzeminska.

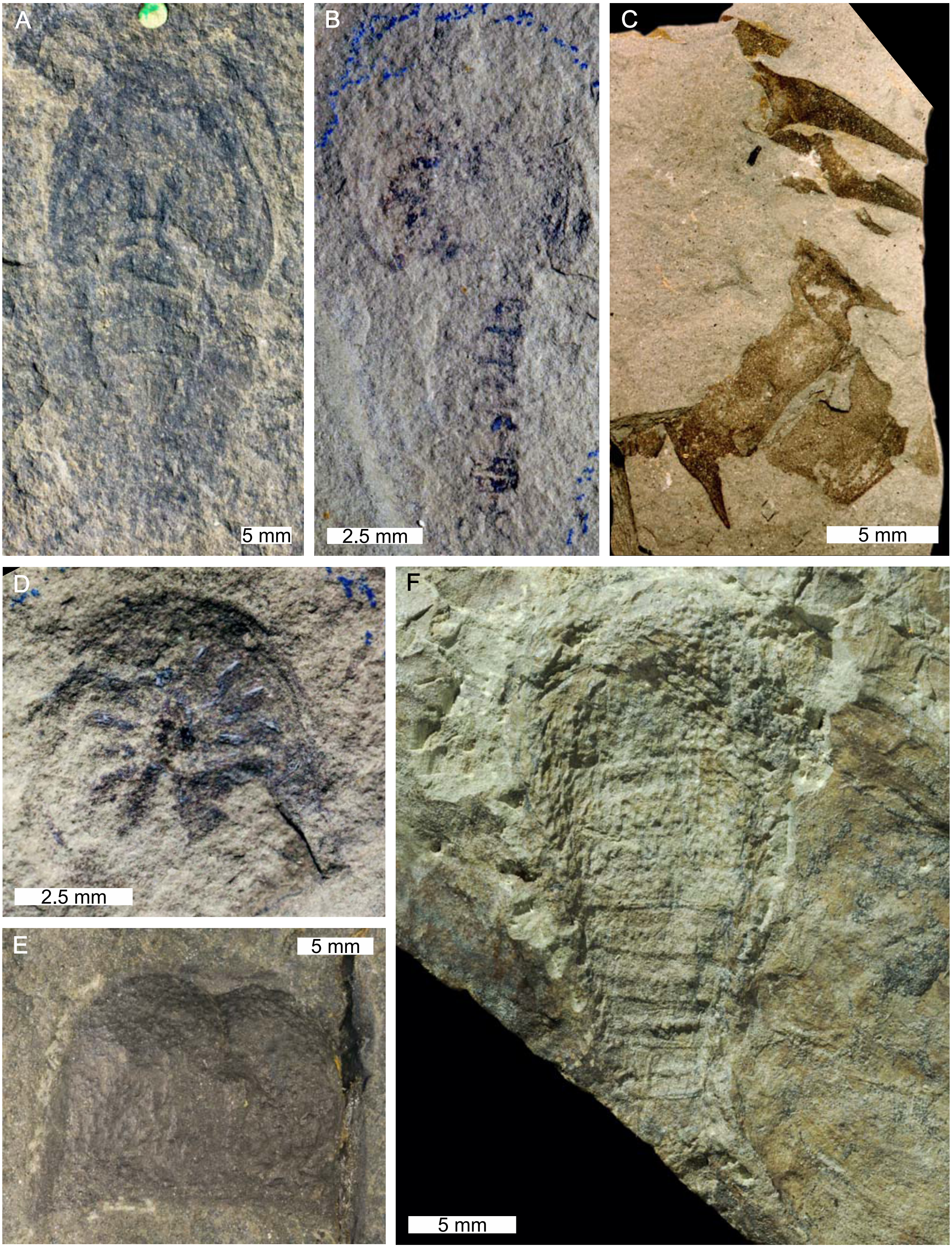

FIGURE 8 | "Synziphosurines" currently lacking a family assignment. **(A)** *Cyamocephalus loganensis* from the Silurian-aged Patrick Burn Formation, Scotland, UK. NHMUK PI. I. 16521, holotype. **(B,D)** *Bunaia woodwardi* from the Silurian-aged Vernon Shale, New York, USA. **(B)** NYSM 9911. **(D)** NYSM 9910. **(C)** Indeterminate *(Continued)*

FIGURE 8 | synziphosurine from the Devonian-aged Klerf Formation, Germany. SPW 831-D. **(E)** *"Bunaia" heintzi* from the Silurian-aged Ringerike Sandstone, Norway. NHM-UIO PMOA4361, holotype. **(F)** *Bembicosoma pomphicus* from the Silurian-aged Reservoir Formation, Scotland, UK. NMS G.1897.32.146, holotype. Photo credit: **(A)** Javier Ortega Hernández; **(B,D)** Russell Bicknell; **(C)** Markus Poschmann; **(E)** Hans Arne Nakrem; **(F)** Bill Crighton.

FIGURE 9 | Species within *Pseudoniscus*. **(A)** *Pseudoniscus falcatus* from the Silurian-aged Patrick Burn Formation, Scotland, UK. NHMUK Pl. In. 44122, holotype. **(B)** *Pseudoniscus aculeatus* from the Silurian-aged Oesel Group, Saaremaa Island, Estonia. AMNH 029281. **(C,D)** *Pseudoniscus roosevelti* from the Silurian-aged Vernon Shale, New York, USA. **(C)** NMS G.2004.45.5a. **(D)** NYSM 4762. **(E)** *Pseudoniscus clarkei* from the Silurian-aged Vernon Shale, New York, USA. NYSM E1030. **(D,E)** were photographed under ethanol. Photo credit: **(A)** Lucie Goodayle, NHM, London; **(B,D,E)** Russell Bicknell; **(C)** Bill Crighton.

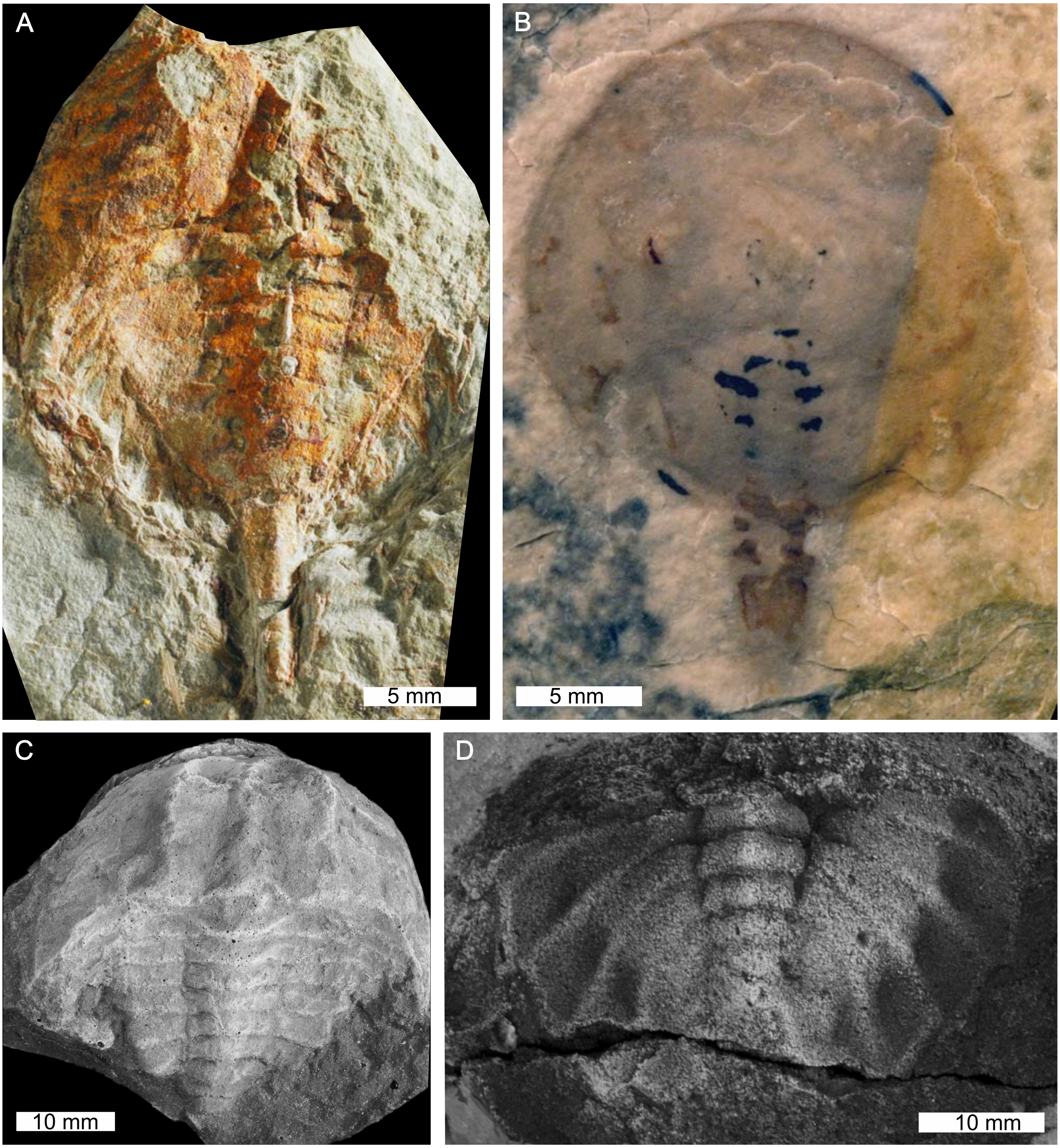

FIGURE 10 | Stem xiphosurids from Canada and the USA. **(A)** *Pickettia carteri* from the Devonian-aged Cattaraugus Formation, Pennsylvania, USA. BMSC E 9644, holotype. **(B)** *Lunataspis aurora* from the Ordovician-aged Churchill River Group, Canada. MM I-4000A, holotype. **(C)** *"Belinurus" alleghenyensis* from the Devonian-aged Chadakoin Formation, New York, USA. Cast of CM11065, holotype. **(D)** *Elleria morani* from the Devonian-aged Venango Formation, Pennsylvania, USA. CM11574, holotype. **(C,D)** were coated with ammonium chloride sublimate. Photo credit: **(A)** KC Kratt; **(B)** Permission to reproduce photographs granted by Graham Young and the Manitoba Museum; **(C,D)** Russell Bicknell.

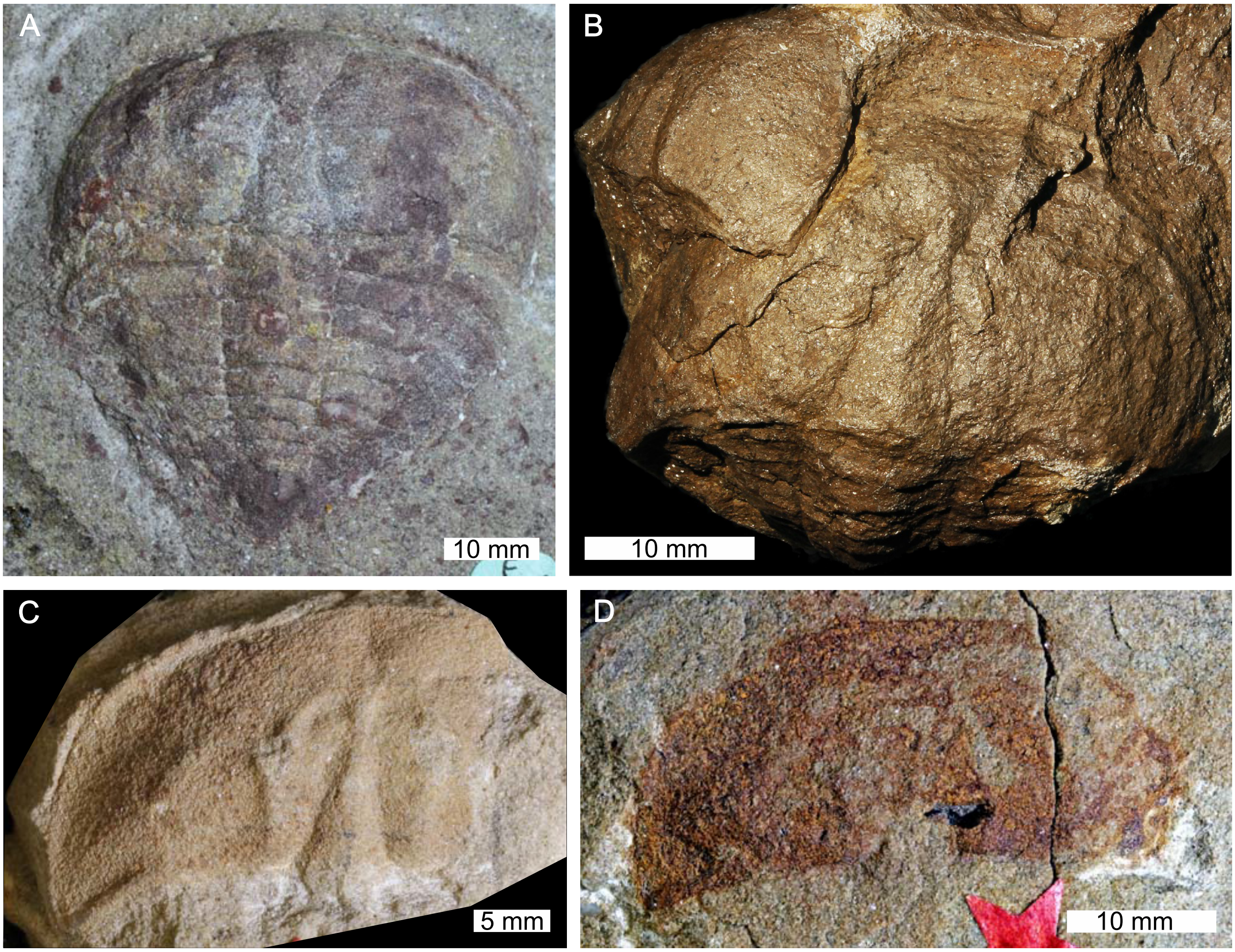

FIGURE 11 | Non-xiphosurid xiphosuran species from Australia and USA. **(A)** *Kasibelinurus amicorum* from the Devonian-aged Mandagery Sandstone, Australia. AM F68969, holotype. **(B)** *"Kasibelinurus" randalli* from the Devonian-aged Chadakoin Formation, Pennsylvania, USA. **(B)** USNM PAL 484524. **(C,D)** *"Kasibelinurus" randalli* from the Devonian-aged Venango Formation, Pennsylvania, USA. **(C)** YPM IP 09010, holotype. **(D)** YPM IP 30656, paratype. Photo credit: **(A)** Josh White; **(B–D)** Russell Bicknell.

although this suggestion remains to be thoroughly explored. The ontogeny of fossil belinurids has been documented using *Euproops* sp. from the Osnabrück Formation (Pennsylvanian) of Germany (Haug et al., 2012), and *E. danae* from the Mazon Creek *Konservat-Lagerstätte* (Pennsylvanian) of the USA (Haug and Rötzer, 2018b). The apparently large belinurid diversity almost definitely reflects over-splitting during the early twentieth century (Anderson, 1997; Lamsdell, 2016) and grouping Euproopidae with Belinuridae (Dunlop et al., 2019). A re-evaluation of the family is therefore needed (Selden and Siveter, 1987) and should build on Anderson (1994), Haug et al. (2012), and Haug and Rötzer (2018b) who synonymised *Euproops* species after determining that cephalothoracic compression produced variable, supposedly species-diagnostic features (Haug and Rötzer, 2018b; Shpinev, 2018).

Limulina

This sub-order comprises the superfamily Limuloidea, the families Paleolimulidae and Rolfeiidae, and the genus *Bellinuroopsis*. Limulina has a fossil record ranging from the Devonian to Recent. The diagnostic feature that separates Limuloidea from Belinurina is the fusion of the two most posterior thoracetronic tergites (*sensu* Lamsdell, 2016).

Paleolimulidae

This family has a fossil record spanning the Carboniferous to Permian (**Table 6**). Three genera construct Paleolimulidae: *Moravurus*, *Paleolimulus*, and *Xaniopyramis* and there are six species within these three genera (**Figure 22**). The morphology of paleolimulids broadly resembles that of modern horseshoe crabs, but members of this group are smaller than extant taxa (Størmer, 1955; Shuster, 2001). Paleolimulids have a domed cephalothorax,

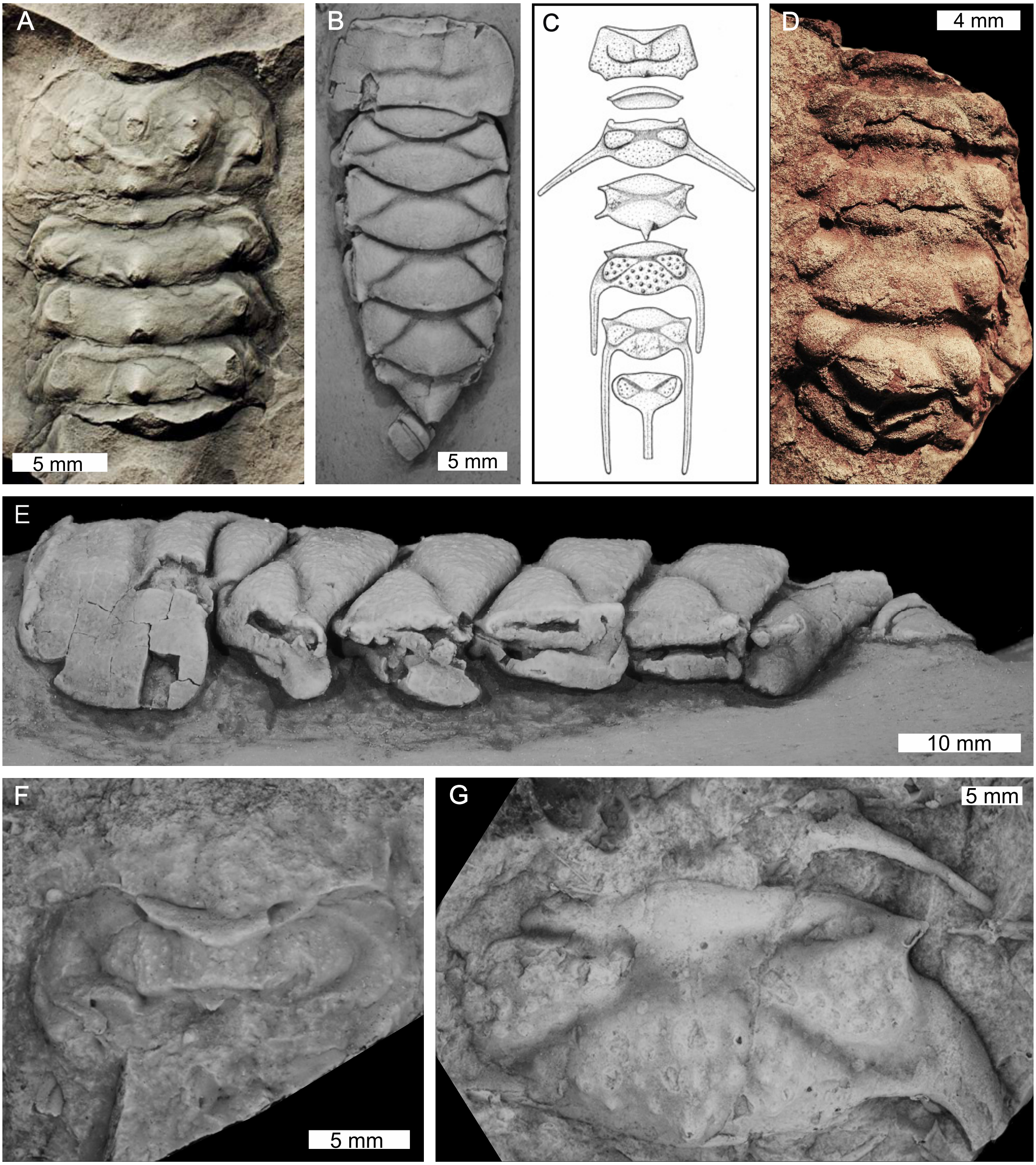

FIGURE 12 | Xiphosuran taxa within genera *Maldybulakia* and *Willwerathia*. **(A)** *Willwerathia laticeps* from the Devonian-aged Klerf Formation, Germany. Cast of Leunissen collection specimen SLK Ib, cast number SPW 1308-D. **(B,E)** *Maldybulakia malcomi* from the Devonian-aged Boyd Volcanic Complex, NSW, Australia. AM F102533, holotype. **(B)** Dorsal view. **(E)** Lateral view. **(C,F,G)** *Maldybulakia angusi* from the Devonian-aged Sugarloaf Creek Formation, NSW, Australia. **(C)** Reconstruction presented in Edgecombe (1998b, Figure 12). **(F)** AM F102560. **(G)** AM F102565, cast of holotype. **(D)** *Maldybulakia mirabilis* from the Devonian-aged Sheshenkarinskoy Suite, Kazakhstan. PIN No. 249/1, holotype. **(B,E–G)** Coated in ammonium chloride sublimate. **(B,E–G)** Converted to gray scale. Photo credit: **(A)** Markus Poschmann; **(B,E–G)** Patrick Smith; **(C)** Permission to use reconstruction granted by Gregory Edgecombe, **(D)** Alexander S. Alekseev.

