An introduction to the Mesozoic biotas of Scandinavia and its Arctic territories

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Abstract: The Mesozoic biotas of Scandinavia have been studied for nearly two centuries. However, the last 15 years have witnessed an explosive advance in research, most notably on the richly fossiliferous Triassic (Olenekian–Carnian) and Jurassic (Tithonian) Lagerstätten of the Norwegian Arctic Svalbard archipelago, Late Cretaceous (Campanian) Kristianstad Basin and Vomb Trough of Skåne in southern Sweden, and the UNESCO heritage site at Stevns Klint in Denmark – the latter constituting one of the most complete Cretaceous–Palaeogene (Maastrichtian–Danian) boundary sections known globally. Other internationally significant deposits include earliest (Induan) and latest Triassic (Norian–Rhaetian) strata from the Danish autonomous territory of Greenland, and the Early Jurassic (Sinemurian–Pliensbachian) to Early Cretaceous (Berriasian) rocks of southern Sweden and the Danish Baltic island of Bornholm, respectively. Marine palaeocommunities are especially well documented, and comprise prolific benthic macroinvertebrates, together with pelagic cephalopods, chondrichthyan, actinopterygians and aquatic amniotes (ichthyopterygians, sauropterygians and mosasauroids). Terrestrial plant remains (lycophytes, sphenophytes, ferns, pteridosperms, cycadophytes, bennettitaleans and ginkgoes), including exceptionally well-preserved carbonized flowers, are also world famous, and are occasionally associated with faunal traces such as temnospondyl amphibian bones and dinosaurian footprints. While this collective documented record is substantial, much still awaits discovery. Thus, Scandinavia and its Arctic territories represent some of the most exciting prospects for future insights into the spectacular history of Mesozoic life and environments.

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The Mesozoic fossil record of Scandinavia and its Arctic territories of Greenland and Svalbard span the dawn of the Triassic some 252 myr ago (Wordie Creek Formation, East Greenland: Nielsen 1935; Bendix-Almgren 1976; Looy et al. 2001; Stemmerik et al. 2001; Bjørager et al. 2006) through to the terminal Cretaceous–Palaeogene boundary 66 myr ago (Møns Klint Formation, Denmark: Damholt & Surylk 2012; Surylk & Adolfsen & Ward 2014; Hansen & Surylk 2014). This interval is marked by the nascence of modern faunal and floral biodiversity, and culminated in one of the most cataclysmic extinction events in Earth history. Much of our knowledge about the Mesozoic world has derived from the long tradition of palaeontological research in Europe (Rudwick 2008; Evans 2010), and yet many key biotas and bioevents from this continent remain comparatively underexplored. Scandinavia and its Arctic territories are therefore extremely important because they encompass not only a Boreal mid–high palaeolatitude setting (Surylk 1990; Ditchfield 1997), but have also witnessed a burgeoning of novel discoveries that reveal significant insights into the global spectrum of Mesozoic organisms, ecosystems and environments.

This Special Publication aims to encapsulate these latest palaeontological advances, and augments them with topical synopses from leading specialists in the field. Our introduction is intended to
provide additional contextual background, and, in particular, emphasizes the broad trends in floral successions and the distribution of faunal finds. Together, these highlight Scandinavia and its Arctic territories as a regional centre for Mesozoic biotic radiations, and a spectacular area for future field exploration with landmark research potential.

**Institutional abbreviations**

LO, Department of Geology, Lund University, Lund, Sweden; MGUH, Natural History Museum of Denmark, Copenhagen, Denmark; OESM, Østsjællands Museum, Store Heddinge, Denmark; PMO, University of Oslo Natural History Museum (Palaeontological Collection), Oslo, Norway; PMU, Palaeontology Collection, Museum of Evolution, Uppsala University, Uppsala, Sweden.

