

A new limulid (Chelicerata, Xiphosurida) from the Lower Jurassic (Sinemurian) of Osteno, NW Italy

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With 2 figures

Abstract: Fossiliferous beds within the Lower Jurassic (Sinemurian) Moltrasio Limestone at Osteno, Italy, preserve a marine fauna including crustaceans, ophiuroids, ammonites, vermiform invertebrates, chondrichthyans, and actinopterygians in Lagerstätte conditions. Excavations during the 1980s and 1990s have greatly expanded the known faunal diversity. Herein, we describe the first horseshoe crab from Osteno, representing the oldest Jurassic limulid and only the second xiphosuran known from Italy. The new taxon, *Ostenolimulus latus* n. gen., n. sp., preserves details of the external morphology along with phosphatized traces of internal muscles and book gills. A number of characteristics, most prominently the possession of a cardiac ridge with rounded cross section, indicate *Ostenolimulus* n. gen. is a limulid resolving outside of the crown group and belongs to a clade including other Jurassic and Cretaceous taxa, such as *Mesolimulus*, *Allolimulus*, *Victalimulus*, and *Casterolimulus*. The discovery of *Ostenolimulus* n. gen. indicates that stem limulids were a diverse and widespread clade during the Jurassic, a time when crown group limulids were beginning to diversify and radiate.

Key words: Horseshoe crabs, Italy, Lagerstätte, Limulidae, taxonomy, Xiphosura.

1. Introduction

Horseshoe crabs, aquatic chelicerates with a fossil record extending back to the Ordovician (RUDKIN et al. 2008), are known from a wide variety of environments (LAMSDELL 2016; LAMSDELL 2020a) across every continent (LAMSDELL 2020b). Known from only 89 species over their 470 million year history, Xiphosura (comprising Xiphosurida and their stem lineage – LAMSDELL 2013) achieve their highest species diversity in the Carboniferous with the radiation of the non-marine belinurines with a second peak in diversity in the Triassic and notable troughs in diversity during the Silurian (from which no xiphosurid species are known) and Jurassic (LAMSDELL, in press). Historical periods of low standing xiphosuran diversity are of particular interest given that only four species of horseshoe crab persist today (LAMSDELL & MCKENZIE 2015), with all under pressure from a variety of factors including hab-

itat loss, exploitation, and climate change (HSIEH & CHEN 2009; BOTTON et al. 2015; PATI et al. 2017). Understanding how evolutionary lineages have responded to similar events in the geologic past can help predict how their descendants may react to current and future changes (DIETL et al. 2015; KOSNIK & KOWALEWSKI 2016; LAMSDELL et al. 2017); in this way, knowledge of the horseshoe crab paleontological record may have a critical role in assisting conservation efforts for the extant species.

Herein we report a new xiphosuran species from the Lower Jurassic (Sinemurian) of Osteno (Como, NW Italy), representing the oldest limulid known from the Jurassic. Study of the fossil layers from Osteno has been intermittent. The fossiliferous outcrop is located nearby the Porto Franco (Crotto del Doglio) locality on the northern shore of Lugano Lake (or Ceresio), around 3 kilometres west of the village of Osteno (Como, NW Italy) (Fig. 1A, B). The first formal re-



Fig. 1. **A** – Geographic map of Lugano Lake with the location of Osteno and “Porto Franco” quarry. **B** – “Porto Franco” quarry, view of the lake. **C, D** – “Porto Franco” quarry, views of the fossiliferous layers.

cord of fossiliferous material was reported by PINNA (1967). Later, PINNA (1968, 1969) described the first decapod crustaceans from Osteno and the interest of the palaeontologists of the Museo di Storia Naturale di Milano (MSNM) in the Osteno fossils increased during the 1970s thanks to private donations of additional specimens and notably in the 1980s to 1990s, when new controlled digs were carried out by the

MSNM at “Porto Franco” quarry. These excavations collected new material promoting several new studies on the faunal assemblage and on its peculiar preservation (see below in Fossil assemblage). The official digs at Osteno quarry have permitted the collection of hundreds of specimens substantially enlarging the MSNM collections. The field excavations ended in 2002, and the quarry was definitively abandoned. The

new limulid described herein was recently donated to the MSNM and increases the faunal diversity at Osteno, as well as being only the second horseshoe crab described from Italy (SELDEN *et al.* 2019).