TABLE 5 | Sub-order Belinurina after Dunlop et al. (2019).

Taxon	Family	Geological information (where detailed) and country	Time period	Environment	Citation for figured specimens	Figured here
Bellinurus kiltorkensis Baily, 1869	Belinuridae	Kiltorcan Formation, Republic of Ireland	Devonian-Carboniferous	Freshwater (*sensu* Bluck, 1967)	Baily, 1870; Cole, 1901; Eller, 1938b	**Figure 14F**
Alanops magnifica Racheboeuf et al., 2002	Belinuridae	Montceau-les-Mines *Konservat-Lagerstätte*, Great Seams Formation, France	Carboniferous	Freshwater	Racheboeuf et al., 2002; Perrier and Charbonnier, 2014; Bicknell et al., 2019b	**Figures 13A,B**
Bellinurus arcuatus Baily, 1863	Belinuridae	Pennine Middle Coal Measures Formation, England, UK; South Wales Lower Coal Measures Formation, Wales, UK,	Carboniferous	Freshwater	Baily, 1863, 1870; Dix and Pringle, 1929; Eller, 1938b; Parkes and Sleeman, 1997	**Figure 13C**
Bellinurus baldwini Woodward, 1907	Belinuridae	Pennine Middle Coal Measures Formation, England, UK	Carboniferous	Freshwater	Woodward, 1907; Eller, 1938b; Novozhilov, 1991	**Figure 13E**
Bellinurus bellulus Pictet, 1846	Belinuridae	South Wales Lower Coal Measures Formation, Wales, UK; Pennine Middle Coal Measures Formation, Lancashire, England, UK	Carboniferous	Freshwater	Pictet, 1846; Baily, 1863; Baldwin, 1905, 1906; Dix and Pringle, 1929; Eller, 1938b	**Figure 13D**
Bellinurus carwayensis Dix and Pringle, 1929	Belinuridae	South Wales Lower Coal Measures Formation, Wales, UK	Carboniferous	Freshwater	Dix and Pringle, 1929	**Figure 13C**
Bellinurus concinnus Dix and Pringle, 1929	Belinuridae	South Wales Lower Coal Measures Formation, Wales, UK	Carboniferous	Freshwater	Dix and Pringle, 1929; Eller, 1938b	**Figure 14B**
Bellinurus grandaevus Jones and Woodward, 1899	Belinuridae	Canso Group, Parrsboro, Nova Scotia, Canada; Riversdale Group, Nova Scotia, Canada	Carboniferous	Freshwater	Jones and Woodward, 1899; Eller, 1938b; Copeland, 1957a	**Figure 14D**
Bellinurus iswariensis (Chernyshev, 1928)	Belinuridae	Almaznaya Formation; Ukraine; Mospinskaya Formation, Ukraine; Smolyaninovskaya (?) Formation, Russia	Carboniferous	Freshwater (*sensu* Eros et al., 2012)	Chernyshev, 1928; Eller, 1938b; Shpinev, 2018	**Figure 14C**
Bellinurus koenigianus Woodward, 1872	Belinuridae	South Wales Lower Coal Measures Formation, Wales, UK; Pennine Middle Coal Measures Formation, England, UK	Carboniferous	Freshwater	Woodward, 1872; Dix and Pringle, 1929; Eller, 1938b; Bergström, 1975	**Figure 14E**
Bellinurus lacoei Packard, 1885	Belinuridae	Mazon Creek *Konservat-Lagerstätte*, Carbondale Formation, Illinois, USA	Carboniferous	Freshwater (*sensu* Fisher, 1979)	Packard, 1885	**Figure 14A**
Bellinurus longicaudatus Woodward, 1907	Belinuridae	Pennine Middle Coal Measures Formation, England, UK	Carboniferous	Freshwater	Woodward, 1907; Eller, 1938b	**Figure 15C**
Bellinurus lunatus (Martin, 1809)	Belinuridae	Pennine Middle Coal Measures Formation, Rochdale, England, UK; Upper Silesia Coal Basin, Czech Republic	Carboniferous	Freshwater	Martin, 1809; Prantl and Přibyl, 1956; Filipiak and Krawczynski, 1996; Krawczynski et al., 1997	**Figures 15A,B**
Bellinurus metschetnensis (Chernyshev, 1928)	Belinuridae	Belaya Kalitva Formation, Ukraine	Carboniferous	Freshwater (*sensu* Eros et al., 2012)	Chernyshev, 1928; Eller, 1938b; Shpinev, 2018	**Figure 15D**
Bellinurus morgani Dix and Pringle, 1930	Belinuridae	South Wales Lower Coal Measures Formation, Wales, UK	Carboniferous	Freshwater	Dix and Pringle, 1930; Fisher, 1982	**Figure 15E**
Bellinurus pustulosus Dix and Pringle, 1929	Belinuridae	South Wales Lower Coal Measures Formation, Wales, UK	Carboniferous	Freshwater	Dix and Pringle, 1929; Eller, 1938b	**Figure 16D**

(Continued)

TABLE 5 | Continued

Taxon	Family	Geological information (where detailed) and country	Time period	Environment	Citation for figured specimens	Figured here
Bellinurus reginae Baily, 1863	Belinuridae	Canso Group, Parrsboro, Nova Scotia, Canada; Karviná Formation (?), Upper Silesia, Poland; South Wales Lower Coal Measures Formation, Wales, UK	Carboniferous	Freshwater	Baily, 1863; Woodward, 1867; Zittel, 1881; Vogdes, 1917; Copeland, 1957a; Novozhilov, 1991; Parkes and Sleeman, 1997	**Figures 16C,E**
Belinurus šustai Prantl and Přibyl, 1956	Belinuridae	Karviná Formation, Czech Republic.	Carboniferous	Freshwater (*sensu* Dopita and Kumpera, 1993)	Prantl and Přibyl, 1956	**Figure 17A**
Bellinurus stepanowi Chernyshev, 1928	Belinuridae	Almaznaya Formation, Ukraine; Kamenskaya Formation, Russia	Carboniferous	Freshwater (*sensu* Eros et al., 2012)	Chernyshev, 1928; Eller, 1938b; Shpinev, 2018	**Figure 16B**
Bellinurus silesiacus Roemer, 1883	Belinuridae	Upper Silesia Coal Basin, Poland	Carboniferous	Freshwater	Roemer, 1883; Eller, 1938b	**Figure 16A**
Bellinurus trechmanni Woodward 1918	Belinuridae	Pennine Upper Coal Measures Formation, England, UK; Sprockhövel Formation, Germany	Carboniferous	Freshwater	Woodward, 1918; Trechmann and Woolacott, 1919; Eller, 1938b	**Figure 17B**
Bellinurus trilobitoides (Buckland, 1837)	Belinuridae	Bickershaw *Konservat-Lagerstätte*, England, UK; Clay Ironstone, England, UK; ?Pennine Upper Coal Measures Formation, England, UK.	Carboniferous	Freshwater	Buckland, 1837; Prestwich, 1840; Anderson et al., 1997; Bicknell and Pates, 2019b	**Figure 17D**
Bellinurus truemani Dix and Pringle, 1929	Belinuridae	South Wales Lower Coal Measures Formation, Wales, UK; Sprockhövel Formation, Germany	Carboniferous	Freshwater	Dix and Pringle, 1929; Eller, 1938b; Schultka, 1994; Brauckmann, 2005	**Figure 17C**
Euproops anthrax (Prestwich, 1840)	Belinuridae	Pennant Sandstone Formation, Wales, UK; South Wales Upper Coal Measures Formation, Wales, UK	Carboniferous	Freshwater	Prestwich, 1840; Størmer, 1955; Bergström, 1975; Novozhilov, 1991	**Figure 18F**
Euproops bifidus Siegfried, 1972	Belinuridae	Flöz Dreibänke Formation, Germany	Carboniferous	Freshwater	Siegfried, 1972; Brauckmann, 1982, 2005	**Figure 18D**
Euproops cambrensis Dix and Pringle, 1929	Belinuridae	South Wales Lower Coal Measures Formation, Wales, UK	Carboniferous	Freshwater	Dix and Pringle, 1929	**Figure 18C**
Euproops danae (Meek and Worthen, 1865)	Belinuridae	Almaznaya Formation; Ukraine; Beeman Formation, New Mexico, USA; Donets Black Coal Basin, Ukaraine; Farrington Group, England, UK; Mazon Creek *Konservat-Lagerstätte*, Carbondale Formation, Illinois, USA; Riversdale Group, Canada; Smolyaninovskaya Formation, Russia; Uffington Shale; West Virginia, USA	Carboniferous	Freshwater	Meek and Worthen, 1865; Packard, 1885; Chernyshev, 1928; Raymond, 1945; Copeland, 1957b; Murphy, 1970; Ambrose and Romano, 1972; Fisher, 1979; Anderson, 1994; Babcock and Merriam, 2000; Shuster, 2001; Rudkin and Young, 2009; Lucas et al., 2014; Bicknell et al., 2018d, 2019b,d; Haug and Rötzer, 2018b; Shpinev, 2018; Tashman et al., 2019; Haug and Haug, 2020	**Figure 19**
Euproops longispina Packard, 1885	Belinuridae	Allegheny Formation, Pennsylvania, USA	Carboniferous	Freshwater	Packard, 1885	**Figures 18A,B**
Euproops mariae Crônier and Courville, 2005	Belinuridae	Graissessac Shale and Coal, Graissessac Basin, France	Carboniferous	Freshwater	Crônier and Courville, 2005	**Figure 18E**
Euproops meeki Dix and Pringle, 1929	Belinuridae	South Wales Upper Coal Measures Formation, Wales, UK	Carboniferous	Freshwater	Dix and Pringle, 1929	**Figure 20D**
Euproops orientalis Kobayashi, 1933	Belinuridae	Jido Series, Korea	Carboniferous	Freshwater	Kobayashi, 1933	**Figure 20C**

(Continued)

TABLE 5 | Continued

Taxon	Family	Geological information (where detailed) and country	Time period	Environment	Citation for figured specimens	Figured here
Euproops rotundatus Prestwich, 1840	Belinuridae	Coal Measures Westhoughton, England, UK; Orzesze Beds, Upper Silesia Coal Basin, Poland; South Wales Upper Coal Measures Formation, Wales, UK; Pennine Middle Coal Measures Formation, Lancashire, England, UK	Carboniferous	Freshwater	Prestwich, 1840; Woodward, 1867; Bölsche, 1879; Baldwin, 1902, 1906; Gaskell, 1908; Vogdes, 1917; Størmer, 1955; Filipiak and Krawczynski, 1996; Krawczynski et al., 1997; Anderson et al., 1999; Schultka, 2000; Lomax et al., 2016; Haug and Haug, 2020	**Figure 20B**
Euproops sp.	Belinuridae	Bear Gulch Limestone, Montana, USA; Mazon Creek *Konservat- Lagerstätte*, Carbondale Formation, Illinois, USA; Piesberg quarry, Osnabrück Formation Germany; Windsor Group, Canada	Carboniferous	Freshwater	Copeland, 1957b; Schram, 1979; Brauckmann, 1982; Schultka, 2000; Haug et al., 2012; Bicknell et al., 2019b; Haug and Haug, 2020	**Figure 20A**
?Liomesaspis birtwelli (Woodward, 1872)	Belinuridae	Pennine Lower Coal Measures Formation, England, UK	Carboniferous	Freshwater	Woodward, 1872: Gaskell, 1908; Bergström, 1975; Fisher, 1984	**Figure 21C**
Prolimulus woodwardi Fritsch 1899	Belinuridae	Kladno Formation, Czech Republic	Carboniferous	Freshwater (*sensu* Hannibal and Feldmann, 1981)	Fritsch, 1899; Prantl and Přibyl, 1956; Novozhilov, 1991; Štamberg and Zajíc, 2008	**Figures 21D–F**
Liomesaspis laevis Raymond, 1944	Belinuridae	Bickershaw *Konservat-Lagerstätte*, England, UK; Meisenheim Formation, Germany; Mazon Creek *Konservat- Lagerstätte*, Carbondale Formation, Illinois, USA; Montceau-les-Mines *Konservat-Lagerstätte*, Great Seams Formation, France	Carboniferous-Permian	Freshwater	Raymond, 1944; Størmer, 1955; Vandenberghe, 1960; Müller, 1962; Novozhilov, 1991; Malz and Poschmann, 1993; Anderson, 1997; Anderson et al., 1997; Schindler and Poschmann, 2012	**Figures 21A,B**
Anacontium brevis Raymond, 1944	Belinuridae	Wellington Formation, Oklahoma, USA	Permian	Freshwater	Raymond, 1944	**Figure 21H**
Anacontium carpenteri Raymond, 1944	Belinuridae	Wellington Formation, Oklahoma, USA	Permian	Freshwater	Raymond, 1944	**Figure 21G**
Liomesaspis leonardensis (Tasch, 1961)	Belinuridae	Wellington Formation, Kansas, USA	Permian	Freshwater	Tasch, 1961	**Figure 21I**
Xiphosuroides khakassicus Shpinev and Vasilenko, 2018	?Belinuridae	Sarskaya Formation, Khakassia, Russia	Carboniferous	Freshwater	Shpinev and Vasilenko, 2018	**Figure 20E**

Taxa order by time-period and then alphabetically by genus. Synonyms mentioned in Dunlop et al. (2019): Belinuridae = Euproopidae and Liomesaspididae*;* Bellinurus = Belinurus, Steropsis and Koenigiella*;* Euproops = Prestwichia and Prestwichianella*;* Liomesaspis = Pringlia and Palatinaspis. *? denotes uncertain taxonomic affinities and formation assignment.*

ophthalmic ridges that converge anteriorly to lateral compound eyes and genal spines that extend posteriorly as far as the fourth thoracic tergite (Lerner et al., 2016). The thoracetron is fused and has an angular axial section with transverse and longitudinal thoracetronic ridges occasionally present (Raymond, 1944; Siveter and Selden, 1987; Novozhilov, 1991), along with a styliform telson (Pickett, 1984; Seegis, 2014). Moveable thoracetronic spines are occasionally preserved (Seegis, 2014). Unique features of select taxa include the additional articulation between the thoracetron and telson known from *Paleolimulus signatus* and the expressed opercular (VIII) tergite producing a free thoracetronic lobe in *Pa. woodae* and *Xaniopyramis linseyi* (Størmer, 1952; Babcock et al., 2000; Lerner et al., 2016). Rare specimens preserve soft-parts. *Paleolimulus signatus* (Insect Hill *Konservat-Lagerstätte*, Wellington Formation, USA, Permian) preserves cephalothoracic and thoracetronic appendages (Dunbar, 1923; Raymond, 1944; Størmer, 1952; Babcock and Merriam, 2000; Bicknell et al., 2019b). These appendages are strikingly similar to modern horseshoe crabs (Størmer, 1955; Bicknell et al., 2019b). *Xaniopyramis linseyi* (Upper Limestone Group, Scotland, Carboniferous) preserves impressions of cephalothoracic appendage muscles (Siveter and Selden, 1987).

TABLE 6 | Taxa in the suborder Limulina.

Taxon	Family	Geological information (where detailed) and locality	Time period	Environment	Citation for figured specimens	Figured here
Moravurus rehori Přibyl, 1967	Paleolimulidae	Kyjovice Formation, Czech Republic	Carboniferous	Marine (*sensu* Bábek et al., 2004)	Přibyl, 1967	**Figure 22C**
Paleolimulus woodae Lerner et al., 2016	Paleolimulidae	Horton Bluff Formation, Nova Scotia, Canada	Carboniferous	Marine	Lerner et al., 2016	**Figure 22B**
Xaniopyramis linseyi Siveter and Selden, 1987	Paleolimulidae	Upper Limestone Group, England, UK	Carboniferous	Marine	Siveter and Selden, 1987	**Figure 22A**
Paleolimulus signatus (Beecher, 1904)	Paleolimulidae	Barneston Limestone Kansas, USA; Francis Creek Shale Member, Illinois, USA; Insect Hill *Konservat-Lagerstätte*, Wellington Formation, Kansas, USA; Pony Creek Shale *Konservat-Lagerstätte,* Wood Siding Formation, Kansas, USA	Carboniferous–Permian	Marine	Beecher, 1904; Dunbar, 1923; Størmer, 1955; Novozhilov, 1991; Babcock et al., 2000; Shuster, 2001; Shuster and Anderson, 2003; Bicknell et al., 2019b	**Figures 22D,F**
Paleolimulus kunguricus Naugolnykh, 2017	Paleolimulidae	Philippovian Formation, Russia	Permian	Marine	Naugolnykh, 2017, 2018	**Figure 22G**
?*Paleolimulus juresanensis* Chernyshev, 1933	Paleolimulidae	Maltchev or Belogor Beds. No certain formation (T. Tolmacheva pers. Comms. 2018)	Permian	Marine	Chernyshev, 1933	**Figure 23E**
Rolfeia fouldenensis Waterston, 1985	Rolfeiidae	Cementstones Group, Scotland, UK	Carboniferous	Marine	Waterston, 1985	**Figure 23B**
Bellinuroopsis rossicus Chernyshev, 1933	Unspecified	Lebedjan Formation, Russia	Devonian	Marine	Chernyshev, 1933; Eller, 1938b; Størmer, 1955; Novozhilov, 1991	**Figure 23A**

The taxa are order by family, time-period and then alphabetically by genus and species. Synonyms mentioned in Dunlop et al. (2019): Paleolimulidae = Moravurdiae*.* Bellinuroopsis = Neobelinuropsis*.* Paleolimulus = Prestwichia*. ? denotes uncertain taxonomic affinities.*

Paleolimulid species were mostly marine taxa and their morphologies, similar to extant horseshoe crabs, reflect this life mode. They may have therefore variably explored swimming and burrowing life modes, with these ecological inferences related to the presence of movable thoracic spines (Siveter and Selden, 1987). *Paleolimulus woodae* lacked thoracetronic movable spines and may have been capable of swimming, while *Xaniopyramis linseyi*, adorned with large thoracetronic spines, would have likely burrowed (Siveter and Selden, 1987; Lerner et al., 2016). The diversity of Paleolimulidae has previously been overstated and *Paleolimulus* is now considered a paraphyletic group (Lamsdell, 2016; Lerner et al., 2017; Bicknell, 2019). Many paleolimulid forms are now considered to be austrolimulids (discussed below), so continued research into these taxa is needed to uncover the true disparity of forms within this family and diversity of both austrolimulids and paleolimulids (Bicknell, 2019).

Rolfeiidae

This monospecific family consists of *Rolfeia fouldenensis* and is known from the Carboniferous-aged Cementstones Group, Scotland (**Table 6**, **Figure 23**). The cephalothorax is domed, exhibiting small genal spines, and a thick cephalothoracic margin. The species has a cardiac lobe narrows anteriorly and ophthalmic ridges that cross the lateral compound eyes, converging at the cardiac lobe (Waterston, 1985). The thoracetron is fused with visible tergal divisions and the opercular tergite is fully expressed. Large fixed and small moveable thoracetronic spines are known from *R. fouldenensis* (Waterston, 1985; Selden and Siveter, 1987; Lamsdell, 2016) and the telson is styliform. Lamsdell (2016) suggested that transverse cephalothoracic ridge nodes were characteristic of the family; however, as the holotype considered here lack these features, this feature may be treated tentatively. Presently, no appendages are known from this group (Waterston, 1985).

Rolfeia fouldenensis is the only species exhibiting large fixed thoracetronic spines extending laterally, coupled with smaller moveable thoracetronic spines (Clarkson, 1985). These spines likely provided the thoracetron with more surface area to prevent individuals from sinking into the substrate (Anderson, 1994) when they were not suspended in water (Siveter and Selden, 1987). Originally thought to be a possible paleolimulid due to tergal expression on the thoracetron (Waterston, 1985), the unique characters of both moveable and overdeveloped fixed spines, coupled with an expressed opercular tergite, were

TABLE 7 | Fossil taxa in superfamily Limuloidea.