**A synthesis of Scandinavian Mesozoic biotas**

**The Triassic**

The long history of Scandinavia’s terrestrial biotas is charted through the palynological record, which manifests liverworts as the seminal colonizers of continental ecosystems in the early Palaeozoic (Late Ordovician) of southern Sweden (Badawy 2014). Increasing abundance and diversity of bryophytes and vascular plants occurred throughout the Silurian and Devonian in Ska˚ne (Mehlqvist et al. 2015) and Gotland (Hagström 1997), with the genesis of characteristic Mesozoic floras around the Permian-Triassic boundary in Greenland, Svalbard and the Oslo Rift: these collectively indicate turnover of regional biomes coincident with increasing aridity (Bercovici et al. 2015). The Permian-Triassic extinction event is represented by the disappearance of dominant hygrophilous Cordaites (which equate to gigantopterids in Cathaysia and glossopterids in Gondwana) and their replacement by emergent seed plants (Anderson et al. 1999; McLoughlin 2011).

The coeval chronicle of Triassic terrestrial faunas is not well represented until the Norian-Rhaetian of the Fleming Fjord Formation in Jameson Land, East Greenland (Klein et al. 2015; Milàn et al. 2015). Here, body fossils and footprints evidence various dinosaurian taxa, especially sauropodomorphs, together with plagiosaur and capitosaurs (primarily temnospondyl amphibians, rare rhamphorhynchoid pterosaurs, and early mammaliforms (e.g. Bendix-Almgreen 1976; Jenkins et al. 1994; Milàn et al. 2012a; Sulej et al. 2014; Clemmensen et al. 2015; Hansen et al. 2015; Klein et al. 2015). Fragmentary Late Triassic (Carnian-Rhaetian) temnospondyls are likewise known from both Svalbard and southern Sweden (Kear et al. 2015 and references therein), and coincide with lush vegetation comprising ginkgoes, cycads and bennettites, lycophytes, sphenophytes, and ferns (Vajda et al. 2013). Fossilized fungi and bacterial traces have also been reported from Hopen Island in the Svalbard archipelago (McLoughlin & Strullu-Derrien 2015). A bone fragment of a Late Triassic sauropodomorph was also recovered from a drill core in the North Sea 2256 m below the seabed (Hurum et al. 2006a).

Earliest Triassic (Induan–Olenekian) marine ecosystems are recognized from the Vardebukta Formation on Svalbard (Vigran et al. 2014), and most prolifically from the world-famous Wordie Creek Formation in East Greenland (Fig. 1a–e). These deposits incorporate bivalves, gastropods and ammonoids, as well as actinopterygian and coelecanth fishes (Speth 1932; Nielsen 1942, 1949; Donovan 1964) that span the Permian-Triassic boundary (Twitchett et al. 2001; Bijrager et al. 2006). Potentially anadromous Early Triassic temnospondyls (primarily tematosaurids, rhytidostians and capitosaurians) have also been described, with approximately equivalent occurrences found on Spitsbergen and other islands in Svalbard (Sæve-Söderbergh 1936; Cox & Smith 1973; reviewed by Kear et al. 2015): these are associated with actinopterygian fishes (Fig. 1f) and hybodontiform sharks (Stensiö 1921, 1925; Blazewiński et al. 2013).

Globally renowned Triassic marine ammonite fossils were recovered from Spitsbergen during the Nordenskjöld expeditions of 1864 and 1868 (Hulke 1873). More complete material was subsequently collected by Swedish scientists in 1908 and 1909 (Wiman 1910, 1916a, b, 1928, 1933), and constitutes a diverse assemblage of ichthyopterygians (Fig. 1g), including the phylogenetically important basal taxon Grippia longirostris (Maxwell & Kear 2013). Isolated pistosaurid sauropterygian remains have also been discovered (Kear & Maxwell 2013), and Hurum et al. (2014) documented Triassic ichthyosaurian material from Edgeøya (Vigran et al. 2014). The classic vertebrate successions of Wiman (1910) are, however, still used to subdivide the horizons on Spitsbergen (see Maxwell & Kear 2013): the lithostratigraphical work of Mørk et al. (1999), equating the actinopterygian- and temnospondyl-dominated ‘Fish Niveau’ to the lower Olenekian Lusitaniadalen Member of the Vikinghøgda Formation; the ‘Grippia Niveau’ and ‘Lower Saurian Niveau’ – both representing sequential components of the Late Olenekian–Anisian Vendomdalen Member of the Vikinghøgda Formation; and derived mixosaurid and shastasaurid ichthyosaurs from the ‘Upper Saurian Niveau’ characterizing the Landinian Blanknuten Member of the upper Botnehei Formation and the Carnian Tschermakfjellet Formation.
The Jurassic