2. Geological setting

The fossiliferous outcrop at Osteno (“Porto Franco” quarry) is a roughly 10-metre-thick strata of rock, grey-white on the exposed surface and bluish-grey when fractured, formed from fine sediments and rich in siliceous sponge spicules (Fig. 1C, D). The exact shape of this “lens” of fossiliferous rock is unknown. It is found within the Moltrasio Limestone Formation, a very thick formation rich in flint nodules and highly developed in the Como and Lugano areas (NW Italy). The sediments were deposited during the Early Jurassic in a deep-sea basin, forming a complex of sediments 3,000 to 4,000 meters thick at the basin’s deepest point. The presence of syndimentary faults, caused by landslides of the muddy deposits, give evidence of currents laden with sediment (turbidites). The Moltrasio Limestone is generally poorly fossiliferous, but the belemnites, ammonites and brachiopods that have been found have enabled a dating between the Hettangian (201 million years ago) and the early Pliensbachian (Carixian, 190 million years ago). The Osteno lens was probably formed under special conditions in a very localized area of the basin; however, as it is impossible to follow its lateral development and, therefore, its relationship with more characteristic Moltrasio Limestone sediments, it is difficult to understand exactly what those conditions were (PINNA 1985). In thin section, the rock usually presents finely layered and rich in fragments of calcareous organisms and spicules from siliceous sponges. The attribution to the lower Sinemurian *Arietites bucklandi* Zone was based on the discovery of the ammonite *Coroniceras bisulcatum* (BRUGUIÈRE, 1789) in association with *Ectocentrites* CANAVARI, 1888 and *Sulciferites* SPATH, 1922 (PINNA 1967; ARDUINI *et al.* 1982).

3. Fossil assemblage

The outcrop contains mainly the remains of marine organisms (invertebrates and fish). Despite being relatively common, fish make up a smaller fraction of

the Osteno faunal assemblage than do the arthropods. The studies conducted so far have identified 12 different types of cartilaginous and bony fish, of which four genera are also known from the marginally older Early Jurassic strata of Lyme Regis (UK), which is used as a point of comparison given its close geologic age to the strata at Osteno. Some terrestrial plants have also been found, suggesting the existence of nearby land.

Flora: The plant remains at the site are largely incomplete and relatively scarce. General morphology is mostly undeformed, albeit rather compressed, the original organic matter reduced to a thin carbonaceous film that has largely altered the fine anatomical details, such as the ribs of the leaves or the stem structures. This has hampered their precise systematic identification. However, studies have identified a terrestrial floral assemblage that is almost exclusively arboreal in nature. Seven genera have been recognized at Osteno among equisetals, ferns, bennettitales, and coniferales, with only a few species, of which three have been identified and ten remain indeterminate (BONCI & VANNUCCI 1986).