Taxon	Family	Geological information (where detailed) and locality	Time period	Environment	Citation for figured specimens	Figured here
?Paleolimulus longispinus Schram, 1979	Austrolimulidae	Bear Gulch Limestone, Montana, USA	Carboniferous	Marginal Marine	Schram, 1979; Hagadorn, 2002; Haug et al., 2012	**Figures 25B,C**
?Paleolimulus jakovlevi Glushenko and Ivanov, 1961	Austrolimulidae	Araukaritovaya Formation, Ukraine	Permian	Marine	Glushenko and Ivanov, 1961	**Figure 26E**
Panduralimulus babcocki Allen and Feldmann, 2005	Austrolimulidae	Maybelle Limestone, Texas, USA	Permian	Marginal marine	Allen and Feldmann, 2005	**Figures 25A,F**
Tasmaniolimulus patersoni Bicknell, 2019	Austrolimulidae	Jackey Shale, Tasmania, Australia	Permian	Freshwater	Ewington et al., 1989; Itow et al., 2003; Bicknell, 2019	**Figure 24B**
Austrolimulus fletcheri Riek, 1955	Austrolimulidae	Beacon Hill Shale, NSW, Australia	Triassic	Freshwater	Riek, 1955; Novozhilov, 1991; Itow et al., 2003; Rudkin and Young, 2009; Bicknell and Pates, 2019b; Bicknell et al., 2019e	**Figure 24A**
Dubbolimulus peetae Pickett, 1984	Austrolimulidae	Ballimore Formation, NSW, Australia	Triassic	Freshwater	Pickett, 1984; Itow et al., 2003	**Figure 24C**
?Paleolimulus fuchsbergensis Hauschke and Wilde, 1987	Austrolimulidae	Exter Formation, Germany	Triassic	Freshwater	Hauschke and Wilde, 1987; Hauschke, 2014	**Figure 26D**
Psammolimulus gottingensis Lange, 1923	Austrolimulidae	Solling Formation, Germany	Triassic	Freshwater	Lange, 1922; Meischner, 1962; Novozhilov, 1991; Kustatscher et al., 2014; Bicknell and Pates, 2019b; Bicknell et al., 2019b	**Figure 26A**
Vaderlimulus tricki Lerner et al., 2017	Austrolimulidae	Thaynes Group, Idaho, USA	Triassic	Marginal marine	Lerner et al., 2017	**Figure 25E**
Casterolimulus kletti Holland et al., 1975	Austrolimulidae	Fox Hills Formation, North Dakota, USA	Cretaceous	Freshwater	Holland et al., 1975	**Figure 25D**
Albalimulus bottoni Bicknell and Pates, 2019b	?Limulidae	Ballagan Formation, Scotland, UK	Carboniferous	Marine	Bicknell and Pates, 2019b	**Figures 27A,B**
Limulitella bronnii Schimper, 1853	Limulidae	Grés á Voltzia Formation, France	Triassic	Freshwater	Schimper, 1853; Pfannenstiel, 1928; Wincierz, 1960; Novozhilov, 1991; Gall and Grauvogel-Stamm, 1999; Röhling and Heunisch, 2010	**Figure 28A**
Limulitella henkeli von Fritsch, 1906	Limulidae	Jena Formation, Germany	Triassic	Marine (*sensu* Błażejowski et al., 2017)	von Fritsch, 1906; Hauschke and Mertmann, 2015	**Figure 28B**
?*Limulitella* sp.	Limulidae	Bernburg Fordmation, Germany	Triassic	Marine to freshwater Hauschke et al., 2005	Hauschke and Wilde, 2000	**Figure 30A**
Limulitella sp.	Limulidae	Sakamena Group, Madagascar	Triassic	Marine	Hauschke et al., 2004	**Figure 29E**
Limulitella sp.	Limulidae	Lower Wellenkalk Member, Muschelkalk, Netherlands	Triassic	Marine	Zuber et al., 2017	**Figure 28C**
?*Limulitella* sp.	Limulidae	Buntsandstein, Germany	Triassic	Marine	Hauschke and Wilde, 2008	**Figures 29C,D**
?*Limulitella* sp.	Limulidae	Lower Muschelkalk, Netherlands	Triassic	Marine	Hauschke et al., 2009; Klompmaker, 2019	**Figure 28D**
Limulitella tejraensis Błażejowski et al., 2017	Limulidae	Ouled Chebbi Formation, Tunisia	Triassic	Freshwater	Błażejowski et al., 2017	**Figure 29B**
Limulitella vicensis (Bleicher, 1897)	Limulidae	Keuper Formation, France	Triassic	Marine	Bleicher, 1897; Fisher, 1984	**Figure 29A**

(Continued)

TABLE 7 | Continued

Taxon	Family	Geological information (where detailed) and locality	Time period	Environment	Citation for figured specimens	Figured here
Limulitella volgensis Ponomarenko, 1985	Limulidae	Rybinsk Formation, Russia	Triassic	Marine	Ponomarenko, 1985	**Figure 30E**
Limulitella liasokeuperinus (Braun, 1860)	Limulidae	?Exter Formation, Germany	Triassic	Freshwater	Braun, 1860; Hauschke and Wilde, 1984	**Figure 30D**
Limulus nathorsti Jackson, 1906	Limulidae	Höör Sandstone, Sweden	Triassic	Marine	Jackson, 1906	**Figure 31E**
Limulus priscus Münster, 1839	Limulidae	Muschelkalk Limestone, Germany	Triassic	Marine	Münster, 1839	**Figure 32F**
Mesolimulus crespelli Vía Boada, 1987	Limulidae	Alcover Limestone Formation, Spain	Triassic	Marine	Vía Boada, 1987a,b; Martí, 1994	**Figure 31B**
Sloveniolimulus rudkini Bicknell et al., 2019e	Limulidae	Strelovec Formation, Slovenia	Triassic	Marine	Križnar and Hitij, 2010; Bicknell et al., 2019e	**Figure 32C**
Tachypleus gadeai (Vía Boada and Villalta, 1966)	Limulidae	Alcover Limestone Formation, Spain	Triassic	Marine	Vía Boada and Villalta, 1966; Romero and Vía Boada, 1977; Vía Boada et al., 1977; Martí, 1993, 1994; Diedrich, 2011; Bicknell et al., 2019e	**Figure 31A**
Tarracolimulus rieki Romero and Vía Boada, 1977	Limulidae	Alcover Limestone Formation, Spain	Triassic	Marine	Romero and Vía Boada, 1977; Vía Boada et al., 1977	**Figure 31C**
Yunnanolimulus luopingensis Zhang et al., 2009	Limulidae	Guanling Formation, Luoping, China	Triassic	Marine	Zhang et al., 2009; Hu et al., 2011, 2017; Bicknell et al., 2019b	**Figures 32A,B**
Limulidae gen. et sp. indet, previously *Limulus kieri*	Limulidae	Muschelkalk Limestone, Germany	Triassic	Marine	Hauschke et al., 1992	**Figure 31D**
Limulidae gen. et sp. indet	Limulidae	Bernburg Formation, Germany	Triassic	Freshwater	Hauschke, 2014	**Figure 32E**
Limulidae gen. et sp. indet	Limulidae	Volpriehausen Formation, Germany	Triassic	Freshwater	Hauschke, 2014	**Figure 32D**
Crenatolimulus sp.	Limulidae	Kcynia Formation, Poland	Jurassic	Marine	Kin et al., 2013; Błazejowski, 2015; Błazejowski et al., 2015, 2016	**Figure 33A**
"Limulus" darwini Kin and Błazejowski, 2014	Limulidae	Kcynia Formation, Poland	Jurassic	Marine	Kin and Błazejowski, 2014; Tashman, 2014; Błazejowski, 2015; Błazejowski et al., 2016, 2019	**Figure 33B**
Limulus woodwardi Watson, 1909	Limulidae	Northampton Sand Formation(?), England, UK	Jurassic	Marine	Watson, 1909	**Figure 33C**
Mesolimulus sibiricus Ponomarenko, 1985	Limulidae	Talynzhansk Formation, Russia	Jurassic	Marginal marine	Ponomarenko, 1985	**Figure 33E**
Mesolimulus sp.	Limulidae	Purbeck Limestone Group, England, UK	Jurassic	Marine	Ross and Vannier, 2002	**Figure 33D**
Mesolimulus walchi (Desmarest, 1822)	Limulidae	*Konservat-Lagerstätte* of Ettling, Germany; Solnhofen Limestone, Germany	Jurassic	Marine	Desmarest, 1822; Koenig, 1825; Zittel, 1881; Malz, 1964; Fisher, 1984; Briggs and Wilby, 1996; Shuster, 2001; Itow et al., 2003; Shuster and Anderson, 2003; Briggs et al., 2005; Novitsky, 2009; Rudkin and Young, 2009; Sekiguchi and Shuster, 2009; Diedrich, 2011; Haug et al., 2011; Ebert et al., 2015; Hauschke and Mertmann, 2016; Bicknell et al., 2018d, 2019b	**Figure 34**

(Continued)

TABLE 7 | Continued

Taxon	Family	Geological information (where detailed) and locality	Time period	Environment	Citation for figured specimens	Figured here
Crenatolimulus paluxyensis Feldmann et al., 2011	Limulidae	Glen Rose Formation, Texas, USA	Cretaceous	Marine	Feldmann et al., 2011; Bicknell et al., 2019b	**Figure 35D**
Limulus coffini Reeside and Harris, 1952	Limulidae	Pierre Shale, Colorado, USA	Cretaceous	Marine	Reeside and Harris, 1952; Shuster, 2001; Shuster et al., 2003; Sekiguchi and Shuster, 2009	**Figure 35F**
Mesolimulus tafraoutensis Lamsdell et al., 2020	Limulidae	Gara Sbaa *Konservat-Lagerstätte*, Kem Kem Beds, Morocco	Cretaceous	Marine	Garassino et al., 2008; Lamsdell et al., 2020	**Figure 35E**
Tachypleus syriacus (Woodward, 1879)	Limulidae	Haqel and Hadjoula *Konservat-Lagerstätten*, Lebanon	Cretaceous	Marine	Woodward, 1879; Novozhilov, 1991; Lamsdell and Mckenzie, 2015; Bicknell et al., 2019b	**Figures 35C,G**
Victalimulus mcqueeni Riek and Gill, 1971	Limulidae	Korumburra Group, NSW, Australia	Cretaceous	Freshwater	Riek and Gill, 1971; Itow et al., 2003; Poropat et al., 2018; Bicknell et al., 2019b,e	**Figures 35A,B**
Limulus decheni Zincken, 1862	Limulidae	Braunkohlen Formation, Germany; Domsen Sands, Weißelster Basin, Germany	Eocene	Marine	Zincken, 1862; Giebel, 1863; Fiebelkorn, 1895; Böhm, 1908; Vetter, 1933; Novozhilov, 1991; Bellmann, 1997; Hauschke and Wilde, 2004; Dunlop et al., 2012; Hauschke, 2013, 2018; Hauschke and Mertmann, 2015; Schimpf et al., 2017	**Figures 36C–E**
Unnamed specimen	Unspecified	Zechstein, Germany	Permian	Marine	Hauschke and Wilde, 1989	**Figures 36A,B**
Unnamed specimen	Unspecified	Trochitenkalk Formation, Germany	Triassic	Marine	Krause et al., 2009; Diedrich, 2011	**Figures 30B,C**
Valloisella lievinensis Racheboeuf, 1992	Unspecified	Bickershaw Complex, England UK; Westphalian B Coal Measures, England, UK; Westphalian C Coal Measures, France	Carboniferous	Freshwater	Dix and Jones, 1932; Racheboeuf, 1992; Anderson and Horrocks, 1995	**Figure 36F**

The taxa are order by family, time-period and then alphabetically by genus and species. Synonyms mentioned in Dunlop et al. (2019): Limulidae = Mesolimulidae*;* Limulitella = Limulites. Tachypleus = Heterolimulus*. Note that due to the paraphyletic status of Paleolimulus, taxa in this genus have been placed into Austrolimulidae. These taxa require revision. ? denotes uncertain taxonomic affinities or formation assignment.*

sufficient to erect a new family (Selden and Siveter, 1987; Siveter and Selden, 1987).

Bellinuroopsis

This Devonian-aged, monospecific genus (*Bellinuroopsis rossicus*) is known from one Russian specimen (Lebedjan Formation, **Table 6**, **Figure 23**; Chernyshev, 1933; Moore et al., 2007). The main characteristics that distinguishes *Bel. rossicus* from other taxa in Limulina are the following: a wedge-shaped cardiac lobe (Størmer, 1955); and an oblong thoracetron with eight, free moving, expressed tergites, tapering slightly to a telson. Furthermore, an expressed opercular (VIII) tergite that is more pronounced than in Rolfeiidae (Størmer, 1955; Novozhilov, 1991). These unique features potentially warrant the erection of a separate family, as suggested by Størmer (1955).

Limuloidea

Taxa in this superfamily are Austrolimulidae, Limulidae, and *Valloisella*. The diagnostic features of these taxa are a "thoracetron showing no lateral expression of individual tergites" (Lamsdell, 2016, p. 190).

Austrolimulidae

This family ranges from at least the Permian to the Cretaceous (**Figure 1**). There are at least seven monospecific genera: *Austrolimulus, Casterolimulus, Dubbolimulus, Panduralimulus, Psammolimulus, Tasmaniolimulus,* and *Vaderlimulus* (**Table 7**, **Figures 24–26**). Austrolimulids have domed cephalothoraxes, with overdeveloped genal spines that terminate as far back as the telson onset. Thoracetrons are mostly fused; occasionally preserve apodemal pits with highly reduced or vestigial moveable spines and styliform telsons (Riek, 1955, 1968; Lerner et al., 2017; Bicknell, 2019). Swallow-tailed thoracetrons are observed in *A. fletcheri* (Beacon Hill Shale, NSW, Australia, Triassic) and *V. tricki* (Thaynes Group, Idaho, USA, Triassic; Lerner et al., 2017), but this character is not known from all taxa in the family, including *T. patersoni* (Jackey Shale, Tasmania, Australia, Permain; Bicknell, 2019). Furthermore, *A. fletcheri* has a thoracetron with two sections, the posterior section of which has three exposed tergites (Riek, 1955; Pickett, 1984; Novozhilov, 1991; Itow et al., 2003). Lamsdell (2016) described a dorsal thoracetronic keel in Austrolimulidae. This feature is noted in *D. peetae* (Ballimore Formation, NSW, Australia, Triassic) and *T. patersoni*, but is not known to the other taxa (Riek, 1955; Pickett, 1984; Allen and Feldmann, 2005; Feldmann et al., 2011; Lerner et al., 2017; Bicknell, 2019). Appendages are known from *T. patersoni*, in which the distal portions of walking legs are observed (Ewington et al., 1989; Bicknell, 2019), and *P. gottingensis* (Solling Formation, Germany, Triassic) shows evidence of pushing legs (Meischner, 1962; Bicknell et al., 2019b).

The large genal spine splay and abnormal forms of austrolimulids represent the strangest and most extreme xiphosurid morphologies (they have been considered odd-ball taxa, Eldredge, 1976; Bicknell, 2019). Their morphologies likely reflect the freshwater and marginal conditions that were exploited by the group, and provide evidence against the highly conserved nature of Xiphosurida (Fisher, 1984; Bicknell, 2019). The hypertrophied spines may have permitted more effective motion within unidirectional fluid-flow in rivers (Bicknell, 2019; Bicknell and Pates, 2019b). As discussed above, Lamsdell (2016) and Lerner et al. (2017) suggested that species in *Paleolimulus* belong in Austrolimulidae (e.g., *Pa. fuchsbergensis*, *Pa. jakovlevi*, and *Pa. longispinus*) using phylogenetic and linear morphometric arguments respectively. These taxa require revision; a direction of research that will begin to uncover the true diversity of these taxa and their interesting morphologies.

Limulidae

This is the most long-lived and most generically diverse xiphosurid family, with a fossil record that spans possibly from the Carboniferous to Recent (**Figure 1**). There are 10 limulid genera: *Albalimulus, Crenatolimulus, Limulitella, Limulus, Mesolimulus, Sloveniolimulus, Tachypleus, Tarracolimulus, Victalimulus,* and *Yunnanolimulus* with 24 species (**Table 7**, **Figures 27–38**; Lamsdell, 2016). Limulids have a domed, horseshoe-shaped cephalothoraces with genal spines that can extend posteriorly up to the first third of the thoracetron (Novozhilov, 1991). Ophthalmic ridges are known from all taxa and the lateral compound eyes are located along these ridges (Størmer, 1955; Novozhilov, 1991). Ophthalmic ridges do not converge anteriorly. The thoracetron is completely fused, unsegmented, trapezoidal to sub-hexagonal, often displaying movable spines, with small fixed spines, and a styliform telson (Størmer, 1955; Tiegs and Manton, 1958; Siveter and Selden, 1987; Lamsdell, 2016). Appendages and soft-bodied material are occasionally preserved in fossil limulids. *Victalimulus mcqueeni* (Latrobe Group, NSW, Australia, Cretaceous), *T. syriacus* (Haqel and Hadjoula *Konservat-Lagerstätten*, Lebanon, Cretaceous) and *Y. luopingensis* (Member II, Guanling Formation, Luoping, China, Triassic) all preserved cephalothoracic and thoracetronic appendages (Riek and Gill, 1971; Hu et al., 2011, 2017; Lamsdell and Mckenzie, 2015; Bicknell et al., 2019b). *Limulitella bronnii* (Grés á Voltzia Formation, France, Triassic) only preserved cephalothoracic appendages (Wincierz, 1960). *Mesolimulus walchi* preserved muscle fibers, and cephalothoracic and thoracetronic appendages (Zittel, 1881; Briggs et al., 2005; Bicknell et al., 2019b). Finally, muscle insertions were identified using and augmented laminography on a *Limulitella* sp. specimen from the Triassic-aged Lower Wellenkalk Member, Muschelkalk, Netherlands (Zuber et al., 2017). Sexual dimorphism has been suggested for select fossil taxa (Bicknell et al., 2019b): *Limulus decheni* (females have longer cephalothoraces; Hauschke and Wilde, 2004), *T. syriacus* (females have broader thoracetrons and males have scalloped anterior cephalothoraces; Lamsdell and Mckenzie, 2015) and *Y. luopingensis* (females have shorter posterior thoracetronic moveable spines and males have modified anterior walking legs; Hu et al., 2017). Most limulids were marine, but *V. mcqueeni, Lim. bronnii*, and *Lim. tejraensis* are considered freshwater species, while *Lim. liasokeuperinus* is considered a marginal marine taxon.

Limulids are thought to represent bradytelic evolution and exhibit strong morphological conservation between extant and fossil taxa. As such, they have been the focus of evolutionary and morphological research (Fisher, 1984; Bicknell and Pates, 2019b; Bicknell et al., 2019b). The limited morphological difference between the 148 Mya Jurassic "*Limulus*" *darwini* (Kcynia Formation, Poland) and modern juvenile *L. polyphemus* has been used to assert stabilomorphism; the "relative morphological stability of organisms in time and spatial distribution, the taxonomic status of which does not exceed genus level" (Błazejowski, 2015, p. 11). The conservation may reflect habitation of similar marine conditions, or convergence on an effective morphology.

Extant limulids have distributions across the east coast of the USA and Asia, with their common names reflecting said distribution (Shuster, 2001; Bicknell and Pates, 2019a): the American, or Atlantic, horseshoe crab, *Limulus polyphemus*; the Indonesian horseshoe crab, *Carcinoscorpius rotundicauda*; the Chinese horseshoe crab, *Tachypleus gigas*; and the Japanese horseshoe crab, *T. tridentatus* (**Figures 35**, **36**; Itow et al., 2003; Zhou and Morton, 2004; Sekiguchi and Shuster, 2009). The ontogeny and morphology of these taxa has been documented thoroughly across the past two centuries (Shuster, 1982; Haug and Rötzer, 2018a) and the morphological similarities are depicted in **Figures 35** and **36**. Extant limulids occupy many environmental conditions and can exploit brackish, freshwater, shallow water, and fully-marine conditions (Siveter and Selden, 1987). *Limulus polyphemus*, *T. gigas,* and *T. tridentatus* are mostly shallow marine, bottom-dwelling taxa that spawn on beaches and inhabit a combination of marine sub-habits during ontogeny (Fisher, 1984). Conversely, *C. rotundicauda* migrates into completely freshwater (Størmer, 1952; Fisher, 1984; Crônier and Courville, 2005; Sekiguchi and Shuster, 2009; Lamsdell, 2016). Despite representing the descendants of a long fossil lineage, they now face an extinction event. Extensive harvesting of specimens for their blood, and as a food source, as well as habitat modification have majorly impacted populations (Botton, 2001; Hsieh and Chen, 2009; Shin et al., 2009; Akbar John et al., 2011; Cartwright-Taylor et al., 2011; Carmichael and Brush, 2012; Nelson et al., 2015; Kwan et al., 2016; Fairuz-Fozi et al., 2018). Measures therefore need to be taken to prevent this group from an extinction event. To this end, *L. polyphemus* and its kin have now been suggested as world heritage species (Tanacredi et al., 2009) and *T. tridentatus* was recently listed as an endangered taxon (Laurie et al., 2019)