The Triassic–Jurassic transition is marked by extinctions coincident with emissions from the Central Atlantic Magmatic Province (Sha et al. 2015). In the Scandinavian territories, this is evidenced by successions from East Greenland (Klein et al. 2015). These reveal an abrupt replacement of the Rhaetian ‘Lepidopteris flora’ (typified by seed ferns, Taxodiaceae and the enigmatic Ricciisporites-producing plants) by the Hettangian ‘Thaumatopteris flora’ (Harris 1931), which was dominated by ferns, Cheirolepidiaceae, Pinaceae and new groups of cycadophytes (Vajda et al. 2013). Compatible earliest Jurassic strata are exposed in southern Sweden and on the Danish Baltic island of Bornholm (Vajda & Wigforss-Lange 2009). Ornithopod and potential thyreophoran footprints (Gierliński & Ahlberg 1994; Milán & Gierliński 2004), together with isolated dinosaurian vertebrae

Fig. 1. Scandinavian Triassic localities and fossils. (a) Earliest Triassic (Induan–Olenekian) strata of the Wordie Creek Formation at Kap Stosch in East Greenland (photograph: Benjamin Kear); (b) actinopterygian fishes Bobastrania groenlandica (PMU 29041) and (c) Australosomus kochi (PMU 29036); (d) pectinoid bivalve Claraia (PMU 29004); and (e) ceratitid ammonoid Ophiceras (PMU 29145). Middle Triassic (Anisian–Landian) vertebrate remains from Spitsbergen: (f) skull of the actinopterygian Saurichthys elongatus (PMU 24010a); and (g) skull of the early ichthyopterygian Phalarodon (PMU 24577). Scale bars are 20 mm in (c) and (e), and 30 mm in (b), (d), (f) and (g).
(Bölaü 1954), have been described from the Rhaetian–Hettangian Höganaäs Formation of the Höganaäs Basin in southern Sweden.

Intense Jurassic volcanism, today revealed by volcanic necks in southern Sweden (Bergelin 2009), created lahar deposits that preserve plant remains in exceptional detail, even including visible cell nuclei (Bornfleure et al. 2014). More recent excavations in similar sediments overlying the Sinemurian–Pliensbachian Höör Sandstone have produced conifer wood with growth increments, permitting reconstruction of palaeoclimate, and pollen assemblages that evince the vegetative community (Vajda et al. 2016).

The Early–Middle Jurassic outcrops on Bornholm are situated within a complex fault block of the NW–SE-trending Sorgenfrei–Tornquist Zone (Gravesen 2009). The stratigraphically oldest finds occur in the Hettangian Sose Bugt Member of the Rønne Formation, and comprise deformation structures interpreted as dinosaurian tracks (Clemmensen et al. 2014). Associated organic-rich beds and abundant plant material otherwise infer a warm and humid palaeoenvironment (Petersen et al. 2003).

