A REVIEW OF AQUATIC VERTEBRATE REMAINS FROM THE MIDDLE–UPPER TRIASSIC JILH FORMATION OF SAUDI ARABIA

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A recent field survey of the Middle–Upper Triassic (upper Anisian to lowermost Carnian) paralic marine deposits of the Jilh Formation in central Saudi Arabia has yielded large quantities of vertebrate fossils. These finds prompt a revision of the existing faunal list and include at least one novel stratigraphical occurrence for the Arabian Peninsula. The remains comprise sauropterygian marine reptiles (*Psephosauriscus* sp., *Nothosaurus cf. tchernovi, Nothosaurus cf. giganteus, Simosaurus* sp.), a lungfish (*Ceratodus* sp.), hybodontiform sharks (*Hybodus* sp.) and saurichthyform actinopterygians (*Saurichthys* sp.). Palaeobiogeographical assessment reinforces Tethyan affinities for the assemblage and reflects the close proximity of the Arabian region to the 'Sephardic Realm', a compositionally distinct circum-Mediterranean faunal province characterized by hypersaline Muschelkalk facies.

Key words: Sauropterygian, dipnoan, actinopterygian, hybodontiform, Anisian-Carnian, Saudi Arabia, Tethys.

SAUDI ARABIA has a geographically important record of Mesozoic marine vertebrates spanning the Middle–Late Triassic (Vickers-Rich et al. 1999; Kear et al. 2010), Late Jurassic (Madden et al. 1995; Halawani 2001), and the Late Cretaceous (Thomas et al. 1999; Kear et al. 2008, 2009). These occurrences represent the only such fossils currently documented from the Arabian Peninsula and are thus a significant indicator of faunal composition from the northeastern Gondwanan shelf. The richest fossil localities are found in the Jilh Formation, an upper Anisian to lowermost Carnian (Middle–lowermost Upper Triassic) paralic marine unit that crops out in a long series of escarpments skirting the eastern margin of the cratonic Arabian Shield in central Saudi Arabia (Fig. 1). The earliest account of vertebrate remains from the Jilh Formation was given by Powers et al. (1966: D36), who listed the presence of "amphibian (?) bone fragments". Sharief (1981) also remarked on the discovery of a thecodont reptile jaw (misspelled "the conodont"; Sharief 1981: 130). Vickers-Rich et al. (1999) provided the first comprehensive assessment of the Jilh Formation vertebrate assemblage (based on a small collection amassed in 1976 and now held at the Queen Victoria Museum and Art Gallery in Launceston, Tasmania), describing fragmentary remains from a diverse range of hybodontiform sharks, actinopterygian fish and marine reptiles including an ichthyosaur, sauropterygians (placodonts, nothosaurs and pachypleurosaurs) and a tanystropheid prolacertiform.

A detailed re-examination of the Jilh Formation outcrops was conducted in 2007 by a joint Saudi-Australian field team. This survey catalogued a number of new sites and recovered a considerable amount of well-preserved, diagnostic fossil material. These specimens have facilitated taxonomic refinement of the current species list and include at least