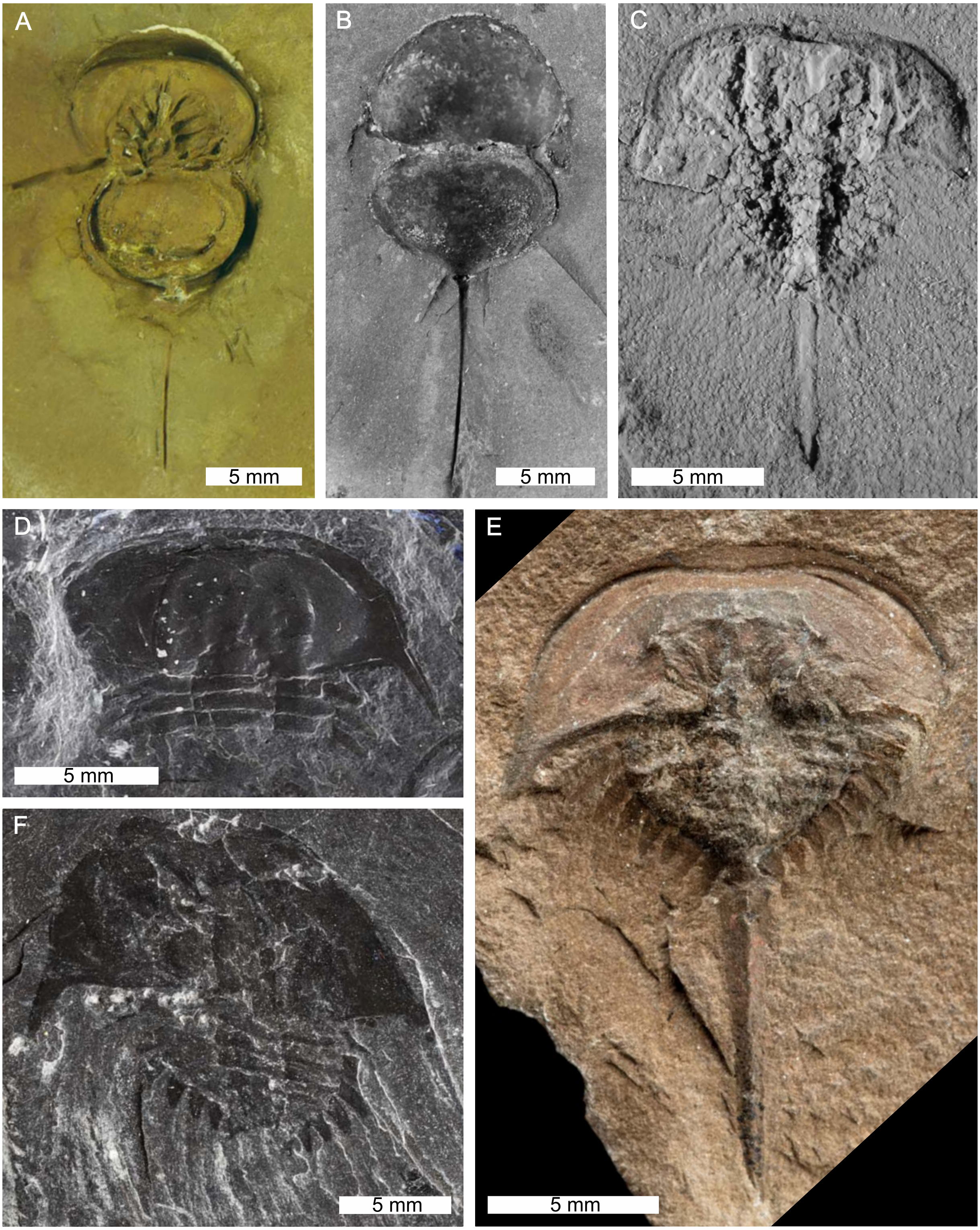

FIGURE 13 | Belinurid species in the genera *Alanops* and *Bellinurus*. **(A,B)** *Alanops magnifica* from the Carboniferous-aged Montceau-les-Mines *Konservat-Lagerstätte*, Great Seams Formation, France. **(A)** MNHN SOT001784, paratype, ventral view. Note appendages. **(B)** MNHN SOT002154, paratype, dorsal view. **(C)** *Bellinurus arcuatus* from the Pennine Middle Coal Measures Formation, England, UK. AM F29886. **(D)** *Bellinurus bellulus* from the Carboniferous-aged South Wales Lower Coal Measures Formation, Wales, UK. NMW 70.17. G9. **(E)** *Bellinurus baldwini* from the Carboniferous-aged Pennine Middle Coal Measures Formation, England, UK. NHMUK PI. In. 18572, holotype. **(F)** *Bellinurus carwayensis* from the Carboniferous-aged South Wales Lower Coal Measures Formation, Wales, UK. NMW 29.197.G3, holotype. **(B,C)** Converted to gray scale. **(C)** Coated in ammonium chloride sublimate. Photo credit: **(A,B)** Dominique Chabard; **(C)** Patrick Smith, **(D,F)** Stephen Pates; **(E)** Lucie Goodayle, NHM, London.

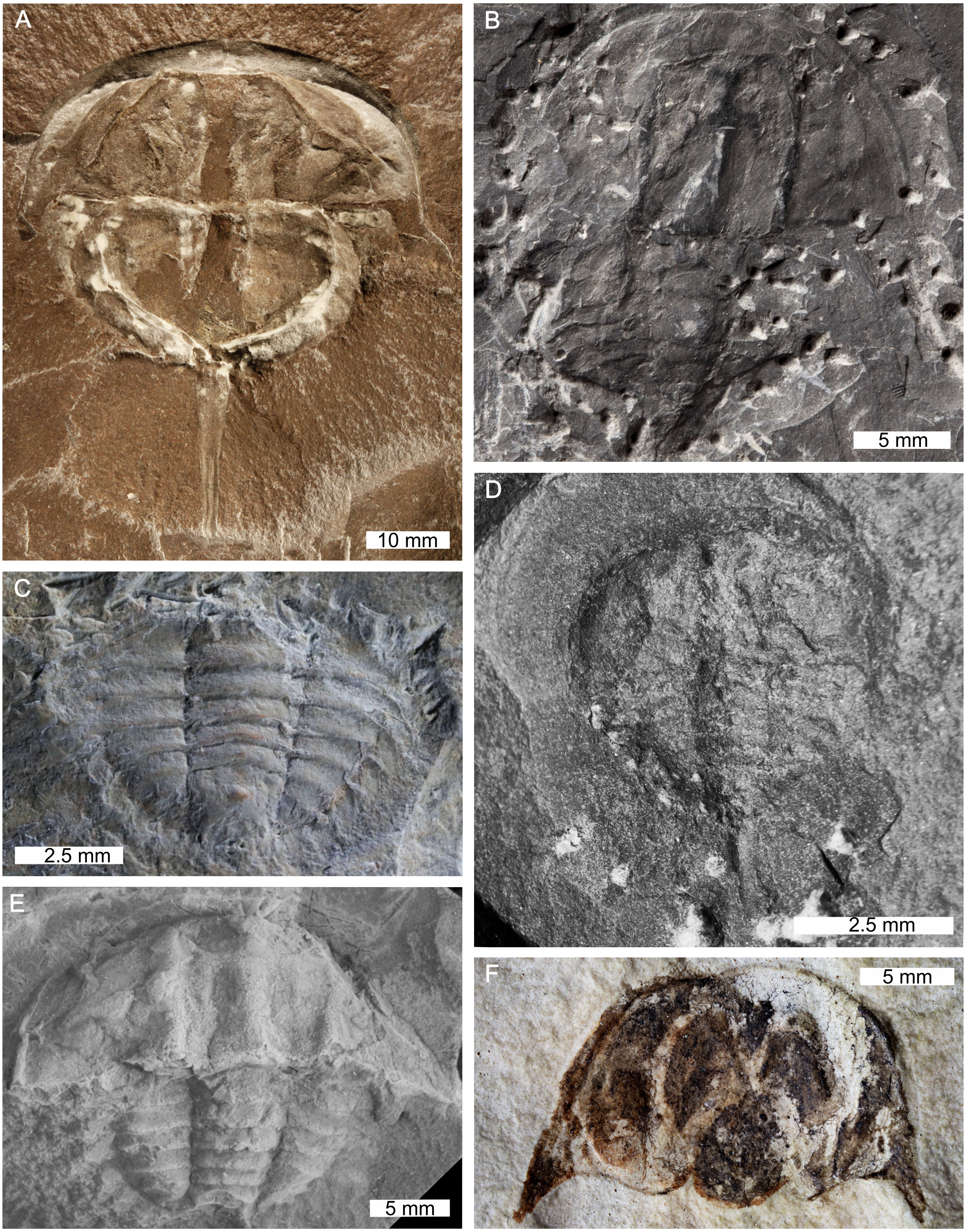

FIGURE 14 | *Bellinurus* species from Canada, UK, Ukraine, and USA. **(A)** *Bellinurus lacoei* from the Carboniferous-aged Mazon Creek *Konservat-Lagerstätte*, Carbondale Formation, Illinois, USA. USNM 38861, cotype. **(B)** *Bellinurus concinnus* from the Carboniferous-aged South Wales Lower Coal Measures Formation, Wales, UK. BGS.GSE 48775, holotype. **(C)** *Bellinurus iswariensis* from the Carboniferous-aged Almaznaya Formation, Ukraine. TsNIGR 3/2095. **(D)** *Bellinurus grandaevus* from the Carboniferous-aged Canso Group, Nova Scotia, Canada. GSC 12806, hypotype. **(E)** *Bellinurus koenigianus* from the Carboniferous-aged Coal Measures Formation, England, UK. CM 11066. **(F)** *Bellinurus kiltorkensis* from the Devonian to Carboniferous-aged Kiltorcan Formation, Ireland. NHMUK PI. In. 25931, cast of original specimen. **(D,E)** Converted to gray scale. Photo credit: **(A,C,E)** Russell Bicknell; **(B)** GB3D image, permission given by Mike Howe © 2018 JISC GB3D Type Fossils Online project partners (Amgueddfa Cymru–National Museum Wales); **(D)** Jodie Francis; **(F)** Lucie Goodayle, NHM, London.

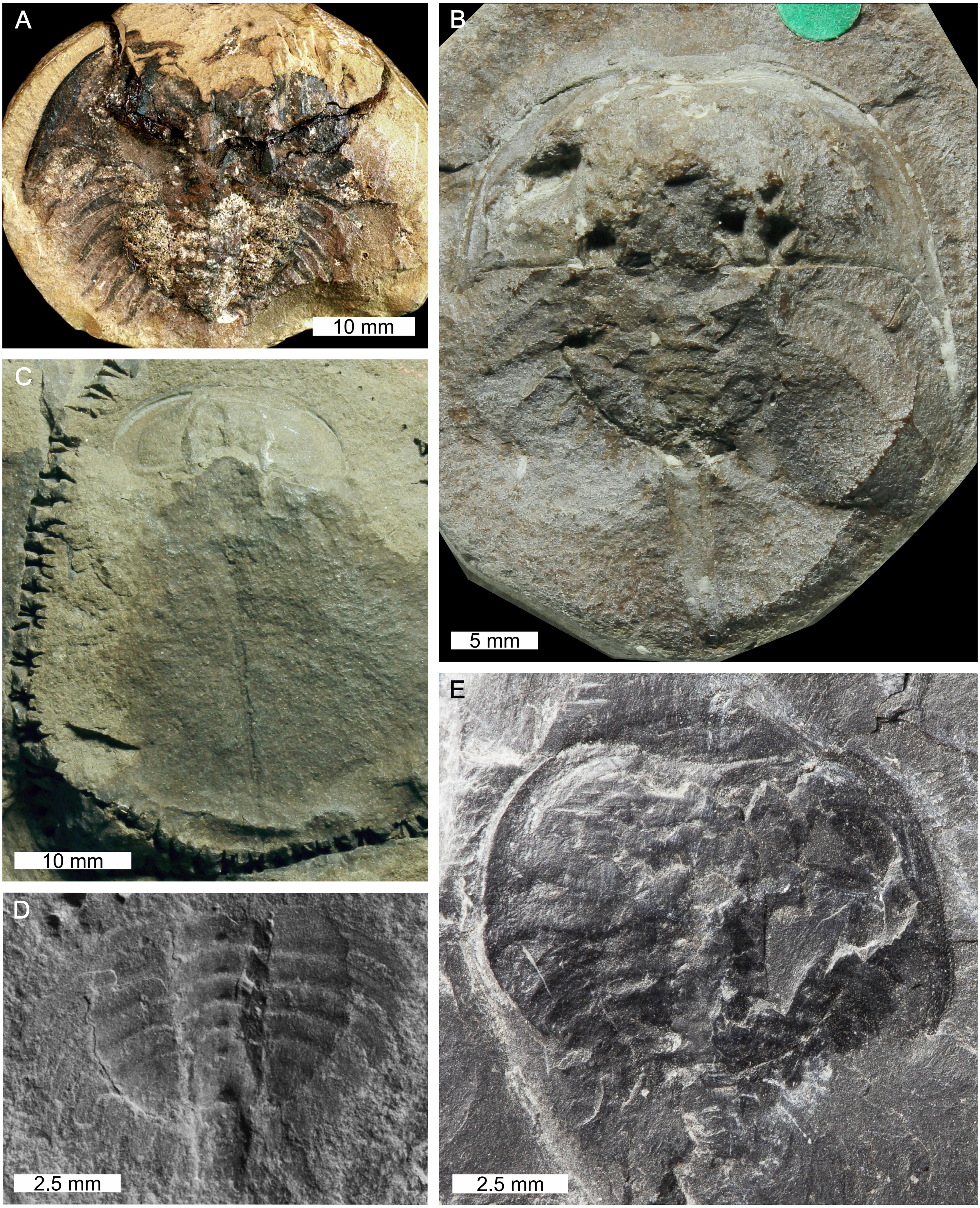

FIGURE 15 | *Bellinurus* species from the Czech Republic, UK, and Ukraine. **(A,B)** *Bellinurus lunatus.* **(A)** Specimen from Carboniferous-aged Upper Silesia Coal Basin, Czech Republic. GIUS 5-845/7. **(B)** Specimen from Pennine Middle Coal Measures Formation, England, UK. NHMUK Pl. I. 2754. **(C)** *Bellinurus longicaudatus* from Carboniferous-aged Pennine Middle Coal Measures Formation, England, UK. NHMUK Pl. In. 18563, holotype. **(D)** *Bellinurus metschetnensis* from Carboniferous-aged Belaya Kalitva Formation, Ukraine. TsNIGR 8/2095. **(E)** *Bellinurus morgani* from Carboniferous-aged South Wales Lower Coal Measures Formation, Wales, UK. BGS.GSE 49362, holotype. **(D,E)** Converted to gray scale. Photo credit: **(A)** Błaże Błażejowski; **(B,C)** Stephen Pates; **(D)** Russell Bicknell; **(E)** GB3D image, permission given by Mike Howe © 2018 JISC GB3D Type Fossils Online project partners (Amgueddfa Cymru – National Museum Wales).

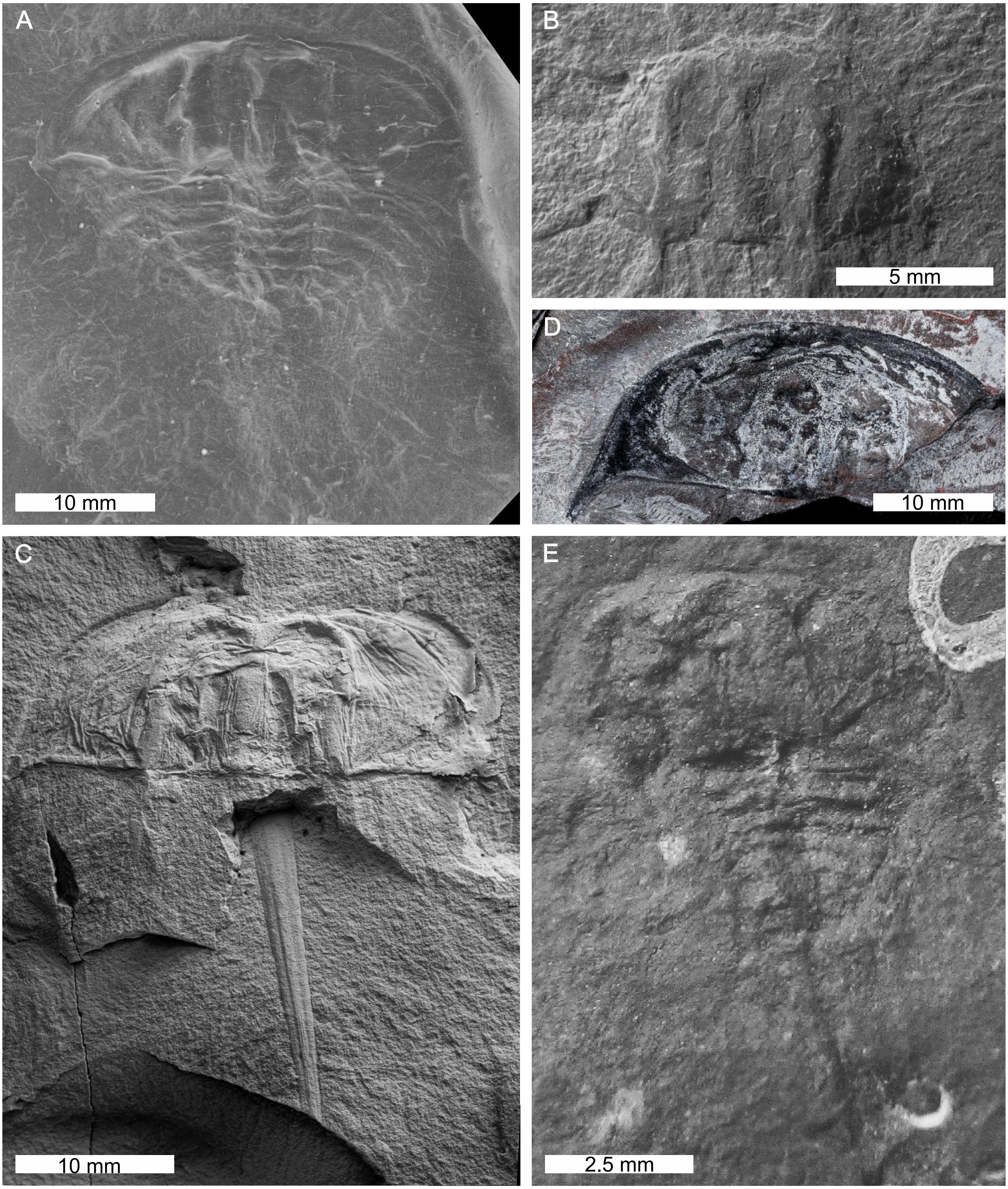

FIGURE 16 | *Bellinurus* species from Canada, Poland, UK, and Ukraine. **(A)** *Bellinurus silesiacus* from the Carboniferous Upper Silesia Coal Basin, Poland. MB.A.1091, cast of original. **(B)** *Bellinurus stepanowi* from the Carboniferous-aged Almaznaya Formation, Ukraine. TsNIGR 6/2095. **(C,E)** *Bellinurus reginae*. **(C)** Specimen from Karviná Formation(?), Upper Silesia, Poland. MB.A.1090. **(E)** Specimen from Carboniferous-aged Canso Group, Nova Scotia, Canada. GSC 12803. **(D)** *Bellinurus pustulosus* from Carboniferous-aged South Wales Lower Coal Measures Formation, Wales, UK. NMW 29.197.G2, holotype. ? denotes uncertain formation assignment. **(A–C,E)** Converted to gray scale. Photo credit: **(A)** Andreas Abele; **(B)** Russell Bicknell; **(C)** Christian Neumann; **(D)** Stephen Pates; **(E)** Matt Stimson. **(A,B,C,E)** Converted to gray scale.

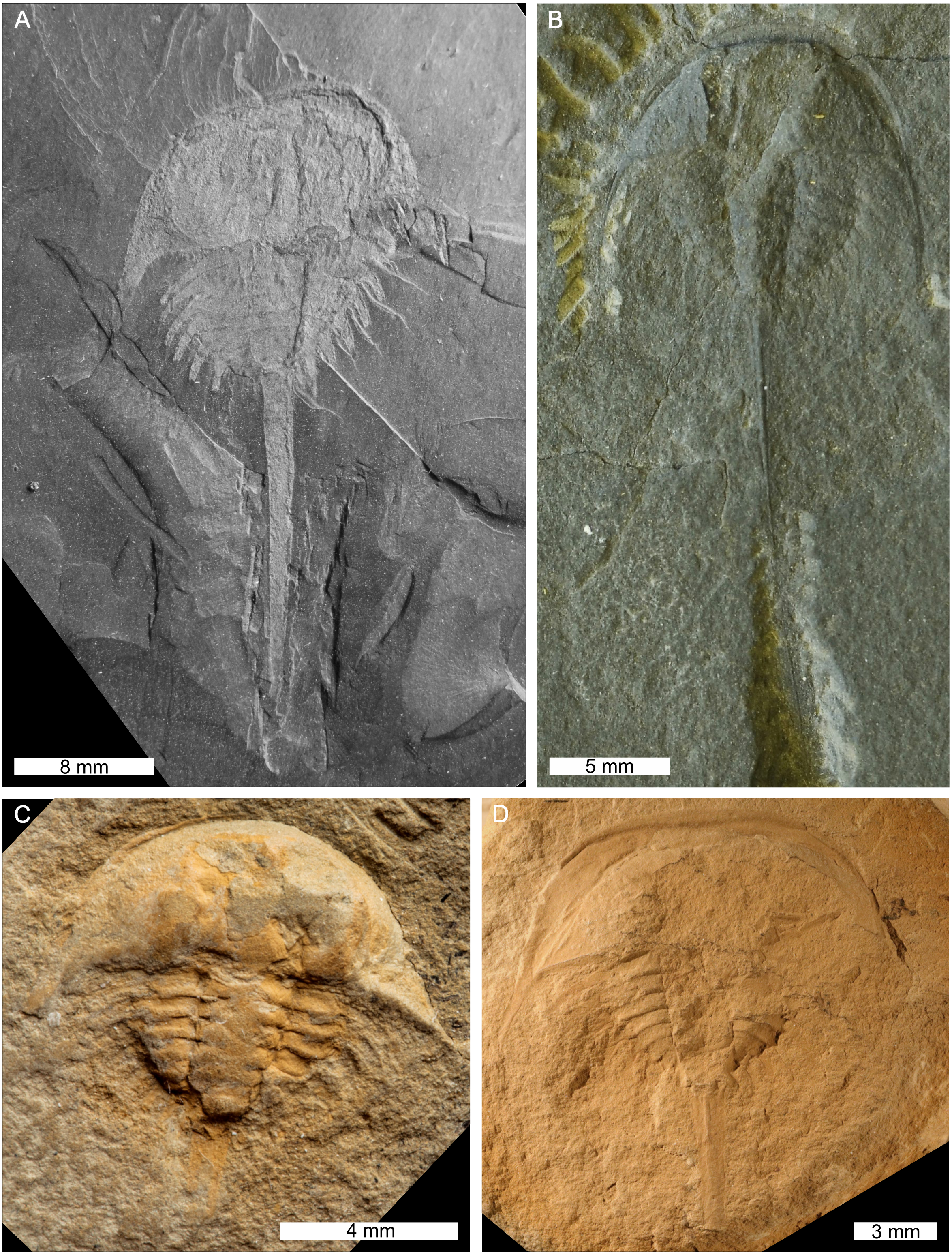

FIGURE 17 | *Bellinurus* species from the Czech Republic, Germany, and UK. **(A)** *Bellinurus šustai* from the Carboniferous-aged Karviná Formation, Czech Republic. MMO B 976, holotype. **(B)** *Bellinurus*. cf. *truemani* from the Carboniferous-aged Sprockhövel Formation, Germany. SMF Viii 314. **(C)** *Bellinurus trechmanni* from the Carboniferous-aged Pennine Upper Coal Measures Formation, England, UK. NHMUK PI. In. 18487, holotype. **(D)** *Bellinurus trilobitoides* from the Carboniferous-aged ?Pennine Upper Coal Measures Formation, England, UK. LL.111267a. **(A)** Converted to gray scale. ? denotes uncertain formation assignment. Photo credit: **(A)** Mertová Eva; **(B)** Monica Solorzano-Kraemer; **(C)** Lucie Goodayle; **(D)** Russell Bicknell.