The Pliensbachian marginal marine Hasle Formation on Bornholm (Fig. 2a) has produced macroinvertebrates, as well as hybodontiform and neoselachian shark remains, together with rhomaeoaurid and plesiosaurid plesiosaurs (Surlyk & Noe-Nygaard 1986; Rees 1998; Milàn & Bonde 2001; Bonde 2004, 2012; Donovan & Surlyk 2003; Smith 2008). Recently, a small theropod footprint was also found in horizons subject to periodic subaerial exposure (Milàn & Surlyk 2015). In addition, enigmatic Pliensbachian marine amniotes have been reported from East Greenland (Bendix-Almgreen 1976), and Toarcian marine amniote and dinosaurian bones and teeth were recognized from Scandinavian erratics transported to northern Germany during Pleistocene glaciations (Sachs et al. 2016).

The Bajocian–Bathonian Bagå Formation exposed in an abandoned clay pit on the Bornholm coast between Hasle and Rønne has yielded sauropod, thyreophoran and theropod footprints (Milân & Bromley 2005; Milàn 2011) (Fig. 2b). These occur in conjunction with well-preserved fern, conifer and ginkgo fossils (Bartholin 1892; Gry 1969; Koppelhus & Nielsen 1994; Mehlqvist et al. 2009).

Late Jurassic (Kimmeridgian) plesiosaurs have been found on Milne Land in Greenland (Bendix-Almgreen 1976; Smith 2007), as well as on Spitsbergen, where both plesiosaursian vertebræ (Wiman 1914) and articulated skeletons (Kear & Maxwell 2013) were recovered with ichthyosaurian remains that have not yet been formally described. Subsequent systematic exploration of the Spitsbergen Jurassic outcrops by field teams from the University of Oslo (2004–12) has correlated this material with the late Tithonian Slottsmyra Member of the uppermost Agardhfjellet Formation (Hurum et al. 2012) (Fig. 2c). Since then, numerous plesiosaurid and large pliosaurid taxa, as well as ophthalmosaurid ichthyosaurians (Fig. 2d), have been identified (Knutsen et al. 2012a, b, c, d; Drucemiller et al. 2012; Roberts et al. 2014). Rich ammonite assemblages (Wierzbowski et al. 2011) (Fig. 2e) and methane seep horizons have further revealed a diverse ecosystem of bivalves and echinoderms (Hryniewicz et al. 2014 and references therein). Delsett et al. (2015) reviewed this current record in the context of its preservation and geological setting.

The Cretaceous

The terrestrial Jurassic–Cretaceous transition is distinguished at Eriksdal in Skåne, southern Sweden (Vajda & Wigforss-Lange 2006). This time frame marks the nascence of angiosperms, the oldest Scandinavian pollen records of which occur in the Hauterivian Nytorp Sand (Vajda 2001; Vajda & Wigforss-Lange 2006). Latest Jurassic–earliest Cretaceous plant fossils, bivalves, ammonites and an ophthalmosaurid ichthyosaurian skeleton are known from Andoya island in northern Norway (Norborg & Wulff-Pedersen 1997; Norborg et al. 1997). Early Cretaceous strata are also exposed on Bornholm, where the Berriasian Rabekeke, Robbe-dale and Jydegaard formations represent an interlinked barrier spit and lagoonal complex (Noe-Nygaard & Surlyk 1988). These rocks crop out along the coastal cliffs east of Arnager (Gravesen 2009), with the Rabekeke Formation having produced a prolific bone-bed assemblage of atroposaurid, bernissartiid and goniopholid crocodyliforms (Schwarz-Wings et al. 2009), actinopterygian fishes, urodelan and anuran amphibians, indeterminate turtles and lepidosauroids, dromaeosaurid and possible avian theropods, and a single tooth of the multituberculate mammal Summivodon (Lindgren et al. 2004, 2008; Rees et al. 2005). A trample ground with abundant large dinosaurian tracks (up to 700 mm in length) and possible lungfish aestivation burrows is also evident in overlying beds (Surlyk et al. 2008).