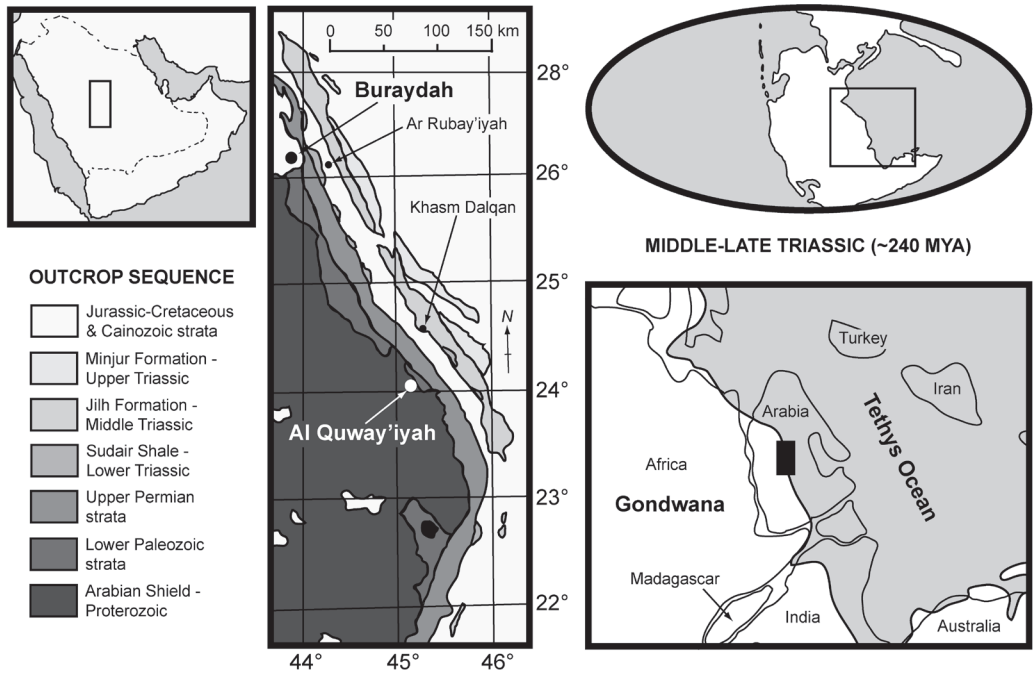

Fig. 1. Locality map (left) with enlargement showing distribution of Jilh Formation outcrops relative to sequential Triassic strata of the Sudair Shale (Scythian) and Minjur Formation (Carnian-?Rhaetian) plus Paleozoic–Cainozoic sediments and Proterozoic basement rocks of the Arabian Shield (modified from Kear et al. 2010). Middle–Late Triassic continental distribution (right) with enlargement indicating geographical placement of the Arabian region and Jilh Formation localities (black fill).

one new stratigraphical occurrence for the Arabian Peninsula (see Kear et al. 2010). This present paper reviews the Jilh Formation vertebrate record in light of these new discoveries and discusses the paleobiogeographical implications of the fauna.

Repository.—All of the fossil material described herein has been registered with the Saudi Geological Survey (**SGS**), Jiddah, Kingdom of Saudi Arabia but is presently housed on long-term loan in the Paleontological Collection at Museum Victoria (**MV**), Australia.

GEOLOGICAL SETTING

Powers et al. (1966), Sharief (1981, 1984, 1986) and Halawani (2001) have provided detailed accounts of stratigraphy and geology (including maps) for the Jilh Formation. In summation, the unit consists of a basal fine-grained sandstone-claystone series with overlying thickly bedded dolomitic sandstone, hematitic sandstone and uppermost stomatolitic dolomite layers. The Jilh Formation represents the middle section of the Buraydah Group, an extensive Lower to Upper Triassic rock sequence that crops out along the eastern margin of the Proterozoic Arabian Shield in central Saudi Arabia (Fig. 1). Age determinations based on conodonts and pollen indicate an Anisian to lowermost Carnian range (Halawani, 2001 and references therein). Sequentially, the Jilh Formation rests conformably on the Scythian Sudair Shale and is overlain by the Carnian-?Rhaetian Minjur Sandstone (Sharief 1981, 1986; Halawani 2001).

Surface exposures of the Jilh Formation form a series of low westward facing escarpments that are partly covered by Quaternary sands and gravels (Sharief 1984). Macrofossils have been found in areas of high topographic relief, near the town of Ar Rubay'iyah (N 26° 23' 20.4" E 44° 14' 3"),

east of Buraydah, and in a section at Khasm Dalqan (N 24° 14' 42.3" E 45° 37' 43.4") northeast of Al Quway'iyah in central Saudi Arabia (Fig. 1). Isolated vertebrate bones and teeth occur randomly throughout thick carbonate beds near the base of the main dolomitic sandstone sequence. Limited surface corrosion suggests post-mortem transport with disarticulation probably via low-energy wave action and/or currents prior to burial. This interpretation is supported by lithological features, which infer sediment deposition under paralic marine conditions (tidal flats) linked to a westward transgression of the Neotethys onto the cratonic Arabian Shield (Sharief 1986). Inter-bedded fluvial sands and clayey strata at the bottom of the dolomitic series are thought to derive from estuarine outlet channels (Sharief 1986). The upper carbonate beds represent a restricted evaporitic lagoon complex bordering a shallow offshore shelf (Sharief 1986).