FIGURE 18 | *Euproops* species from France, Germany, UK, and USA. **(A,B)** *Euproops longispina* from the Carboniferous-aged Allegheny Formation, Pennsylvania, USA. **(A)** USNM 38857, cotype. **(B)** USNM 38858, cotype. **(C)** *Euproops cambrensis* from the Carboniferous-aged South Wales Lower Coal Measures Formation, *(Continued)*

FIGURE 18 | Wales, UK. NMW 29.198.G1, holotype. **(D)** *Euproops bifidus* from the Carboniferous-aged Flöz Dreibänke Formation, Germany. B7.135 holotype. **(E)** *Euproops mariae* from the Carboniferous-aged Graissessac Shale and Coal, Graissessac Basin, France. USTL-CC026, holotype. **(F)** *Euproops* cf. *anthrax* from the Carboniferous-aged South Wales Upper Coal Measures Formation, Wales, UK. NMW 27.177.G3. Photo credit: **(A,B)** Russell Bicknell; **(C,F)** Stephen Pates; **(D)** Markus Bertling; **(E)** Jessie Cuvelier.

showing that progress is being made in preventing the human-driven extinction of Xiphosurida.

Valloisella

This monospecific genus from the Carboniferous Coal Measures in England and France (**Figure 36**) was originally considered a belinurid (Anderson and Horrocks, 1995) but has since been placed at the base of Limuloidea by recent phylogenetic analyses (Lamsdell, 2016). The genus is defined by an almond-shaped cephalothorax, genal spines that extend almost to the thoracetron terminus, and a flange located along the thoracetronic margin (Anderson and Horrocks, 1995). The fused thoracetron is trapezoidal with expressed tergal divisions, contrasting most other species in Limuloidea. No appendages are known from this genus.

HORSESHOE CRAB EVOLUTIONARY HISTORY AND DIVERSITY

Horseshoe crabs experienced three major evolutionary events across the Phanerozoic (**Figure 1**). The Palaeozoic horseshoe crab record was the most exploratory anatomically and evolutionarily (Błażejowski et al., 2017). The rise of synziphosurines began in the Lower Ordovician (Rudkin et al., 2008; Rudkin and Young, 2009; Dunlop, 2010; Van Roy et al., 2010, 2015). Across the Silurian and Devonian, the marine and marginal marine forms were abundant and represent the first evolutionary radiation of this group, before the diversification of Xiphosurida (Størmer, 1955). Synziphosurine diversity declined heavily, reducing to one taxon in the Carboniferous, when they subsequently went extinct (Selden and Drygant, 1987; Selden and Siveter, 1987; Babcock et al., 1995; Anderson and Selden, 1997; Moore et al., 2007; Lucas et al., 2014). Non-xiphosurid xiphosurans also arose in the Upper Ordovician, potentially even the Lower Ordovician, and are unknown after the Devonian (Bicknell et al., 2019c). Xiphosurida arose in the late Devonian with *Bellinuroopsis* (Moore et al., 2007). After this, at least four xiphosurid families arose in the Carboniferous: the Belinuridae, Limulidae, Paleolimulidae and Rolfeiidae (Selden and Drygant, 1987; Selden and Siveter, 1987; Babcock et al., 1995; Anderson and Selden, 1997; Lucas et al., 2014; Bicknell, 2019; Bicknell and Pates, 2019b; Bicknell et al., 2019e), with evidence suggesting that Austrolimulidae may also have arisen at this time (Lamsdell, 2016). Carboniferous Coal Measures and *Konservat-Lagerstätten* record the highest specific diversity and first radiation of Xiphosurida (Anderson, 1997; Moore et al., 2007; Rudkin and Young, 2009). Exploitation of brackish and freshwater conditions by the late Palaeozoic Xiphosurida may reflect adaptation to inconsistent coastlines and fluctuating shallow-marine conditions (Błażejowski et al., 2017). Xiphosurid diversity apparently decreased drastically during the Permian, reflecting the closure of exceptional preservation windows and an increase in xiphosurids inhabiting marginal environments that are poorly preserved in the geological record (Rudkin and Young, 2009). At the end of the Carboniferous, there is no further record of Rolfeiidae, while the first definite austrolimulid species arose in the Permian (Bicknell, 2019). The Permian-Triassic "Great Dying" drove belinurids and paleolimulids to extinction, while austrolimulids and limulids survived into the Mesozoic (Bicknell and Pates, 2019b). The Triassic was a period of extensive exploration in morphology and the second radiation of xiphosurids and the third evolutionary pulse in horseshoe crabs (Bicknell and Pates, 2019b; Bicknell et al., 2019e). An aspect of this radiation was size increase: Mesozoic taxa were much larger (30–60 cm long, including telson) than the Palaeozoic counterparts (3–5 cm) (Størmer, 1955; Bicknell and Pates, 2019b). Austrolimulid diversity peaked in the Triassic (**Figure 1**) but then decreased into the Cretaceous, during which time the group went extinct. Limulid diversity peaked in the Triassic with 12 species and decreased to five during the Cretaceous (Bicknell et al., 2019e). Only limulids survived into the Tertiary with one named Cenozoic species: the Eocene *Limulus decheni* (Rudkin and Young, 2009; Schimpf et al., 2017), a suggested "missing link" between extant Asian and American taxa (Hauschke and Wilde, 2004). This evolutionary history is one of generally low generic diversity, such as in the four extant species (Anderson and Selden, 1997; Anderson, 1999; Shuster et al., 2003; Sekiguchi and Shuster, 2009; Dunlop et al., 2012). However, the habitation of marginal environments with poor conditions for exceptional preservation of un-biomineralised exoskeleton cuticle also may have impacted this observed low diversity (Babcock, 1998; Anderson, 1999; Babcock and Merriam, 2000; Lamsdell and Mckenzie, 2015).

GEOGRAPHICAL DISTRIBUTION OF XIPHOSURAN MATERIAL

Distribution of horseshoe crab fossils is uneven in space and time; reflecting historical biases in collecting that favored North America and Western Europe. The UK has the highest number of taxa ($n = 35$), followed by the USA ($n = 23$) and Germany ($n = 22$). Other areas with much larger landmasses have far fewer known taxa: South America ($n = 1$), Australia ($n = 7$), Asia ($n = 5$), and Africa ($n = 6$). This uneven geographical sampling also partly reflects uneven temporal sampling (e.g., 25 UK taxa are Carboniferous, and eight are Silurian and 11 of 22 German taxa are Triassic). Within countries, well-explored horizons or formations also provide apparent diversity peaks. Notably the South Wales Coal Measures formations (South

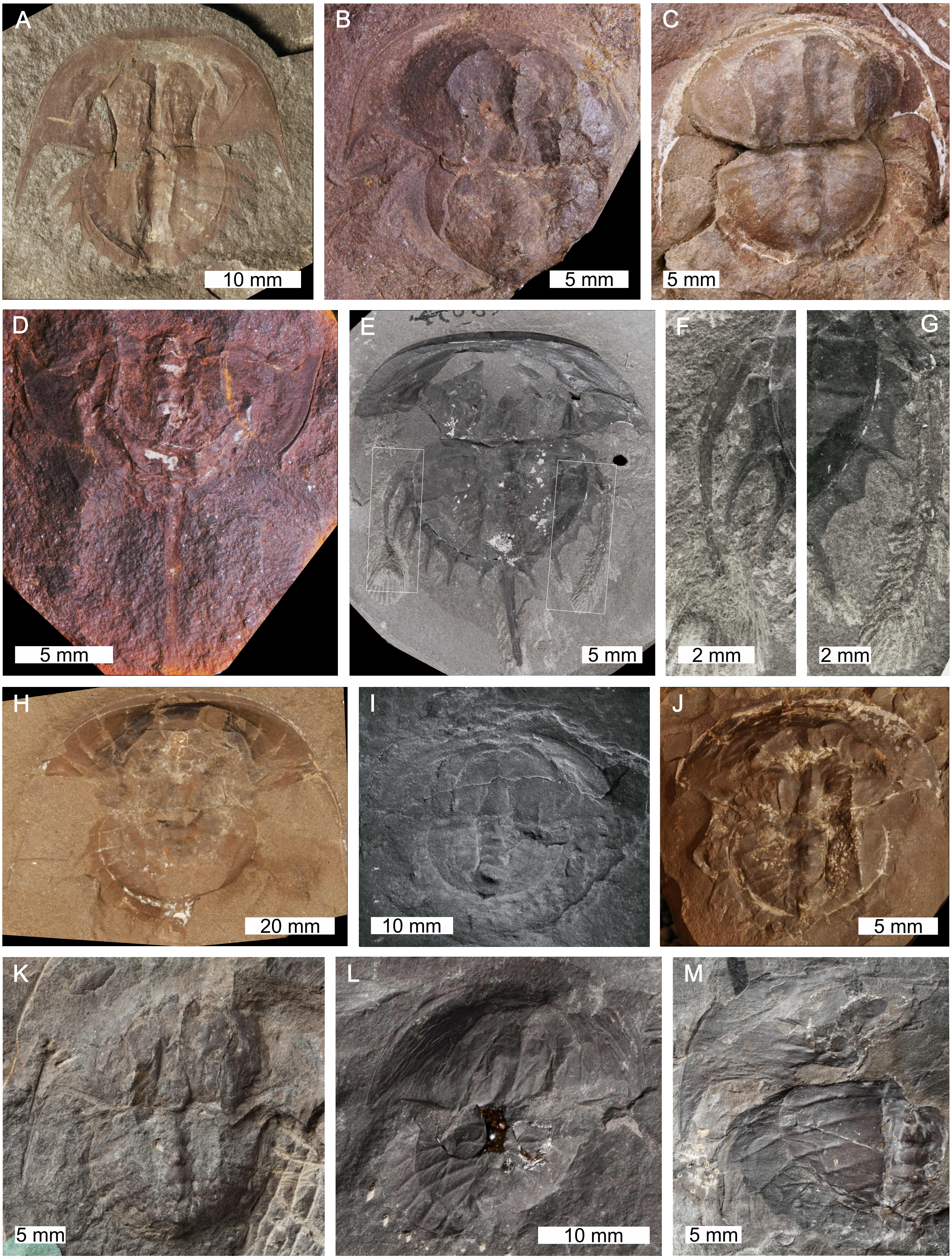

FIGURE 19 | *Euproops danae* from Carboniferous-aged deposits and select species that have been synonymised with *E. danae*. **(A)** Specimen from Carboniferous-aged lower Mercer Shale, Pennsylvania, USA. USNM 697642. **(B–H,J)** Specimens from the Carboniferous-aged Mazon Creek *Konservat-Lagerstätte*, *(Continued)*

FIGURE 19 | Carbondale Formation, Illinois, USA. **(B)** YPM IP 16912. **(C)** YPM IP 25590. **(D)** Specimen that is completely enrolled, ideas mentioned in Fisher (1977) and Anderson (1994) and discussed in Haug et al. (2012). YPM IP 50963. **(E–G)** Specimen with cephalothoracic appendages preserved. YPM IP 28514 **(E)** Complete specimen. **(F)** Close up of left appendage. **(G)** Close up of right appendage. **(H)** USNM 38855, hypotype. **(J)** CM 11061. **(M)** Specimen from the Carboniferous-aged South Wales Upper Coal Measures Formation, Wales, UK. NMW 70.17.G11 **(I)** *Euproops darrahi=E. danae* from the Carboniferous-aged Conemaugh Formation, Pennsylvania, USA. MCZ 109528, holotype. **(K)** *Euproops gwenti=E. danae* from the Carboniferous-aged South Wales Upper Coal Measures Formation, Wales, UK. BGS.GSE 48524, holotype. **(L)** *Euproops graigola =E. danae* from the Carboniferous-aged South Wales Upper Coal Measures Formation, Wales, UK. BGS.GSE 25424, holotype. **(I)** Converted to gray scale. **(I)** Coated with ammonium chloride sublimate. Photo credit **(A–H,J)** Russell Bicknell; **(I,M)** Stephen Pates; **(K,L)** GB3D image, permission given by Mike Howe © 2018 JISC GB3D Type Fossils Online project partners (Amgueddfa Cymru – National Museum Wales).

Wales, UK) where six belinurids are known from the South Wales Lower Coal Measures Formation and three belinurids from the South Wales Upper Coal Measures Formation. These nine taxa, within a limited geographic and temporal sample, provide an apparently high Carboniferous diversity skewing the understanding of overall belinurid diversity and geographic spread as well as reflecting an over-splitting of the group. To address these sampling issues (which are by no means limited to horseshoe crabs) further exploration needs to be targeted to under-sampled regions (Africa, Asia, South America) and time periods (Jurassic and younger), as well as reassessing the apparent high diversity of taxa that have not been recently studied. Such efforts, combined with a concerted effort to redescribe and refine horseshoe crab taxonomy will allow ranges of different groups to be compared without the current underlying biases.

FUTURE DIRECTIONS

Horseshoe crabs are an iconic group of chelicerates and, as depicted here, have been thoroughly, if somewhat sporadically, scientifically explored over the past two centuries. However, in conducting this review we highlighted four main research areas that should be addressed. To conclude this review, potential future directions for horseshoe crab research are presented.

(1) Bicknell (2019), and Bicknell et al. (2019e) highlighted that the traditional views that horseshoe crabs represent evolutionary conservatism, stasis, and bradytelic evolution (Fisher, 1984; Selden and Siveter, 1987; Rudkin et al., 2008) is overstated. In reality, the group experienced three major changes across the Phanerozoic: increased size, thoracetronic fusion, and restriction to marine habitats (Størmer, 1955; Crônier and Courville, 2005; Bicknell and Pates, 2019b). Lamsdell (2016) thoroughly explored the record of habitat change, but the remaining two points should be considered. Thoracetronic fusion has been attributed to a change in ecology, from enrolment to burrowing, but this remains fairly unexplored (Fisher, 1977, 1981, 1982; Waterston, 1985; Lamsdell, 2016; Błażejowski et al., 2017). A study considering when complete fusion developed in the context of palaeoenvironmental and palaeoecological conditions may confirm this hypothesis. Size change is likely associated with exploitation of different niches: smaller Xiphosurida likely preferred freshwater conditions, reflected today in the smallest taxon—*Carcinoscorpius rotundicauda* (Hauschke and Wilde, 1991; Dunlop et al., 2012). A study considering shape and size change through time would allow this hypothesis to be tested. In addition, modern descriptive and statistical tools, such as multivariate geometric morphometrics, semilandmark, and landmark analyses could be employed to explore this topic in more detail (Bicknell, 2019; Bicknell and Pates, 2019b; Bicknell et al., 2019e).

(2) Rates of morphometric change in horseshoe crabs have not been thoroughly explored (Fisher, 1984). The same morphometric data outlined above could be used to address possible evolutionary rates and quantify whether the group, especially limulids, represent arrested evolution. Time series analyses can also be conducted with these data to study modes and models of evolution (Hunt and Carrano, 2010; Hunt et al., 2015; Bicknell et al., 2018a).

(3) As **Tables 6** and **7** outline there are many specimens have been identified as xiphosurids but not formally (re)described in light of recent progress in the field (Lamsdell et al., 2020). Formally describing these specimens would thoroughly aid understanding patterns of horseshoe crab diversity through time. Similarly, new collecting efforts should be focussed on under-represented parts of the globe such as Asia, Africa and South America, as well as Jurassic and younger deposits, where knowledge of this group is hindered by a lack of specimens.

(4) Computer tomography (CT) scanning to document fossil and extant species has become a major tool over the past decade, which has started to positively impact horseshoe crab research. Schimpf et al. (2017) CT scanned *Limulus decheni* specimens to accelerate digital transfer of important morphological information (**Figure 35**). Zuber et al. (2017) used CT scans and augmented laminography to document muscle detail in a *Limulitella* sp. specimen (**Figure 24**), and Bicknell et al. (2018b) conducted micro-CT scans of iodine stained appendages to show *L. polyphemus* muscles *in situ*. Scanning and 3D reconstructions of specimens are still developing and therefore ripe for research, especially for documenting and disseminating information on holotypes.

CONCLUSIONS

The atlas presented here is the first comprehensive collation of named taxa and other unnamed specimens considered horseshoe

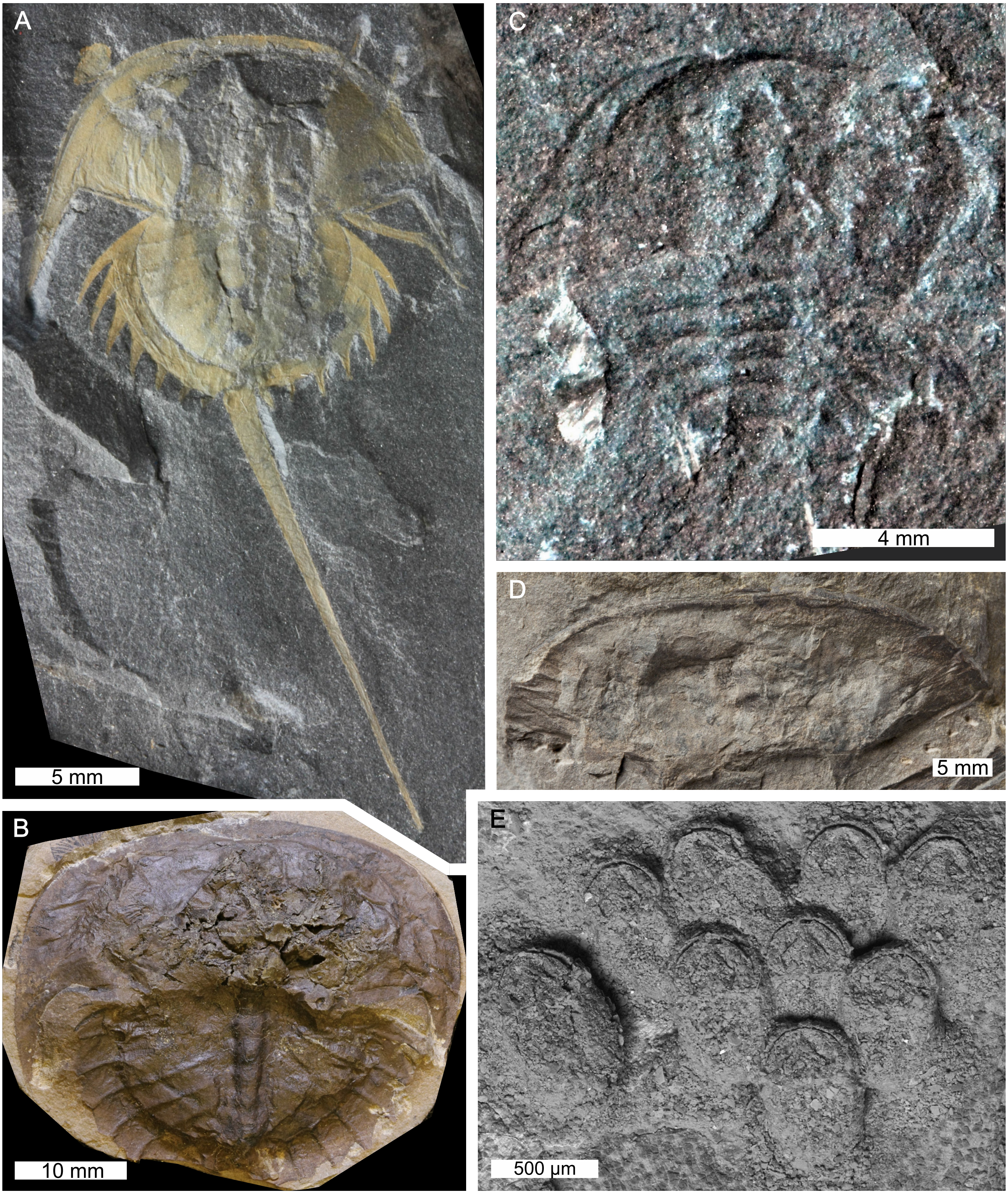

FIGURE 20 | *Euproops* species from Germany, Korea (formerly the Chōsen region) and UK, and *Xiphosuroides*. **(A)** *Euproops* sp., so call "Piesproops", from the Carboniferous-aged Osnabrück Formation, Germany. MAS Pal. 1308. **(B)** *Euproops rotundatus* specimens from the Carboniferous-aged Pennine Upper Coal Measures Formation (?) England, UK. YPM IP 428963. **(C)** *Euproops orientalis* from the Carboniferous-aged Jido Series, Korea. UMUT PA 00433, holotype. **(D)** *Euproops meeki* from the Carboniferous-aged South Wales Upper Coal Measures Formation, Wales, UK. BGS.GSE 48529, holotype. **(E)** *Xiphosuroides khakassicus* from the Carboniferous-aged Sarskaya Formation, Khakassia, Russia. Scanning electron microscope image. PIN 384/211, holotype. **(E)** Converted to gray scale. ? denotes uncertain formation assignment. Photo credit **(A)** Angelika Leipner; **(B)** Russell Bicknell; **(C)** Tai Kubo; **(D)** GB3D image, permission given by Mike Howe © 2018 JISC GB3D Type Fossils Online project partners (Amgueddfa Cymru – National Museum Wales); **(E)** Constantine Tarásenko.