Fauna (invertebrates): Although sponges are poorly preserved at the site, they were probably abundant in the original environment, becoming an important component of the limestone. Very rare are small ophiuroids, molluscs (cephalopods and bivalves), and brachiopods. Rare but interesting components of the faunal assemblage are a variety of “worm-like” organisms, a term used to denote invertebrates with a very elongate body lacking a mineralized exoskeleton. These organisms include the only specimen of an enteropneust (acorn worm; Enteropneusta) found at the site, nematodes (Nematoda), and polychaete annelids (Annelida) (for a complete list see GARASSINO & TERUZZI 2015). The cephalopod molluscs, which are very rare, have been attributed primarily to two subclasses, Ammonoidea and Coleoidea (GARASSINO & DONOVAN 2000). The decapod crustaceans make up the largest portion of Osteno’s faunal assemblage: seven genera have been described, including 15 species (PINNA 1968; PINNA 1969; GARASSINO & TERUZZI 1990; TERUZZI 1990; GARASSINO 1996), some of them later revised by CHARBONNIER *et al.* (2013) and DEVILLEZ & CHARBONNIER (2017, 2019). Stomatopods are very rare in the fossiliferous strata of Osteno: indeed, in almost twenty years of excavations only three specimens have been unearthed and studied (BRAIG *et al.*, *in press*). However, the most interesting scientific dis-

covery at Osteno is undoubtedly that of an odd group of crustaceans, the Thylacocephala, the largest component of the invertebrate fauna whose anatomy and systematic position are still being debated (PINNA et al. 1982; TERUZZI et al. work in progress).

Fauna (vertebrates): Chondrichthyan, holocephalian, and actinopterygian fish are the minor component of Osteno's faunal assemblage. The Mesozoic chondrichthyes belong to one of two groups: the now extinct hybodonts and the neoselachians, which includes sharks and stingrays. Unlike Lyme Regis, where the former dominate, only the latter have been found at Osteno. Two shark species have been recognized (DUFFIN 1987; DUFFIN 1998). Two species of holocephalian have been identified in the quarry with one of them, *Squaloraja polyspondyla* (AGASSIZ, 1836), previously known only in the Sinemurian of Lyme Regis (DUFFIN 1992).

Coelacanths populated the waters of the Osteno sea, as evidenced by isolated scales which are very similar to those of *Holophagus gulo* (EGERTON, 1861), previously reported from Lyme Regis.

Several scarce actinopterygians and teleostean fish are also presents in the faunal assemblage (for a complete list see GARASSINO & TERUZZI 2015).

4. Preservation

The fossils are very compressed and flattened, often with superimposed structures which make reconstruction difficult. Soft body parts are preserved mostly as thin films of grey or blackish kerogen, a substance of organic origin whose mechanism of formation at Osteno has not yet been clarified. Among the invertebrates, the best-preserved remains belong to arthropods and coleoid cephalopods. The reason for this appears to be that those organisms had phosphorus-rich structures – such as the chitinous exoskeleton of the arthropods – that, during the *post-mortem* decomposition phase, provided a saline component essential for bacteria covering the soft tissues (e.g., muscles) to quickly preserve their morphology, for example allowing the preservation of individual muscle fibres (WILBY & BRIGGS 1997).

Several hypotheses have been put forward to explain the formation of the fossiliferous lens at Oste-

no, but so far none have proved to be satisfactory or sufficiently confirmed either by the sedimentological data or by the analysis of the fossilized remains. The sediments do not show traces of bioturbation – the activity of organisms living on or inside the bottom, such as tunnel digging in search of food or shelter – so it is very probable that the organisms that were entirely or partially linked to life on the sea bottom were transported there from a certain distance away. The fossils are often preserved almost intact, with their structures in anatomical connection: decapod crustaceans retain all appendages, even the most delicate ones (BRIGGS & KEAR 1994; HOF & BRIGGS 1997). Nonetheless, fragmentary specimens are not uncommon, such as of fish, which, along with arthropods, make up by far the most abundant fraction of Osteno's faunal assemblage. It is highly likely, then, that the organisms found in the fossiliferous lens and transported to the site by currents did not undergo lengthy transportation; moreover, once the corpses were deposited onto the seabed bottom anoxic conditions and high sedimentation rate must have quickly ensured that they were covered by sediments. Thus, relatively short transport of organic remains and rapid burial in a milieu that was strongly reducing, oxygen-free and lacking scavengers may have been the principal factors favoring their peculiar state of preservation.