The uppermost horizons of the Jydegaard Formation likewise hosts a diverse range of hybodontiform sharks and bony fish, including the lepisosteiform Lepidotes, amioids, pycnodonts and stem teleosts: these occur in conjunction with unidentified turtles, the neosuchian crocodylomorph Pholidosaurus and a scincomorph lizard (Bonde 2004, 2012). Finally, isolated teeth of a dromaeosaurid and possible juvenile sauropod (Bonde & Christiansen 2003; Christiansen & Bonde 2003),
vertebrate coprolites (Milàn et al. 2012a, b), and
mass accumulations of non-marine bivalves and
gastropods have been reported (Noe-Nygaard
et al. 1987; Noe-Nygaard & Surlyk 1988).

Barremian–Aptian ornithopod tracks are known
from the Festningen Sandstone Member of the
Helvetiafjellet Formation on Spitsbergen (Hurum
et al. 2006b). These were first published in the
1960s (Lapparent 1960, 1962), and have been used
to elucidate Boreal high-latitude dinosaurian as-
semblage composition in Fennoscandia during the
Early Cretaceous (Gangloff 2012; Hurum et al.
2016a).

A potential avian femur was recently reported
from the Alban of Spitsbergen (Hurum et al.
2016b), and abundant plant fossils are recognized
from the Nuusuaq Basin in central-west Greenland
(Heer 1883; Koch 1964; Pedersen 1968; Boyd
This region further exposes a substantial marine section (Dam et al. 2009) with diverse Albian–Maastrichtian faunas comprising bivalves (including one of the world’s largest inoceramids measuring 1.78 m), gastropods, decapod crustaceans, brachiopods, bryozoans, corals, sponges (Floris 1967, 1972; Collins & Wienberg Rasmussen 1992), abundant pelagic belemnites, ammonites and actinopterygian fish (Birkelund 1956, 1965; Bendix-Almgreen 1969; Kennedy et al. 1999). The Wendel Hav Basin in NE Greenland (Stemmerik et al. 1998; Alsen 2007) similarly produces occasional Cretaceous ammonites and plesiosaurian remains (Bruhn 1999; Milàn 2009).

The Cenomanian marine Arnegger Greensand Formation on the west coast of Bornholm represents the earliest part of the Scandinavian Late Cretaceous. The representative fauna comprises ammonites, belemnites, bivalves, gastropods, brachiopods and foraminifera, together with abundant invertebrate burrow traces and isolated shark teeth (Kennedy et al. 1981; Larsson et al. 2000). The overlying Coniacian Arnegger Limestone Formation also preserves sponges, ammonites, belemnites and large numbers of bivalves, includingpectinids and inoceramids (Ravn 1916, 1925; Noe-Nygaard & Surylk 1985; Kennedy & Christensen 1991; Tröger & Christensen 1991). The Bavneodde Greensand Formation, which constitutes the youngest Mesozoic unit on Bornholm, contains abundant belemnites, bivalves, gastropods and brachiopods (Surylk 2006).

Charcoalified flowers from late Santonian and/or early Campanian fluvio-lacustrine argillaceous clays in the Kristianstad Basin of Skåne in southern Sweden are world renowned for their assemblage completeness and remarkable preservation (Skarby 1968; Friis et al. 2011). However, it is the highly fossiliferous early Campanian marine succession (Fig. 3a), especially within the restricted Belemmilocammaxammililatus belemnite zone (Christensen 1975), that initiated Mesozoic research in Sweden during the nineteenth (e.g. Nilsson 1827, 1836, 1857; Hisinger 1837; Schröder 1885; Lundgren 1888) and twentieth centuries (Wiman 1916c; Troedsson 1954; Persson 1959, 1962, 1963, 1967). The Kristianstad Basin Campanian fauna (see Sørensen et al. 2013 for the list) represents a distinctive rocky shore benthic invertebrate community (Surylk & Sørensen 2010; Einarssson et al. 2016), coexisting with actinopterygian fish, sharks, rays and chimaeroids (Siverson 1992; Bazzi et al. 2015; Siversson et al. 2015), cheloniod and trionychid turtles (Persson 1959; Scheyer et al. 2012) (Fig. 3b), various mosauridan lizards (e.g. Persson 1959; Lindgren & Siverson 2002, 2004; Lindgren 2004), elasmosaurid and polycotylid plesiosaurians (e.g. Persson 1959, 1962, 1963, 1967, 1990; Einarssson et al. 2010; Sachs et al. 2015), the dyrosaurid crocodilian Aigialosuchus villandensis (Persson 1959), and aquatic hesperornithiform birds (Rees & Lindgren 2005). Terrestrial non-avian dinosaurs, represented by neoceratopsians, ornithopods and a possible theropod (Lindgren et al. 2007; Poropat et al. 2015), inhabited island archipelagos (Surlyk & Christensen 1974), along with a mixed flora (lackland of angiosperms (Debeva) and conifers indicated by leaves and pollen from coeval sediments in the Vomb Trough (Halamski et al. 2016).