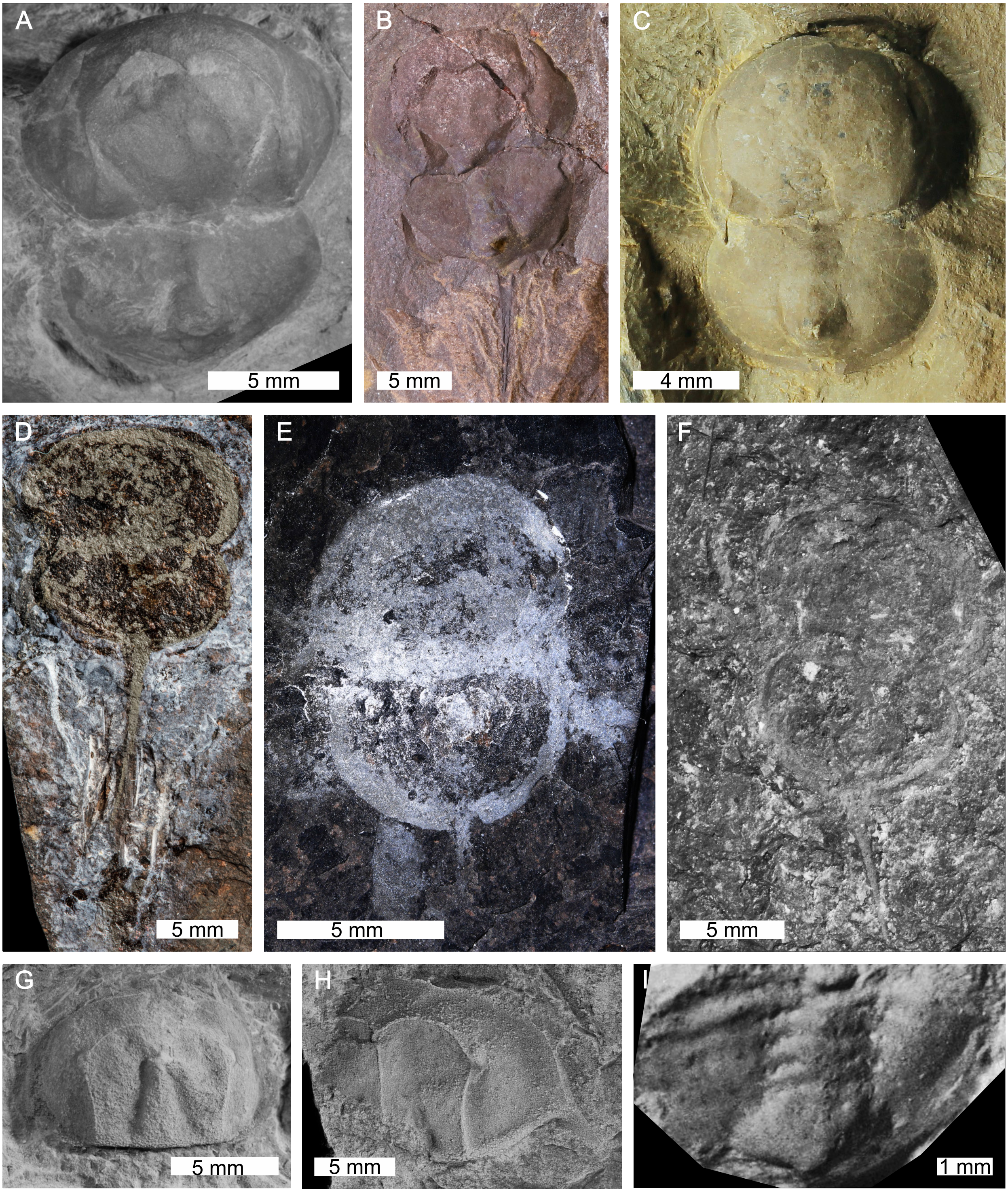

FIGURE 21 | Belinurids in the genera *Anacontium, Liomesaspis*, and *Prolimulus*. **(A,B)** *Liomesaspis laevis* specimens from the Carboniferous-aged Mazon Creek *Lagerstätte*, Illinois, USA. **(A)** MCZ 109536, holotype. **(B)** YPM IP 16913, paratype. **(C)** ?*Liomesaspis birtwelli* from the Carboniferous-aged Pennine Middle Coal Measures Formation, England, UK. NHMUK PI. I. 13882. **(D–F)** *Prolimulus woodwardi* from the Carboniferous-aged Kladno Formation, Czech Republic. **(D)** NHMUK PI. In. 18588, syntype. **(E)** MCZ 109537, hypotype. **(F)** MB.A.1989. **(G)** *Anacontium carpenteri* from the Wellington Formation, Oklahoma, USA. MCZ 109531, paratype. **(H)** *Anacontium brevis* from the Permian-aged Wellington Formation, Oklahoma, USA. MCZ 109533, holotype. **(I)** *Liomesaspis leonardensis* from the Permian-aged Wellington Formation, Kansas, USA. Image reproduced from Tasch (1961) as the specimen has been lost (C.D. Burke, pers. comms. 2018). W.U. 200, holotype. **(A,F)** Converted to gray scale. ? denotes uncertain taxonomic assignment. **(G,H)** Coated with ammonium chloride sublimate and converted to gray scale. Photo credit: **(A,B)** Russell Bicknell; **(C)** Monica **(C,E,G,H)** Stephen Pates; **(D)** Lucie Goodayle, NHM, London; **(F)** Lorenzo Lustri; **(G)** Mark Renczkowski; **(I)** Permission to reproduce holotype granted by Kathleen Huber.

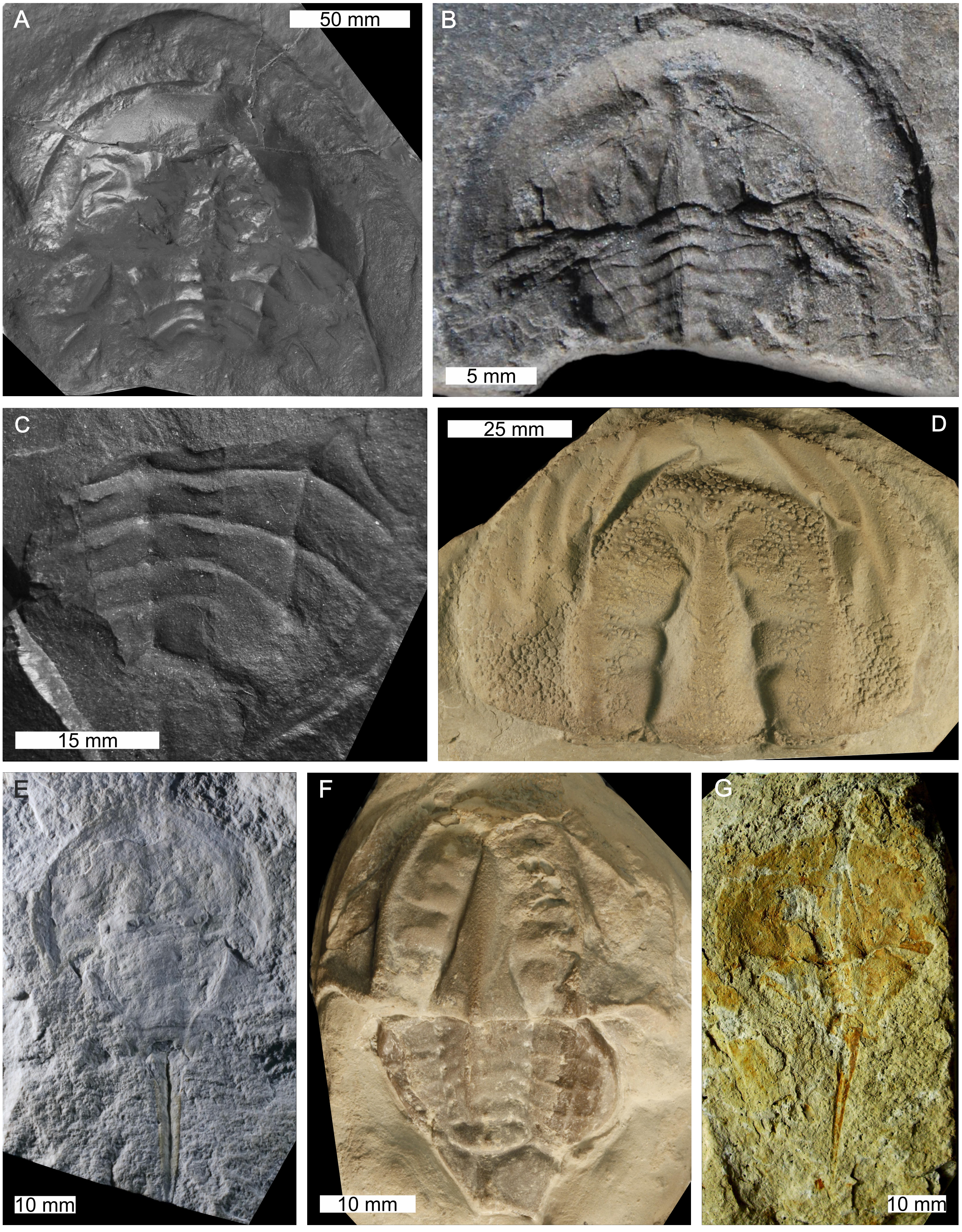

FIGURE 22 | Examples of Carboniferous and Permian paleolimulids. **(A)** *Xaniopyramis linseyi* from the Carboniferous-aged Upper Limestone Group, Weardale, England, UK. OUMNH E.03994, rubber cast of holotype. **(B)** *Paleolimulus woodae* from the Carboniferous-aged Horton Bluff Formation, Nova Scotia, Canada.

(Continued)

FIGURE 22 | NSM005GF045.374, paratype. **(C)** *Moravurus rehori* from the Carboniferous-aged Kyjovice Formation, Czech Republic. MMO B 8169, holotype. **(D,F)** *Paleolimulus signatus* from the Carboniferous-aged Pony Creek Shale *Konservat-Lagerstätte,* Wood Siding Formation, Kansas, USA. **(D)** USNM 484411, hypotype. **(F)** USNM PAL 484408, hypotype. **(E)** ?*Paleolimulus juresanensis* from the Permian-aged Maltchev or Belogor Limestone Beds. CCMGE CM2/3694, holotype. **(G)** *Paleolimulus kunguricus* from the Permian-aged Philippovian Formation, Russia. GIN PH-18, holotype. ? denotes uncertain taxonomic assignment. Photo credit: **(A)** GB3D image, permission given by Mike Howe © 2018 JISC GB3D Type Fossils Online project partners (Amgueddfa Cymru – National Museum Wales); **(B)** Allan Lerner; **(C)** Mertová Eva; **(D–F)** Russell Bicknell; **(G)** Serge Naugolnykh.

FIGURE 23 | *Bellinuroopsis rossicus* and *Rolfeia fouldenensis*. **(A)** *Bellinuroopsis rossicus* from the Devonian-aged Lebedjan Formation, Russia. CCMGE CM1/3694, holotype. **(B)** *Rolfeia fouldenensis* from the Carboniferous-aged Cementstones Group, Scotland, UK. NMS 1984.67.1A, holotype. Photo credit: **(A)** Russell Bicknell; **(B)** Bill Crighton.

crabs. The work builds on research presented during the early- to middle-twentieth century and, its presentation in an open-access environment will allow all researchers interested in horseshoe crabs access to key anatomical information needed for new taxonomic studies. Brief notes detailing the characteristic features and supposed life modes of families within Xiphosurida are presented, synthesizing other key works on the group. A brief evolutionary history of horseshoe crabs is presented, which outlines diversity changes from the Lower Ordovician to today. Finally, we highlight four major avenues for future research: most notably analyses of morphometric data of horseshoe crabs to mathematically probe the evolutionary history of the group. These same data may represent an important step toward reconciling synziphosurines with true horseshoe crabs.

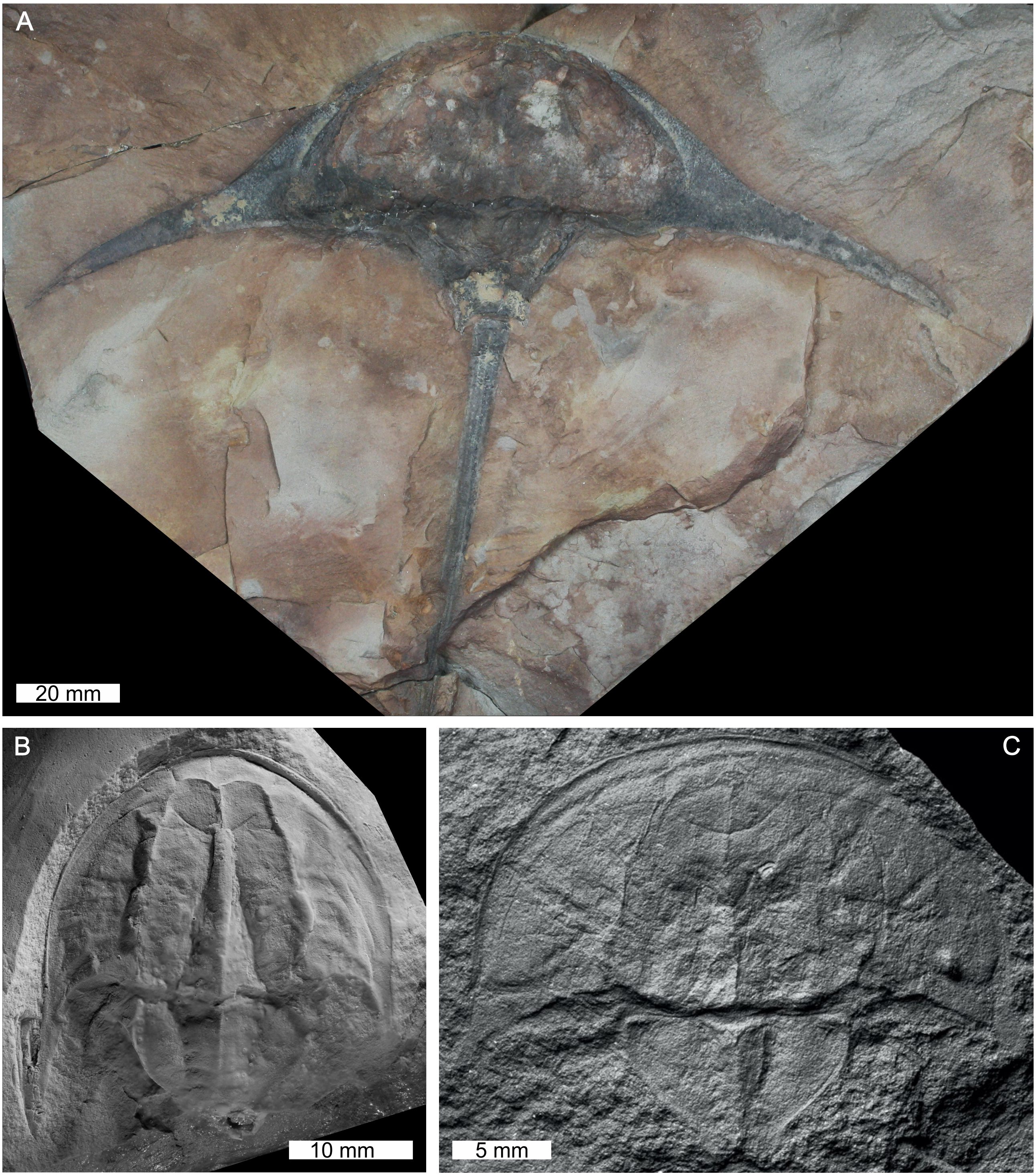

FIGURE 24 | Austrolimulids from Australia. **(A)** *Austrolimulus fletcheri* from the Triassic-aged Beacon Hill Shale, NSW, Australia. AM F38274, holotype. **(B)** *Tasmaniolimulus patersoni* from the Permian-aged Jackey Shale, Tasmania, Australia. UTGD 123979, holotype. **(C)** *Dubbolimulus peetae* from the Triassic-aged Ballimore Formation, NSW, Australia. MMF 27693, holotype. **(B,C)** Converted to gray scale. Photo credit: **(A)** Josh White; **(B)** Russell Bicknell; **(C)** David Barnes. **(B)** Coated in ammonium chloride sublimate.

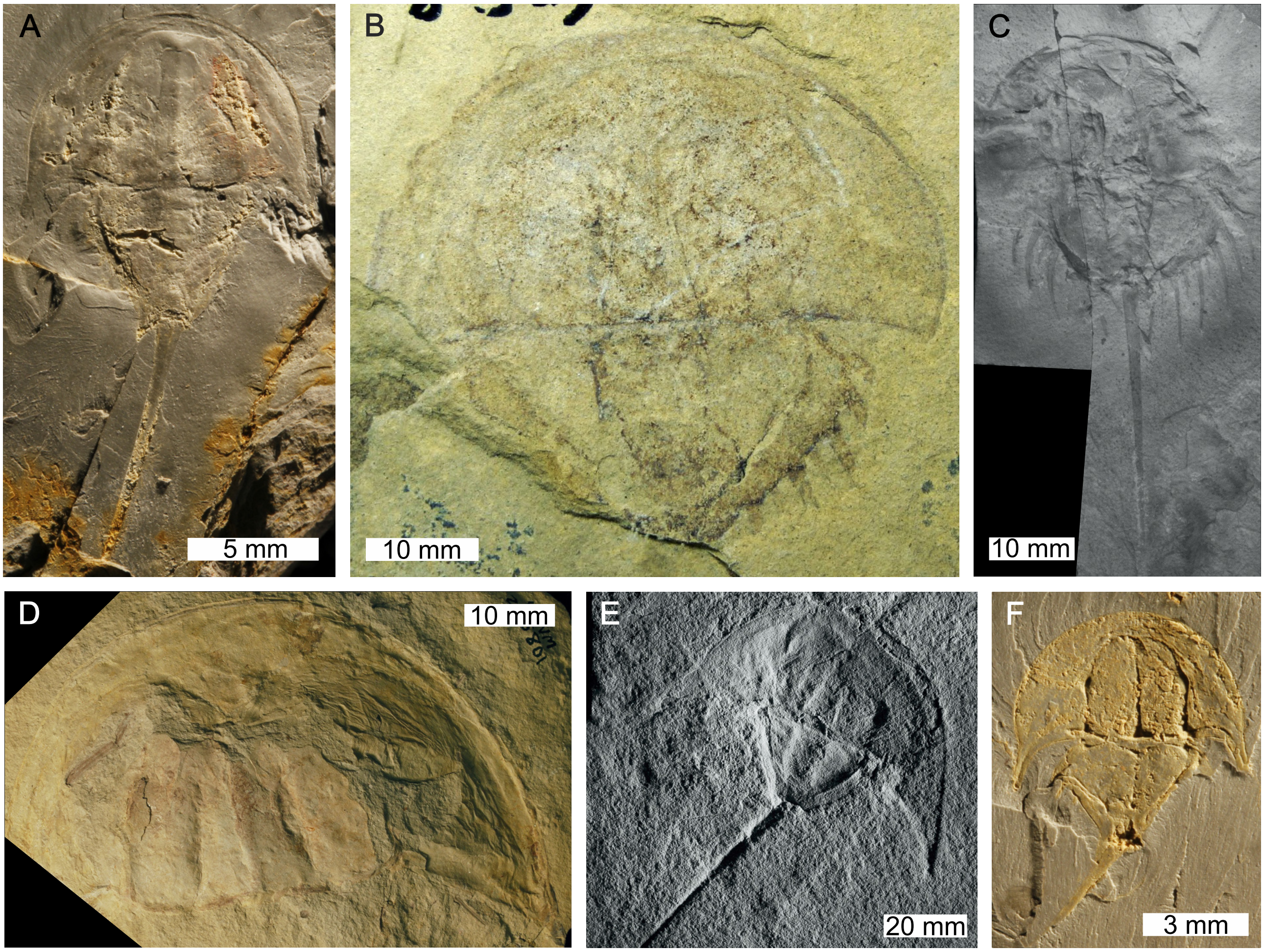

FIGURE 25 | Austrolimulids from the USA. **(A,F)** *Panduralimulus babcocki* from the Permian-aged Maybelle Limestone, Texas, USA. **(A)** USNM 520723, holotype. **(F)** USNM 520724, paratype. **(B,C)** *Paleolimulus longispinus* specimens from the Carboniferous-aged Bear Gulch Limestone, Montana, USA. **(B)** UM 81-8-5-1. **(C)** CM 54050. **(D)** *Casterolimulus kletti* from the Cretaceous-aged Fox Hills Formation, North Dakota, USA. USNM 206801, holotype. **(E)** *Vaderlimulus tricki* from the Triassic-aged Thaynes Group, Idaho, USA. UCM 140.25, holotype. **(C)** Converted to gray scale. Photo credit: **(A,C,D,F)** Russell Bicknell; **(B)** Kallie Moore; **(E)** Allan Lerner.