5. Material

One specimen preserving prosomal carapace and incomplete thoracetron, lacking the telson (total length *c.* 81 mm, as preserved). The studied specimen is dorsally exposed, preserved as part and counterpart, compressed dorso-ventrally, flattened, with superimposed structures; the chitinous exoskeleton is partially preserved and crushed. Photos were taken under natural and ultraviolet lights to highlight the morphological details.

The specimen is housed in the palaeontological collections of the Museo di Storia Naturale di Milano (MSNM).

6. Systematic palaeontology

Class Xiphosura LATREILLE, 1802
 (= Merostomata DANA, 1852)
 Order Xiphosurida LATREILLE, 1802
 Suborder Limulina RICHTER & RICHTER, 1929
 Superfamily Limuloidea LEACH, 1819
 Family Limulidae LEACH, 1819
 (= Mesolimulidae STÖRMER, 1952; = Heterolimulidae
 VÍA BOADA & DE VILLALTA, 1966)

Genus *Ostenolimulus* nov.

Etymology: From Osteno, the village close to “Porto Franco” quarry where the studied specimen was collected.

Type species: *Ostenolimulus latus* n. gen., n. sp., by monotypy.

Diagnosis: Limulid with prosomal carapace wider than long; cardiac lobe narrow but greater in width than one third its length, lacking scalloped margin with moderate to shallow cardiac furrows; cardiac lobe bearing well-defined cardiac ridge with rounded cross section, terminating posteriorly in a single dorsal spine; lateral eyes located centrimedially, associated with ophthalmic ridges that converge anteriorly, becoming progressively more effaced as they do so; genal spines with genal facet expanding distally; thoracetron with single axial spine located anteriorly; apodemal pits located within axial furrow; moveable spines likely increasing in size posteriorly.

Discussion: The new genus exhibits a number of characteristics indicating a close relationship to the clade of limulids comprised of the genera *Mesolimulus* STÖRMER, 1952, *Allolimulus* LAMSDALL, 2020b, *Casterolimulus* HOLLAND, ERICKSON & O'BRIEN, 1975, and *Victalimulus* RIEK & GILL, 1971, particularly the possession of a cardiac ridge with rounded cross section. *Ostenolimulus* is distinct from the other genera within the clade in having a wider cardiac lobe than in *Victalimulus* and *Casterolimulus*, while the lack of a scalloped margin to the cardiac lobe differentiates *Ostenolimulus* n. gen. from the four species of *Mesolimulus* (see LAMSDALL et al. 2020). The centrimedial position of the lateral eyes in *Ostenolimulus* n. gen. further distinguishes the new genus from *Allolimulus*, *Casterolimulus* and *Victalimulus*, which all exhibit a posteromesial lateral eye configuration. The lack of deep grooves defining the cardiac lobe also sets *Ostenolimulus* n. gen. aside from all other genera within the clade, suggesting that *Ostenolimulus* may resolve as the sister-taxon to the rest of the clade.

Ostenolimulus latus n. gen., n. sp.
 Fig. 2A–D

Etymology: The species epithet, *latus*, is latin for “wide” and refers to the broad dimensions of the species.