AQUATIC VERTEBRATES FROM THE JILH FORMATION

Sharks and bony fish

Vickers-Rich et al. (1999) recorded a typical array of Middle–Late Triassic Tethyan shark and actinopterygian taxa from the Jilh Formation at Ar Rubay'iyah. Teeth of hybodontiform sharks were especially common and have been found elsewhere at Khasm Dalqan. The majority of specimens are characterized by a prominent central cusp (up to 15 mm high, e.g. SGS 07-25-141; Fig. 2A) with strong vertical ridges, two pairs of lateral cusplets and irregular horizontal foramina at the crown/root junction; features that are coherent with the form-genus *Hybodus* Agassiz, 1837 (Maisey 1987; Rees 1998). Vickers-Rich et al. (1999) also attributed other isolated teeth to *Acrodus* Agassiz, 1837 and possibly *Lissodus* Brough, 1935. Fragmentary shark fin spines (Vickers-Rich et al. 1999: p. 209, fig. 3A) cannot be conclusively assigned to a specific taxon, but their large size (up to 80 mm long), conspicuous ornamentation of strong lateral ridges and posterior denticles suggest affinity with hybodontiforms (Maisey 1978).

The Jilh Formation actinopterygian fauna was tentatively reconstructed on the basis of isolated teeth (Vickers-Rich et al. 1999) and incorporates possible semionotiforms (?*Paralepidotus* Stolley, 1920, ?*Sargodon* Plieninger, 1847), palaeonisciforms (?*Gyrolepis* Agassiz, 1833, *Birgeria* Stensiö, 1919), a perleidoform (*Colobodus* Agassiz, 1844) and saurichthyform (?*Saurichthys* Agassiz, 1834). Subsequent finds from Ar Rubay'iyah include a section of rostro-premaxilla with an anterior portion of the vomers preserved in articulation (maximum width across vomers 9.6 mm, maximum height of rostro-premaxilla 20.4 mm, SGS 07-03-62; Fig. 2B); a section of jaw with well preserved teeth was also recovered from Khasm Dalqan (maximum tooth height 8.5 mm, SGS 07-25-106; Fig. 2C). The marginal dentition in both specimens comprises robust, conical crowns with a small cap of smooth enamel, longitudinal crenations around the base and an expansive pulp cavity; there is also a patina of tubercle-like denticles across the palate in SGS 07-03-62. These features, together with the slender rostrum, are diagnostic for *Saurichthys* (Rieppel 1992; Mutter et al. 2008) and compare well with remains from the Ladinian of Palestine and Turkey (Beltan et al. 1979; Martin et al. 1991).

An important new find from the Jilh Formation at Ar Rubay'iyah is the single pterygopalatine tooth plate of a lungfish (maximum length/width 30.8/19.7 mm, SGS 07-03-63; Fig. 2D). This specimen can be referred to the ubiquitous taxon *Ceratodus* Agassiz, 1838 on the basis of its acutely angled, medially originating ridges, a trait that together with the absence of obvious cusps along the labial margin and a procumbent lingual keel, serve to distinguish it from all other Triassic genera for which tooth plates are known (see Vorobyeva 1967; Martin 1979, 1981; Kemp 1996, 1997, 1998; Cavin et al. 2007). Previous records of lungfish fossils from the Arabian Peninsula include only Late Cretaceous (Kear et al. 2008) and Palaeogene (Whitmore 1995) occurrences. Thus the discovery of a dipnoan in the predominantly Middle Triassic Jilh Formation is significant, both as an extension of the group's stratigraphic range within Arabia and the largely Laurasian distribution of Triassic *Ceratodus* species (see Cavin et al. 2007; Kear et al. 2010).