FIGURE 26 | Austrolimulids from Europe. **(A–C)** *Psammolimulus gottingensis* from the Triassic-aged Solling Formation, Germany. **(A)** Complete specimen, GZG INV 15356a. **(B)** Specimen with pushing leg preserved (black arrow). GZG INV 15376a. **(C)** Complete specimen with appendage impressions in cephalothorax, GZG.INV.45730a. **(D)** *?Paleolimulus fuchsbergensis* from the Triassic-aged Exter Formation, Germany. SMF VII I 311, holotype. **(E)** ?*Paleolimulus jakovlevi* from Permian-aged Araukaritovaya Formation Novoselovka, Ukraine. CCMGE CM1/8886, holotype. ? denotes uncertain taxonomic assignment. Photo credit: **(A–C)** Gerhart Hundertmark; **(D)** Norbert Hauschke; **(E)** Russell Bicknell.

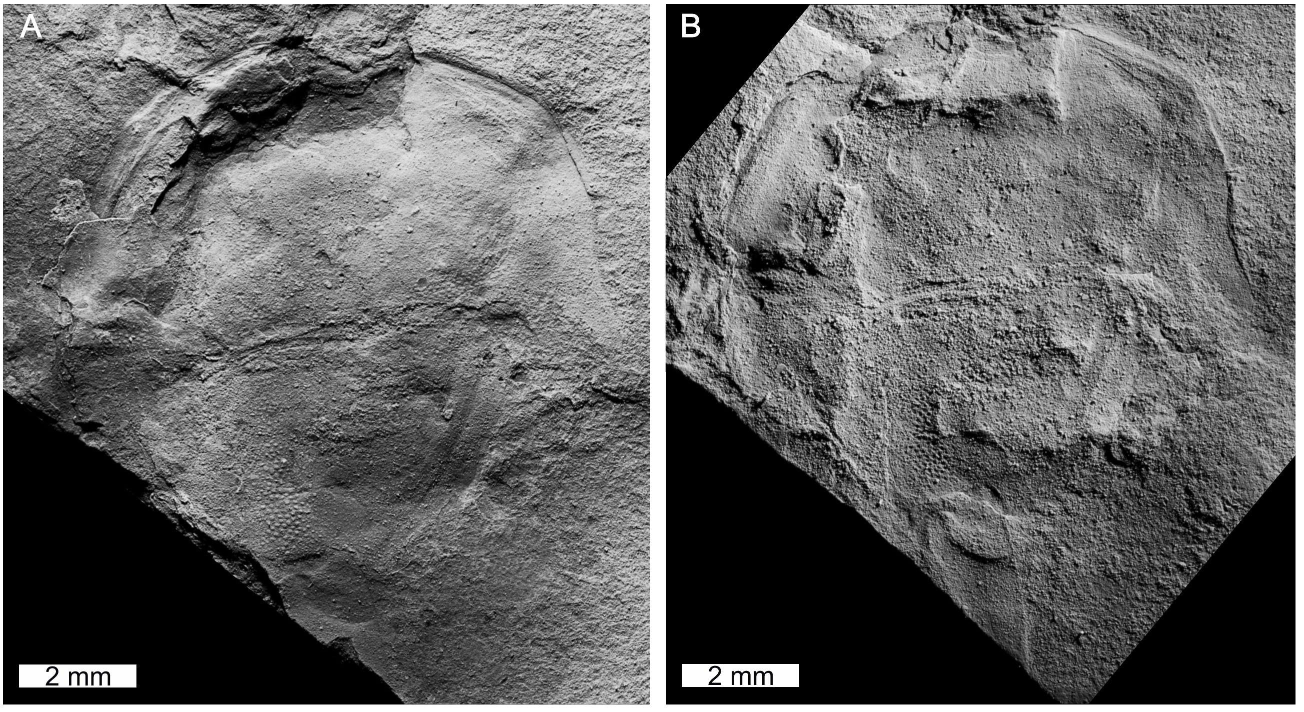

FIGURE 27 | The oldest suggested limulid from the lower Carbonifeous-aged Ballagan Formation, Scotland, UK; *Albalimulus bottoni*. **(A)** BSG.GSE2028, holotype, part. **(B)** BGS.GSE9680, holotype, counter-part. Image mirrored to align with **(A)** Phylogenetic analyses of Xiphosurida placed this taxon close to the base of Limulidae (Bicknell and Pates, 2019b). Specimens were coated with ammonium chloride sublimate and converted to gray-scale. Photo credit: Russell Bicknell.

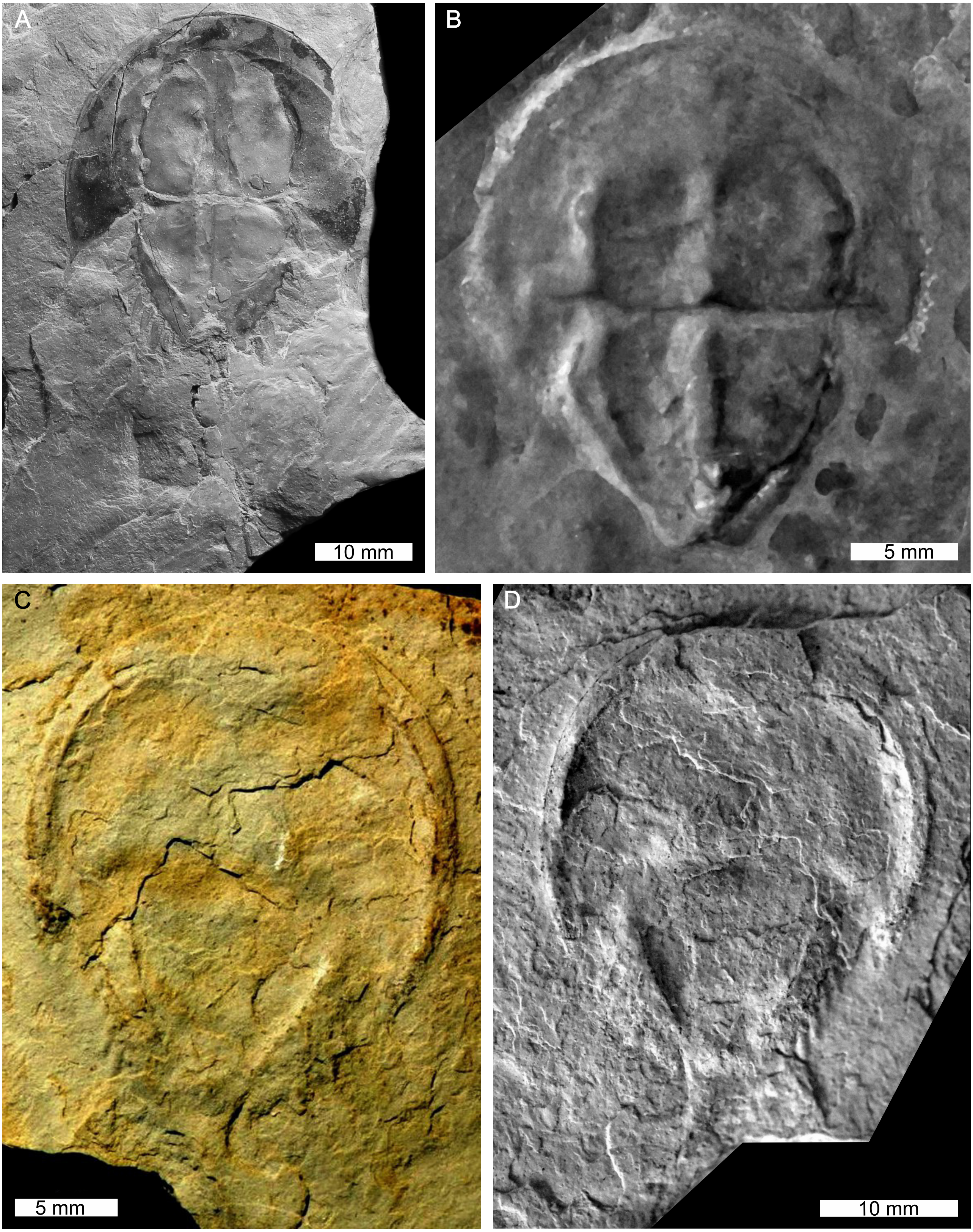

FIGURE 28 | Triassic-aged *Limulitella* species from France, Germany, and the Netherlands. **(A)** *Limulitella bronnii* from the Triassic-aged Grés á Voltzia Formation, France. State Museum of Natural History Stuttgart specimen in Grauvogel collection, LIM 68. **(B)** *Limulitella henkeli* from the Triassic-aged Jena Formation, Germany. *(Continued)*

FIGURE 28 | Slg-TC-4/MLU.Fri1906.VII/5, holotype. **(C)** *Limulitella* sp. from the Triassic-aged Lower Wellenkalk Member, Muschelkalk, Netherlands. Specimen within Oosterink private collection. **(D)** ?*Limulitella* sp. from the Triassic-aged Lower Muschelkalk, Netherlands, no specimen number. **(A,B,D)** Converted to gray scale. ? denotes uncertain taxonomic assignment. Photo credit: **(A)** Dieter Seegis; **(B)** Norbert Hauschke; **(C)** Thomas König; **(D)** Martien Oosterink.

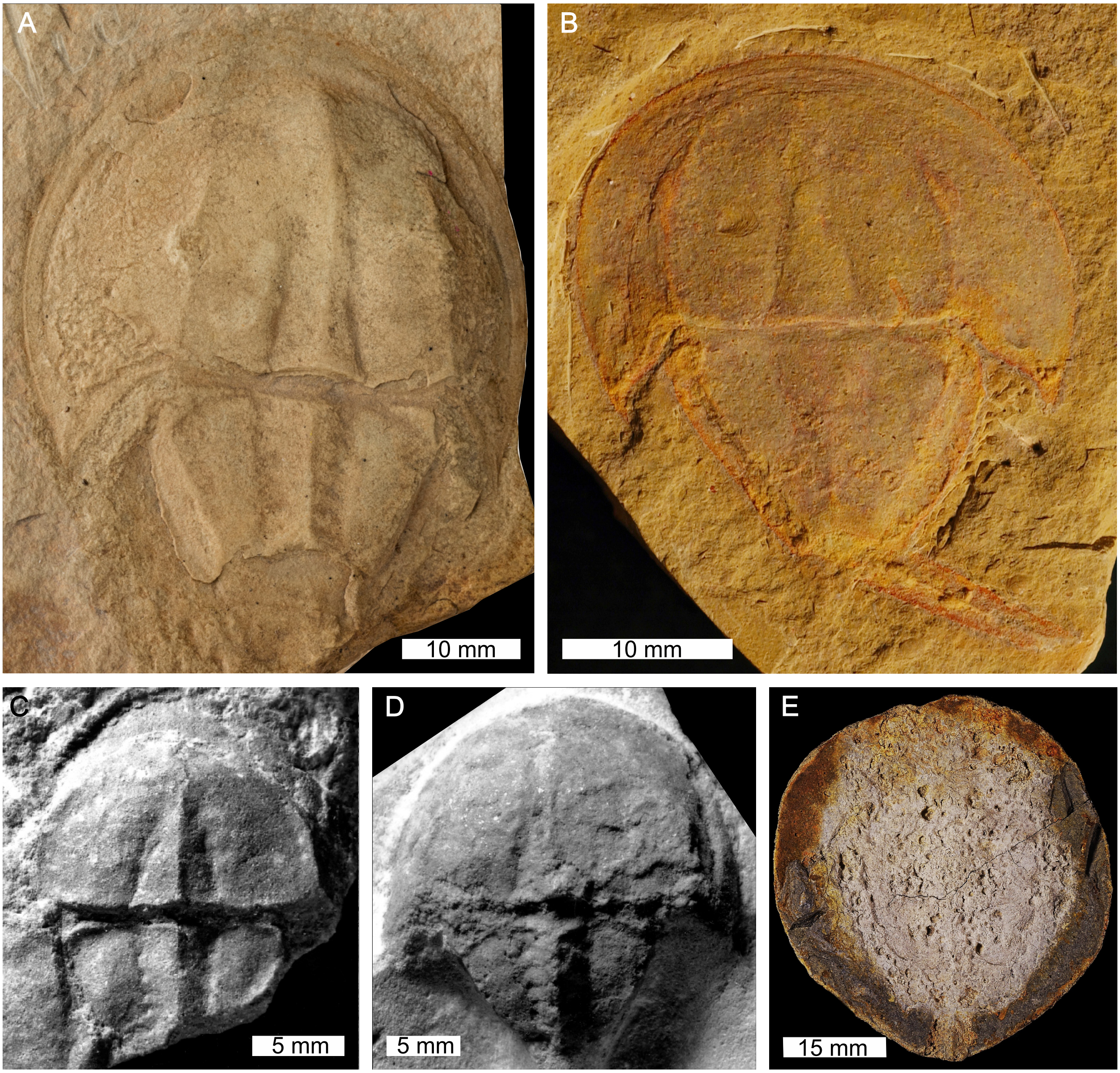

FIGURE 29 | Triassic-aged *Limulitella* species from France, Germany, Madagascar, and Tunisia. **(A)** *Limulitella vicensis* from the Triassic-aged Keuper Formation, France. MAN 8240, holotype. **(B)** *Limulitella tejraensis* from the Triassic-aged Ouled Chebbi Formation, Tunisia. ZPAL V. a6/101, holotype. **(C,D)** ?*Limulitella* sp. from the Triassic-aged Buntsandstein, Germany. **(C)** Exemplar 2 figured in Hauschke and Wilde (2008). **(D)** Exemplar 1 figured in Hauschke and Wilde (2008). **(C,D)** Geologisch-Paläontologischen Instituts der Ruprecht-Karls-Universität Heidelberg specimens and associated with Ph.D. thesis No. 3R.8.34-4. Specimens are likely lost as they were not found again in the collection. **(E)** *Limulitella* sp. from the Triassic-aged Sakamena Group, Madagascar. MSNMi11170, counterpart. ? denotes uncertain taxonomic assignment. Photo credit: **(A)** Lukáš Laibl; **(B)** Błażej Błażejowski; **(C,D)** Permission to reproduce photographs granted by Norbert Hauschke; **(E)** Giorgio Teruzzi.

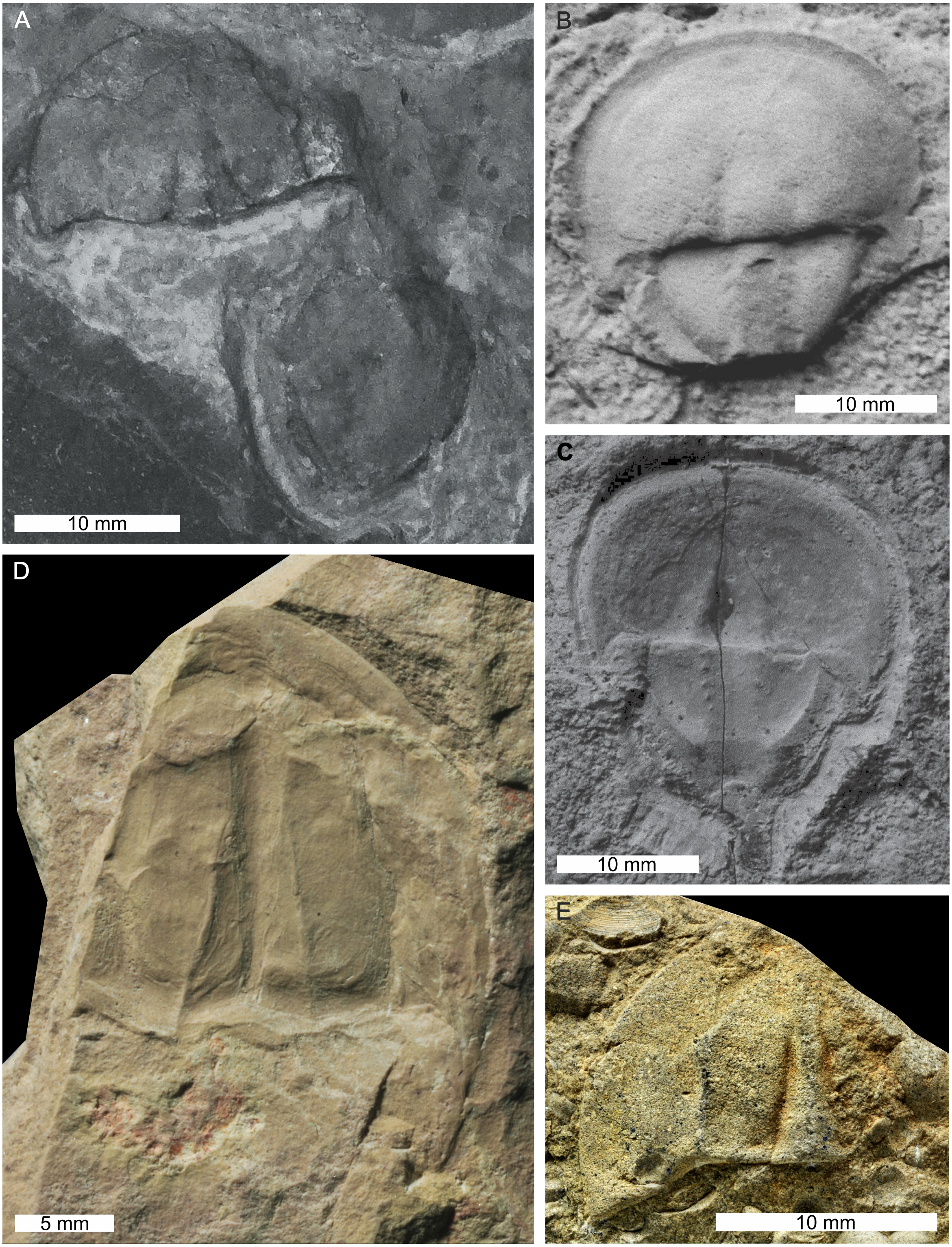

FIGURE 30 | Triassic and Jurassic *Limulitella* from Germany and Russia. **(A)** ?*Paleolimulus* sp., likely *Limulitella* sp., from the Triassic-aged Bernburg Formation, Germany. HAU-WIL2000. **(B,C)** Unnamed specimen from the Triassic-aged Trochitenkalk Formation, Germany. **(B)** Part of specimen. NME 07-56a. **(C)** Counter-part of specimen. NME 07-56b. **(A)** may have been lost. **(B,C)** May be lost (Hartmann pers. comms.). **(D)** *Limulitella* cf. *liasokeuperinus* from the Triassic-aged ?Exter Formation Germany. SNSB-BSPG 1967 XVI 27. Note: holotype lost in World War II. **(E)** *Limulitella volgensis* from the Triassic-aged Parshinskaya Formation, Russia. PIN 4048/7. **(A–C)** Converted to gray scale. ? denotes uncertain taxonomic or formation assignment. Photo credit: **(A–C)** Permission to reproduce photographs granted by Norbert Hauschke; **(D)** Mike Reich; **(E)** Constantine Tarásenko.