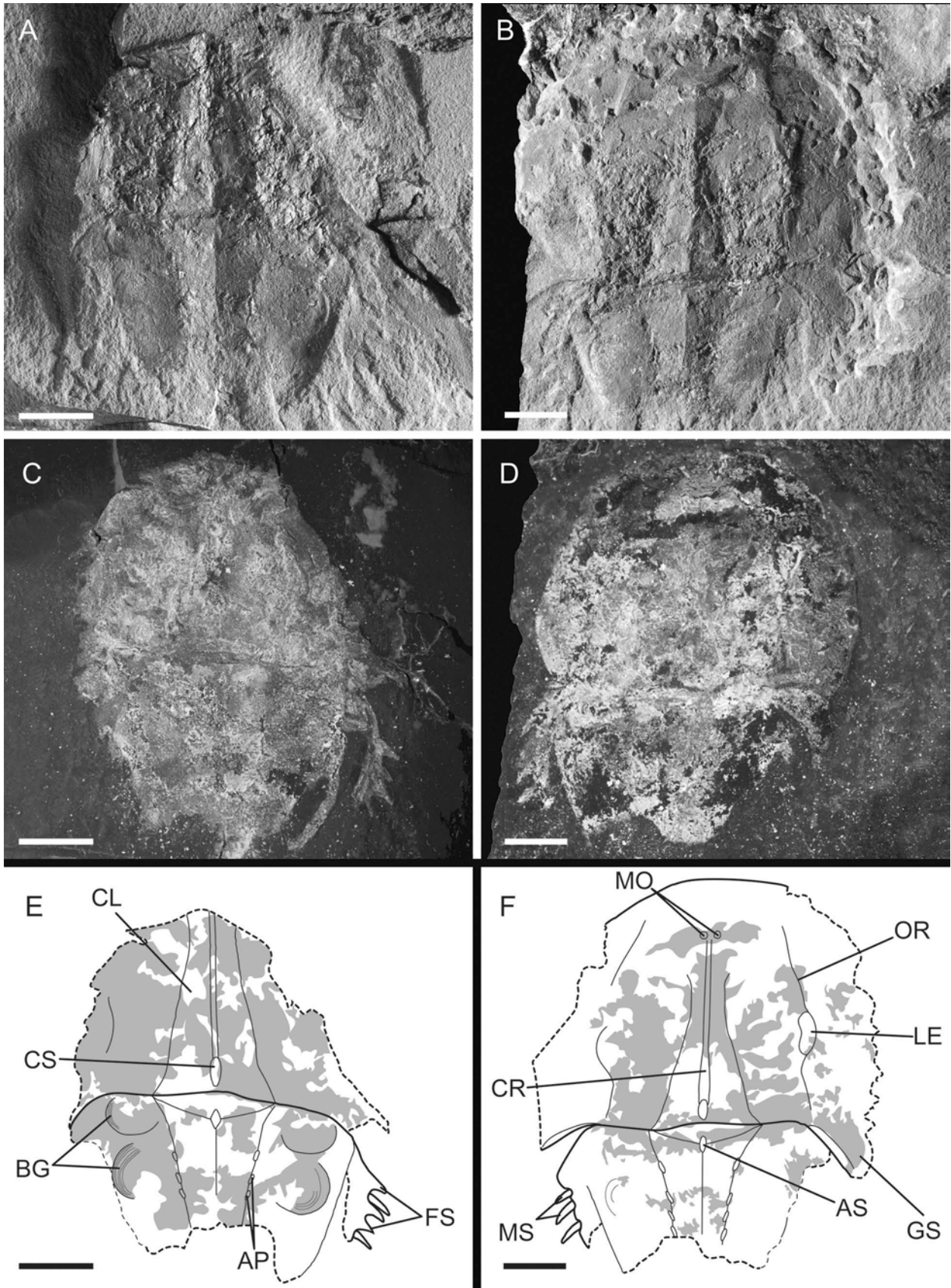
Holotype: MSNM i29339.

Diagnosis: As for the genus.

Description: Part and counterpart of prosomal carapace and thoracetron in dorsal view. Maximum preserved length of specimen 81 mm, maximum preserved width 72 mm. Specimen preserved in three-dimensional relief, with cuticle preserved as a dark brown kerogen that fluoresces under ultraviolet light. Phosphatized muscle tissue is preserved in patches around the center of the prosomal carapace between the cardiac lobe and the ophthalmic ridge, most likely representing the muscle blocks for limb attachment (Fig. 2C). Phosphatized material around the apodemes of the thoracetron represent further muscle tissue, while laminated oval pyritized structures either side of the axis are the remains of the book gills. The prosomal carapace preserves details of the external structures including the cardiac lobe, ophthalmic ridges, lateral eyes, and median ocelli (Fig. 2A, B). The thoracetron is less complete but preserves evidence of the axis and apodemes as well as the portions of the fixed and moveable spines and ventral doublure (Fig. 2C, D). The telson articulation, along with the telson itself, is not preserved.