Lindgren (2004) recorded mosasaur teeth and bones from late Campanian and earliest Maastrichtian marine strata in Skåne, together with a virtually intact gavialid crocodilian skull (Fig. 3c) with associated postcranial elements of Thoracosaurus scanicus (Troedsson 1924; reassigned to the Cretaceous–Palaeogene species T. macrorhynchus by Brochu 2004) from the marine lower Paleocene (late–middle Danian) of Annetorp near Malmö in SW Sweden (Milàn et al. 2010). Latest Cretaceous fluvial and marine successions are also known from the Kangerlussuaq Basin of SE Greenland (Larsen et al. 2001). These are, as yet, incompletely documented but manifest ammonites, belemnites and bivalves, invertebrate trace fossils, and wood and leaf imprints (Larsen et al. 1999, 2001). Palynological studies have also been undertaken on latest Maastrichtian units in Greenland (Nøhr-Hansen 2012) and the North Sea (Rasmussen & Sheldon 2015).

Undoubtedly, the most famous Scandinavian latest Maastrichtian–Danian boundary section is exposed along the coastal cliffs at the Stevns Klint UNESCO World Heritage site in eastern Denmark (Fig. 3d). Extensive exposures of Maastrichtian chalk also occur on the adjacent islands of Møn and Falster. Collectively, these outcrops form the Møns Klint Formation, which has yielded a profuse marine fauna of approximately 450 invertebrate species (Damholt & Surylk 2012; Hansen & Surylk 2014) (Fig. 3e, f), in addition to an abundant ichnofauna (Bromley & Ekdale 1984; Ekdale & Bromley 1984), coprolites (Milàn 2015), and vertebrate body remains representing 31 identifiable chondrichthyan species (Adolfsson & Ward 2014) actinopterygians (Bonde et al. 2008) and marine amniotes, including mosasaurs (Lindgren & Jagt 2005), cheloniod sea turtles (Karl & Lindow 2009) and gavialid crocodylians (Gravesen & Jakobsen 2012).

**Future directions for research**

Mesozoic research has a long history in Scandinavia that has contributed to the development of palaeontology as a modern science (Ebbestad 2016). This
proud tradition continues to this day, with dynamic international collaborations and cutting-edge infrastructure facilitating innovative approaches and intensive exploration of its unique fossil resources. In particular, work undertaken in the remote Arctic regions of Svalbard and Greenland has garnered popular appeal, yet continued investigations into the well-documented localities of southern Sweden and Denmark have, over the last 15 years, generated more novel data than ever before. Aspects of this rapidly expanding work are highlighted in this Special Publications volume, which we hope will inspire new lines of inquiry. Indeed, a number of key areas are already attracting attention, such as the Triassic of Greenland, Svalbard and southern Sweden, and the Cretaceous–Palaeogene transition in Denmark. The rapid progress of these studies bodes exciting potential for the future, with
Scandinavia and its Arctic territories likely to reveal further significant discoveries that will have a major impact on the global perspective of Mesozoic biotas and bioevents.

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