Marine reptiles

Marine reptiles represent the dominant component of the Jilh Formation aquatic vertebrate assemblage. Vickers-Rich et al. (1999) recorded disarticulated axial/appendicular bones and teeth from a variety of taxa including an indeterminate ichthyosaur, a tanystropheid prolacertiform (closely resembling *Tanystropheus* von Meyer, 1855) and sauropterygians:

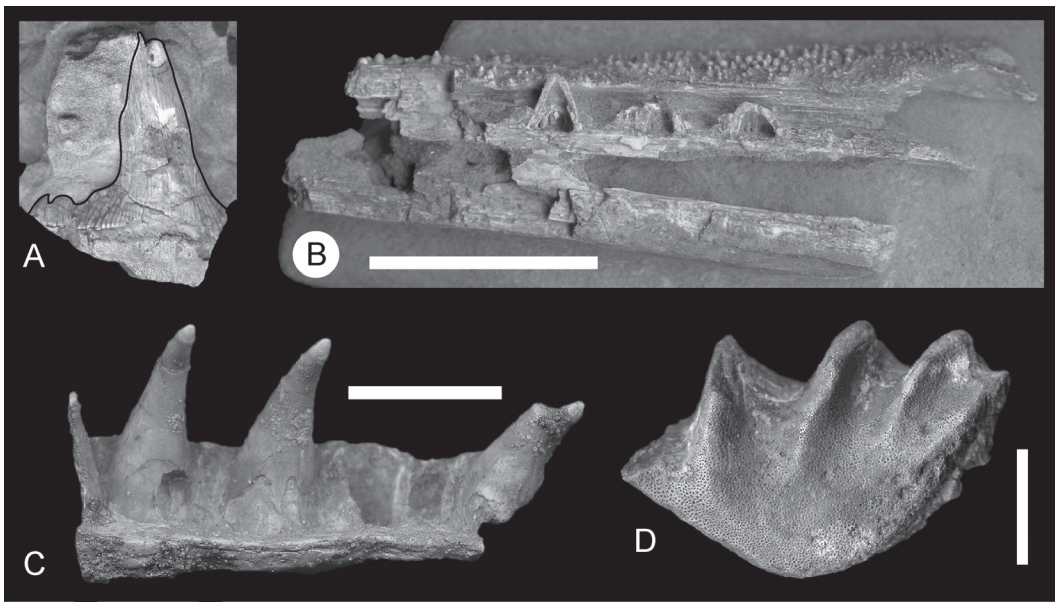

Fig. 2. Shark and fish remains from the Jilh Formation of Saudi Arabia. A, Hybodontiform shark tooth referable to *Hybodus* sp. (SGS 07-25-141); B, *Saurichthys* sp. rostro-premaxilla fragment (SGS 07-03-62); C, jaw fragment attributed to *Saurichthys* sp. (SGS 07-25-106). D, *Ceratodus* sp. pterygopalatine tooth plate (SGS 07-03-63). Scale bars represent 20 mm in A, B; 5 mm in C; 10 mm in D.

cyamodontoid placodonts, nothosaurids (*Nothosaurus* Münster, 1834, *Simosaurus* von Meyer, 1842) and indeterminate pachypleurosauroids. Subsequent collecting at Ar Rubay'iyah has yielded numerous fragments of placodont dermal armour, mostly comprising aggregations of fused osteoderms derived from the carapace of cyamodontoids. Individual osteoderms (up to 16 mm maximum diameter, 17 mm maximum thickness) are hexagonal in outline with a slight central depression and deep grooves indicating the contours of irregularly shaped epidermal scutes (e.g. SGS 07-03-03, SGS 07-03-07; Fig. 3A, B). Rieppel (2002) attributed this morphotype to *Psephosauriscus* Rieppel, 2002, a genus otherwise known only from Anisian-Ladinian strata in the Negev and Sinai Peninsula. Vickers-Rich et al. (1999) reported other carapace osteoderms with a prominent central keel similar to cyamodontoid material from the Negev and Turkey (Beltan et al. 1979; Rieppel 2002).

Broken placodont crushing teeth and a squamosal+?parietal fragment (37.1 mm in length, SGS 07-03-02; Fig. 3C) have been recovered at Ar Rubay'iyah. The squamosal bears at least one conical dermal encrustation as is diagnostic for Cyamodontoidea (Rieppel & Zanon 1997).