Prosomal carapace 53 mm long, total width 72 mm. Cardiac lobe 34 mm long and 18 mm wide at base with curved margins that bow rapidly inward, narrowing to 3 mm at its anterior. Cardiac furrow moderate to shallow. Broad keel running down center of cardiac lobe developed into cardiac ridge with rounded cross section. Spine positioned centrally at posterior of cardiac lobe, 3 mm long by 3 mm wide. Raised triangular node likely bearing median ocelli located anterior to cardiac lobe; ocelli positioned 31 mm from prosomal carapace posterior. Each ocellus is 1.5 mm long and 1 mm wide, with 0.2 mm spacing between them. Lateral eyes positioned midway between the cardiac lobe and prosomal carapace lateral margin, approximately midway along the prosomal carapace length. Lateral eyes are crescentic in shape, 6 mm long and 2 mm wide. Ophthalmic ridges associated with lateral eyes, 37 mm in length with the lateral eyes positioned midway along. The ophthalmic ridges exhibit a distinct kink at the eyes, converging inward anteriorly with an interior angle of 122 degrees. The ophthalmic ridges get progressively more effaced anterior to the eyes, with a slight indication of them meeting medially at the ocellar node to form a very faint m-shape. The posterior termination of the ophthalmic ridges preserves no indication of ophthalmic spines. Genal spines of moderate length, extending 14 mm in length beyond the prosomal carapace posterior, narrowing evenly distally from a width of 12 mm proximally. Occipital bands shallow and broad, widening from the posterior of the ophthalmic ridges distally onto the genal spines.

Thoracetron subtriangular in outline and apparently broader than long although it is broken away along its posterior, resulting in a preserved length of 28 mm. Width 60 mm anteriorly, narrowing to 29 mm wide at preserved posterior. Free lobes not well preserved, with their distal portions weathered away or overlapped by the genal spines, but project beyond the thoracetron lateral margin. Axial region of thoracetron 20 mm wide at anterior, narrowing to 11 mm posteriorly. Axis with medial keel running along its length, terminating anteriorly at an axial spine, which is diamond-shaped in outline, with a width of 2 mm and a length of 4 mm. At least three apodemal pits run alongside



the thoracetrone axis within the groove of the axial furrow. Apodemes are each 2.5 mm long and associated with strands of phosphatized muscle fibres. Subaxial region of thoracetrone preserves details of two pairs of phosphatized book gills (Fig. 2A). The book gills are lamellate, oval in outline, the first pair each being 8 mm long by 16 mm wide and the second pair each being 10 mm long and 14 mm wide. Thoracetrone lateral margin produced into at least four fixed spines, with moveable spines inserting in between. The four preserved fixed spines are 4 mm long and 2 mm wide; the three preserved moveable spines (as preserved), likely increase in size posteriorly, with first being 4 mm long and 2 mm wide while the third is 5 mm long and 2 mm wide. Ventral thoracetrone double 5 mm wide.

7. Discussion

The ichnological record indicates that horseshoe crabs were more abundant during the Jurassic than their body fossil suggests, with trackways known from France (GAILLARD 2011; MOREAU et al. 2014), India (ALBERTI et al. 2017), Morocco (OUKASSOU et al. 2019), and the United Kingdom (ROMANO & WHYTE 1987; ROMANO & WHYTE 2003; ROMANO & WHYTE 2013; ROMANO & TAYLOR 2016; ROMANO & TAYLOR 2019; ROMANO 2020). However, the trace fossil record is of limited use for determining the diversity of Jurassic horseshoe crabs due to the fact that horseshoe crab appendages (and hence their trackways) show a strong degree of morphological conservatism (BICKNELL et al. 2019) and cannot be used to differentiate between the different xiphosurid families. The existing body fossil record suggests a moderately diverse global horseshoe crab fauna, with the crown group limulid *Crenatolimulus darwini* (KIN & BŁAŻEJOWSKI, 2013) known from the Upper Jurassic along with the stem limulid (i.e., a limulid that resolves outside of the crown group, which is defined as the least inclusive clade accommodating all extant species) *Mesolimulus walchii* (DESMAREST, 1822). Crown group limulids are absent from the Middle Jurassic, although two