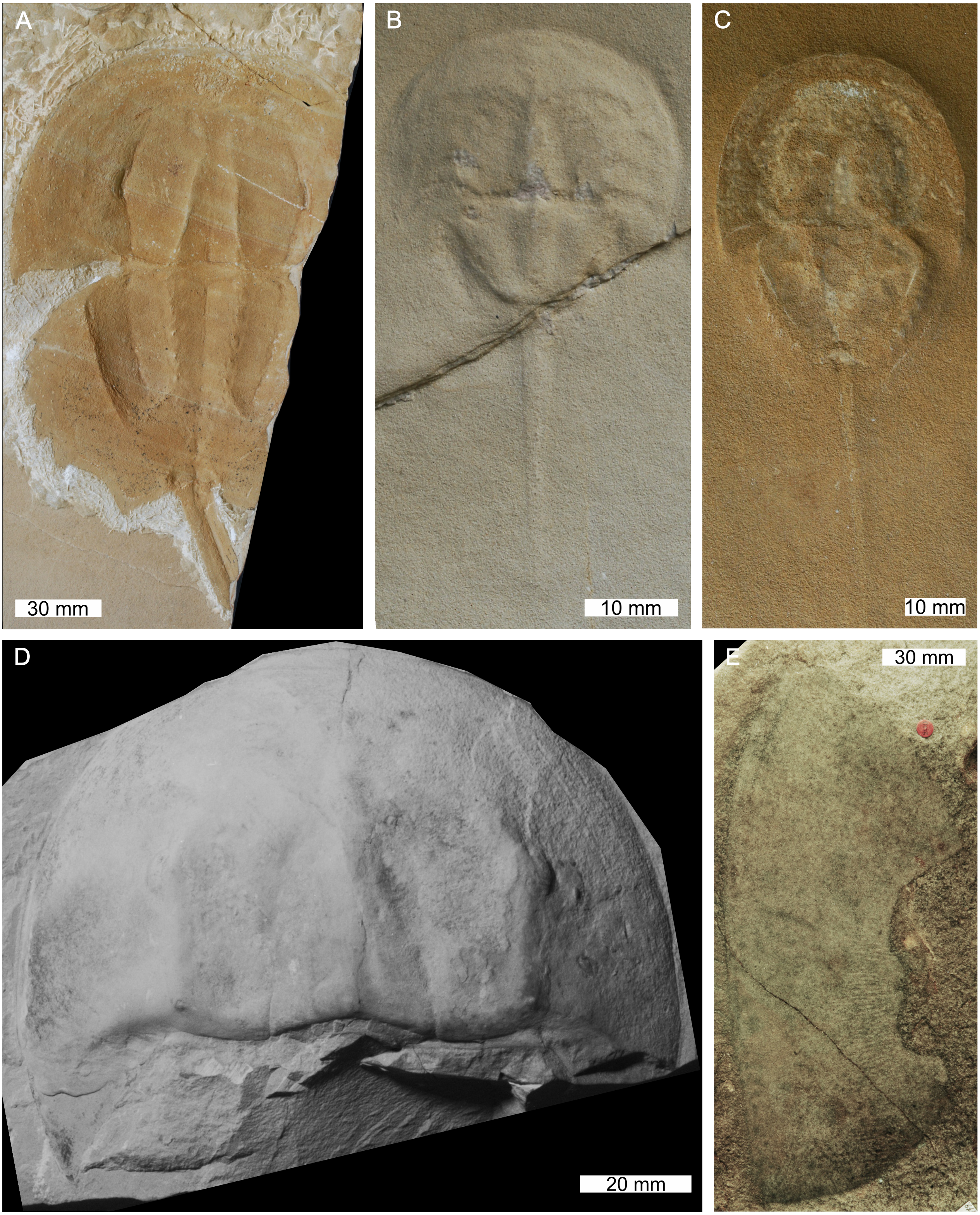

FIGURE 31 | Triassic-aged limulids from Germany, Spain, and Sweden. **(A)** *Tachypleus gadeai* from the Triassic-aged Alcover Limestone Formation, Spain. MGSB 19195, holotype. **(B)** *Mesolimulus crespelli* from the Triassic-aged Alcover Limestone Formation, Spain. MGSB 35088, holotype. **(C)** *Tarracolimulus rieki* from the Triassic-aged Alcover Limestone Formation, Spain. MGSB M 262, holotype. **(D)** Limulidae gen. et sp. indet, previously *Limulus kieri* from the Triassic-aged Muschelkalk Limestone, Germany. MB.A.0207. **(E)** *Limulus nathorsti* from the Triassic-aged Höör Sandstone, Sweden. SMNH Ar33179, holotype. **(D)** Converted to gray scale. Photo credit: **(A–C)** Pedro Adserà; **(D)** Lorenzo Lustri; **(E)** Liping Liu.

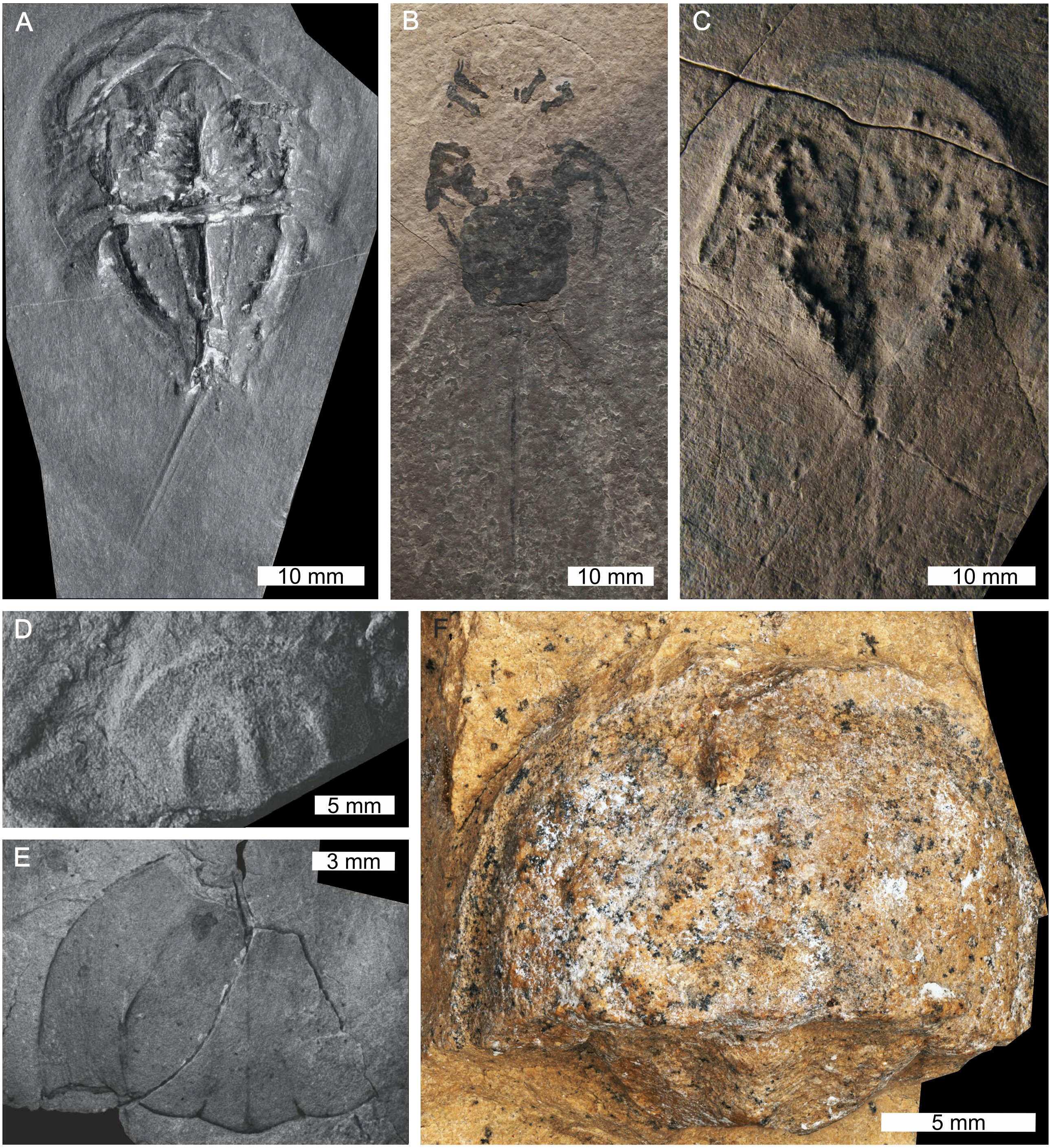

FIGURE 32 | Triassic-aged limulids from China and Europe. **(A,B)** *Yunnanolimulus luopingensis* from the Triassic-aged Member II, Guanling Formation, Luoping, China. **(A)** LPI-61299, holotype. **(B)** Specimen displaying walking legs and book gills. LPI-61734. **(C)** *Sloveniolimulus rudkini* from the Triassic-aged Strelovec Formation, Slovenia. PMSL T-993, holotype. **(D,E)** Limulidae gen. et sp. indet from the Triassic-aged Volpriehausen Formation, Germany. GPS. MLU 2018.23. **(E)** Limulidae gen. et sp. indet from the Triassic-aged Bernburg Formation, Germany. GPS. MLU 2018.24. **(F)** *Limulus priscus* from the Triassic-aged Muschelkalk Limestone, Germany. SNSB-BSPG AS I 939, holotype. **(D,E)** Converted to gray scale. Photo credit: **(A,B)** Shixue Hu; **(C)** Tomaž Hitij; **(D,E)** Permission to reproduce photographs granted by Norbert Hauschke; **(F)** Mike Reich.

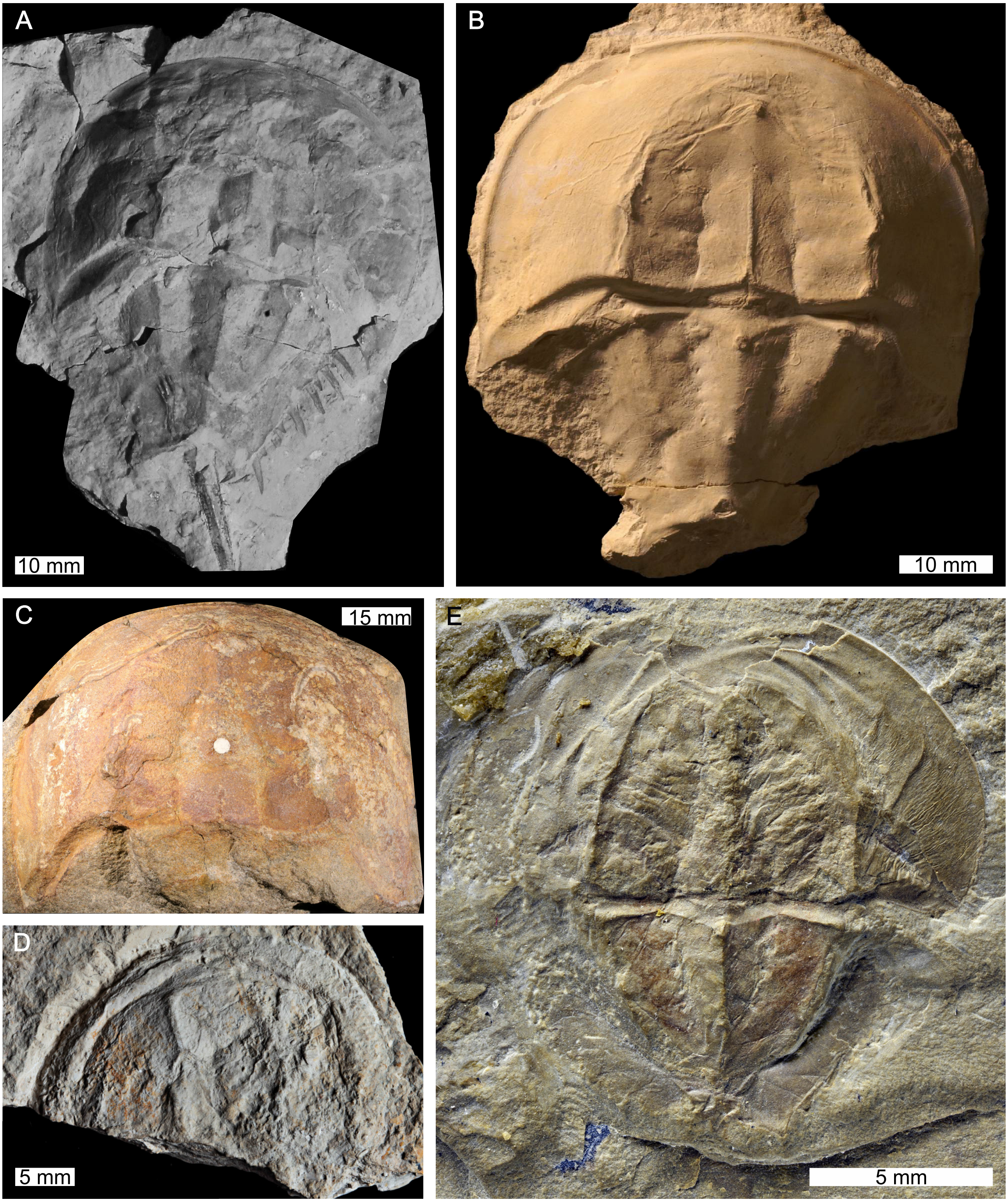

FIGURE 33 | Jurassic-aged limulids from Poland, Russia, and UK. **(A)** *Crenatolimulus* sp. from the Jurassic-aged Kcynia Formation, Poland. ZPAL X.1/O-B/XA 13.B. **(B)** *"Limulus" darwini* from the Jurassic-aged Kcynia Formation, Poland. ZPAL X.1O-BXA, holotype. **(C)** *Limulus woodwardi* from the Jurassic-aged Northampton Sand Formation (?), England, UK. L8627, holotype. **(D)** *Mesolimulus* sp. from the Jurassic-aged Purbeck Limestone Group, England, UK. NHMUK PI. I. 3042. **(E)** *Mesolimulus sibiricus* from the Jurassic-aged Talynzhansk Formation, Russia. PIN 3290-21, holotype. **(A)** Converted to gray scale. Photo credit: **(A,B)** Błażej Błażejowski; **(C)** Russell Bicknell; **(D)** Lucie Goodayle, NHM, London; **(E)** Sergey Bagirov.

FIGURE 34 | Examples of the iconic Jurassic-aged *Mesolimulus walchi* from Germany. **(A–H, J–L)** Specimens from the Solnhofen Limestone, Germany. **(A)** MNHN.F.A33516. **(B)** TMP 1984.69.5. **(C)** YPM IP 9011. **(D)** SMNS 27585. **(E)** CM 28515. **(F)** USNM 706404. **(G)** MCZ 106368. **(H)** OUMNH F11569. **(J)** Specimen preserving gut tract, YPM IP 8975. **(K)** SMNS 694513. **(L)** Specimen preserving gut tract, YPM IP 10183. **(I)** Specimen from the Nusplingen Plattenkalk, Germany, SMNS 70204. Photo credit: **(A)** Lilian Cazes; **(B,C,E–G,J,L)** Russell Bicknell; **(D,I,K)** Guenter Schweigert; **(H)** Javier Ortega Hernández.

FIGURE 35 | Cretaceous-aged limulids. **(A,B)** *Victalimulus mcqueeni* from the Korumburra Group, NSW, Australia. **(A)** Part, NMV P22410B, holotype. **(B)** Counter-part showing appendage impressions, NMV P22410A. **(C,G)** *Tachypleus syriacus* from the Haqel *Konservat-Lagerstätte*, Lebanon. **(C)** NHMUK PI. OR. 59783, holotype. **(G)** Specimen showing possible sexual dimorphic trait of scalloped anterior cephalothorax, NHMUK PI. OR. 187. **(D)** *Crenatolimulus paluxyensis* from the Glen Rose Formation, Texas, USA. **(D)** USNM 545241, cast of holotype. **(E)** *Mesolimulus tafraoutensis* from the Gara Sbaa *Lagerstätte*, Morocco. MSNM i26844, holotype. **(F)** *Limulus coffini* from the Pierre Shale, Colorado, USA, USNM 129043, holotype. Photo credit: **(A,B)** Frank Holmes; **(C,G)** Stephen Pates; **(D,F)** Russell Bicknell; **(E)** Giorgio Teruzzi.

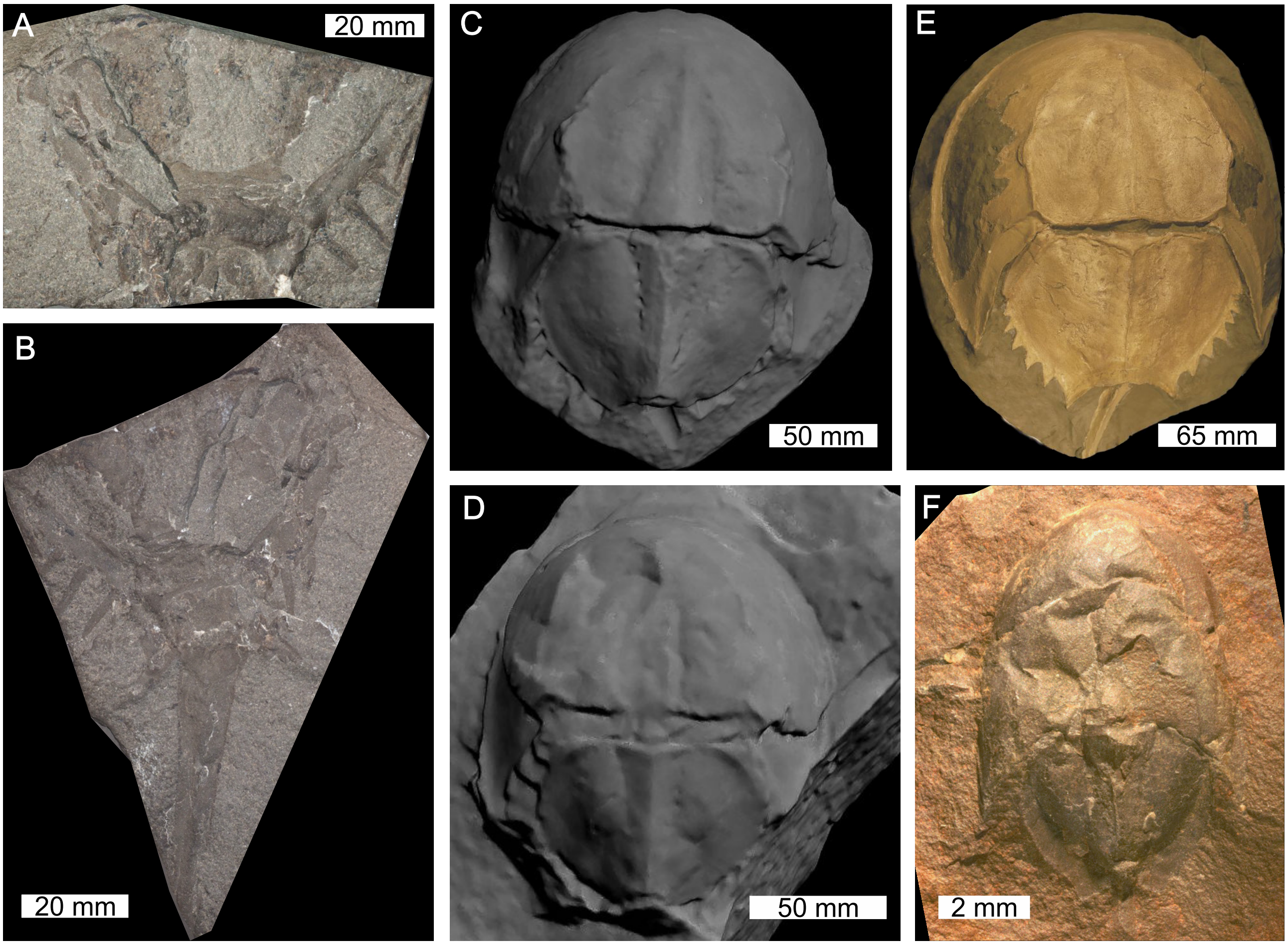

FIGURE 36 | Unnamed Permian xiphosurid, *Limulus decheni* and *Valloisella lievinensis*. **(A,B)** Unnamed xiphosurid from the Permian-aged Zechstein, Germany. **(A)** Counterpart showing thoracetron, NMK D2.11b. **(B)** Part showing thoracetron and telson, NMK D2.11a. **(C–E)** *Limulus decheni* from the Eocene-aged Domsen Sands, Germany. **(C)** 3D reconstruction of a surface scan, VET1931.1.MLU. **(D)** 3D reconstruction of a surface scan, GIE1863.1a.MLU, holotype. **(E)** Specimen with part of telson preserved, MB.A.1901. **(F)** *Valloisella lievinensis* from the Carboniferous-aged Bickershaw Complex, England, UK; LL11133. Photo credit: **(A,B)** Peter Mansfeld; **(C,D)** Permission to use 3D reconstructions granted by Lars Schimpf; **(E)** Andreas Abele; **(F)** Russell Bicknell.

FIGURE 37 | Examples of extant male and female *Tachypleus* species. **(A,B)** Male *T. tridentatus*, YPM IZ 55603. **(A)** Dorsal view. **(B)** Ventral view. **(C,D)** Male *T. gigas*, YPM IZ 55578. **(C)** Dorsal view. **(D)** Ventral view. **(E,F)** Female *T. tridentatus*, YPM IZ 55576. **(E)** Dorsal view. **(F)** Ventral view. **(G,H)** Female *T. gigas*, YPM IZ 103393. **(G)** Dorsal view. **(H)** Ventral view. Photo credit: Russell Bicknell.

FIGURE 38 | Examples of extant male and female *Limulus polyphemus* and *Carcinoscorpius rotundicauda*. **(A,B)** Male *C. rotundicauda*, YPM IZ 55595. **(A)** Dorsal view. **(B)** Ventral view. **(C,D)** Male *L. polyphemus*, YPM IZ 55605. **(C)** Ventral view. **(D)** Dorsal view. **(E,F)** Female *C. rotundicauda*, YPM IZ 55574. **(E)** Dorsal view. **(F)** Ventral view. **(G,H)** Female *L. polyphemus* YPM IZ 55601. **(G)** Ventral view. **(H)** Dorsal view. Photo credit: Russell Bicknell.

AUTHOR CONTRIBUTIONS

RB designed the study and made the figures, with input from SP. RB and SP photographed material and wrote the manuscript.

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