Nothosaurs are the most abundant marine reptiles in the Jilh Formation. Isolated vertebrae (typically around 31.4 mm in length and 31.8 mm in diameter, e.g. SGS 07-03-17; Fig. 3D) display platycoelous articular surfaces characteristic of eusauropterygians. The neural arches have high neural spines (up to 110 mm maximum height), which are synapomorphic for several *Nothosaurus* species from the Middle East (Rieppel et al. 1999). Indeed, some Jilh Formation vertebrae (e.g. SGS 07-10-02; Fig. 3E) can be provisionally attributed on the basis of size (maximum vertebral height ~170 mm) to *Nothosaurus cf. tchernovi*, a species recorded elsewhere from the Ladinian Makhtesh Ramon fauna of central Negev (see Rieppel et al. 1999: p. 40, fig. 37 for comparisons).

A very large tooth (preserved fragment 21.3 mm high, SGS 07-03-58; Fig. 3F) from Ar Rubay'iyah was found in close proximity to a fragmentary limb bone (maximum proximal articular surface width 68.2 mm, SGS 07-03-31) and a vertebral centrum (maximum articular surface diameter 37.4 mm, SGS 07-03-59). The massive proportions of these elements

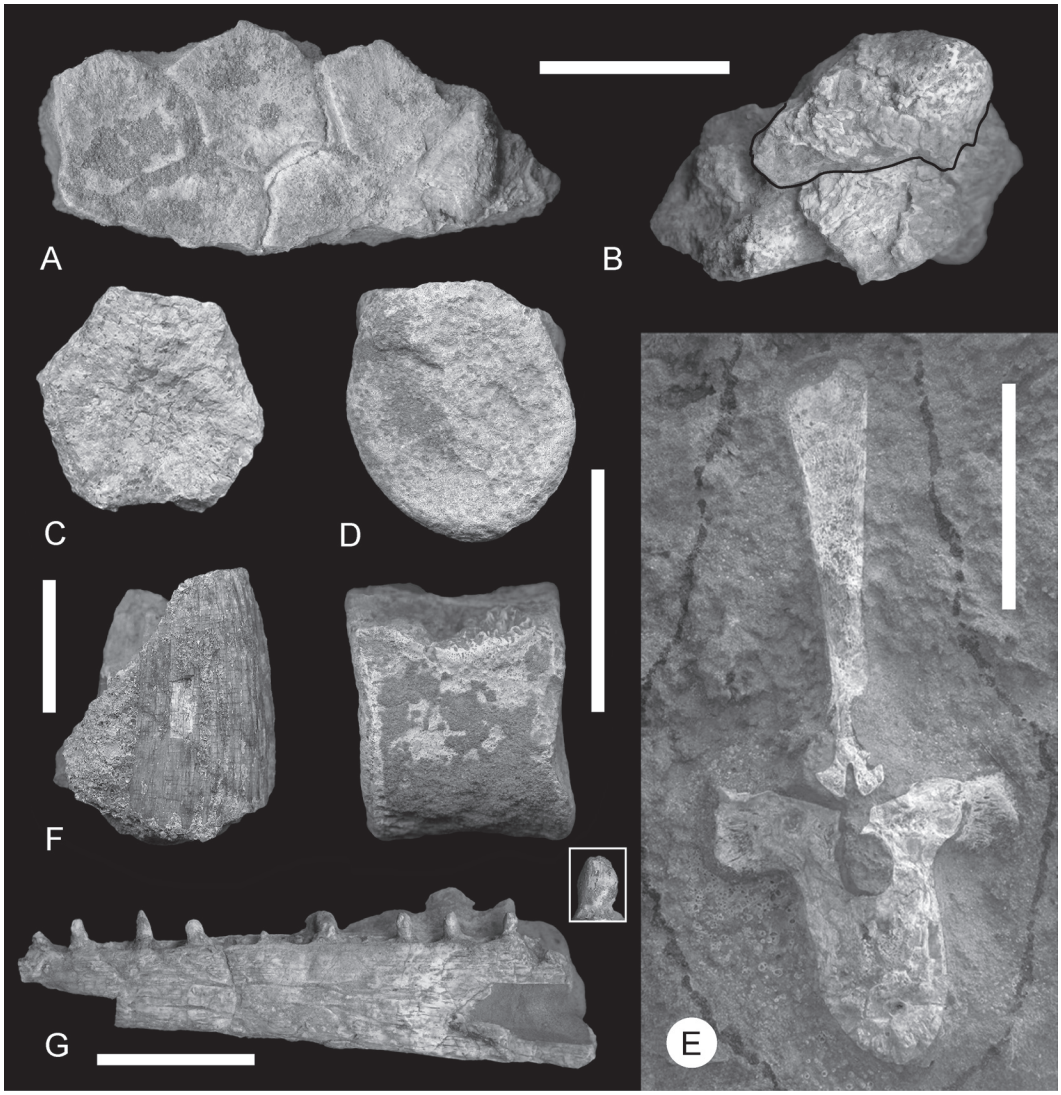

Fig. 3. Marine reptile remains from the Jilh Formation of Saudi Arabia. A, Placodont carapace fragment (SGS 07-03-07), and B, an enlarged isolated osteoderm (SGS 07-03-03), both referred to *Psephosauriscus*; C, cyamodontoid placodont cranial fragment (SGS 07-03-02) showing dermal encrustation (black outline); D, eusauropterygian dorsal vertebral centrum (SGS 07-03-17; *Nothosaurus* sp.) in anterior (top) and lateral (bottom) views; E, *Nothosaurus cf. tchernovi* vertebra (SGS 07-10-02); F, *Nothosaurus cf. giganteus* tooth fragment (SGS 07-03-58); G, *Simosaurus* sp. incomplete dentary ramus (SGS 07-25-262) with an enlargement (white outline) showing one of the characteristically 'expanded' tooth crowns. Scale bars represent 20 mm in A, B, G; 10 mm in C, F; 30 mm in D; 50 mm in E.