stem limulids, *Mesolimulus sibiricus* PONOMARENKO, 1985 and *Allolimulus woodwardi* (WATSON, 1909) are known from Siberia and the United Kingdom, respectively. Only one horseshoe crab species has been previously recorded from the Lower Jurassic, the recently described austrolimulid *Franconiolimulus pochankei* from the Hettangian of Germany (BICKNELL et al. 2021). *Ostenolimulus latus* n. gen., n. sp. is the first limulid described from the Lower Jurassic and is a temporal intermediary between *Franconiolimulus*, which precedes *Ostenolimulus* by 5 million years, and *Allolimulus*, which *Ostenolimulus* predates by 16 million years.

As well as filling a stratigraphic gap, the species extends the known range of Jurassic horseshoe crabs into southern Europe and is only the second horseshoe crab, and the first limulid, to be found in Italy. The morphology of *Ostenolimulus* n. gen. indicates it resolves outside of the limulid crown group, demonstrating that stem limulids were still common in the Mesozoic as crown group limulids were radiating. The size of *Ostenolimulus* n. gen. is greater than the majority of known Palaeozoic and Triassic xiphosurids, with the notable exceptions of *Xaniopyramis* SIVETER & SELDEN, 1987, from the Carboniferous of the United Kingdom, and *Heterolimulus* VÍA BOADA & DE VILLALTA, 1966 from the Triassic of Spain. *Ostenolimulus* n. gen. is of a more comparable size to the other known Jurassic limulids, indicating that a marked shift in size within the lineage occurred during the early Mesozoic and became established by the Jurassic.

The occurrence of horseshoe crabs among the Osteno fauna increases the faunal diversity and is a rare occasion of horseshoe crabs as part of a more normal marine assemblage. The clade of stem limulids to which *Ostenolimulus* n. gen. belongs exhibits a transition to a non-marine life habit, with *Victalimulus* and *Casterolimulus* known from lacustrine deposits (HOLLAND et al. 1975; RIEK & GILL 1971), a shift in habitat known to have occurred independently at least three times of the course of horseshoe crab evolution-

Fig. 2. *Ostenolimulus latus* n. gen., n. sp., MSNM i29339. **A** – Counterpart, photographed under normal light. **B** – Part, photographed under normal light. **C** – Counterpart, photographed under ultraviolet light. **D** – Part, photographed under ultraviolet light. **E** – Counterpart, interpretive drawing showing outline of the specimen with dashed lines indicating broken margins and the shaded areas corresponding to areas of phosphatic preservation. **F** – Part, interpretive drawing showing outline of the specimen with dashed lines indicating broken margins and the shaded areas corresponding to areas of phosphatic preservation. Abbreviations: AP: Apodemal pits; AS: Axial spine; BG: Book gills; CL: Cardiac lobe; CR: Cardiac ridge; CS: Cardiac spine; FS: Fixed spines; GS: Genal spine; LE: Lateral eye; MO: Median ocelli; MS: Moveable spine; OR: Ophthalmic ridge. Scale bars equal 10 mm.

ary history (LAMSDSELL 2020a). *Ostenolimulus* n. gen. is known from unequivocally marine sediments, reinforcing that the habitat shift observed in *Victalimulus* and *Casterolimulus* represents a distinct episode of the phenomenon, likely occurring during the latest Jurassic or Early Cretaceous.

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