and the coarsely striated tooth ornamentation suggest referral to the widespread nothosaurine *Nothosaurus cf. giganteus* (Rieppel 1996). Other nothosaurid taxa are indicated by an incomplete mandible from Khasm Dalqan, which exhibits short, blunt teeth with expanded, coarsely striated crowns and vertical implantation distinctive of the genus *Simosaurus* (mandible fragment length 75.5 mm, mean tooth crown height 4 mm, SGS 07-25-262; Fig. 3G: see Rieppel 1994).

PALAEOBIOGEOGRAPHICAL IMPLICATIONS OF THE ASSEMBLAGE

Taxonomic comparison of the Jilh Formation vertebrate assemblage supports previous assertions of close affinities to faunas from elsewhere in the Middle East and North Africa (Vickers-Rich et al. 1999). The marine reptiles in particular incorporate taxa that are either endemic to the northern Gondwanan region (e.g. *Psephosauriscus*, *Nothosaurus cf. tchernovi*; see Rieppel et al. 1999; Rieppel 2002) or represent geographically widespread, larger-bodied forms (e.g. *Nothosaurus cf. giganteus*, *Simosaurus*; see Rieppel et al. 1999); these were presumably capable of long-distance dispersal via the contiguous marine carbonate shelf rimming the western margin of the Neotethys during the Middle–Late Triassic (Hirsch 1987). The Jilh Formation sharks and fish, although less paleobiogeographically informative, are of typical Tethyan aspect (Vickers-Rich et al. 1999) and include a high frequency of eurytopic taxa (hybodont sharks, *Saurichthys*, *Ceratodus*; Patterson 1966; Rieppel 1992; Cavin et al. 2007) possibly reflecting the unit's complex estuarine-paralic setting. Hirsch (1984, 1987) proposed that during the Middle and Late Triassic (Ladinian-Carnian) marine biotas in the Arabian region formed part of the 'Sephardic Realm', a compositionally distinct circum-Mediterranean faunal province characterized by hypersaline 'Muschelkalk' facies. The predominance of reptiles in the Jilh Formation accords with this paleoecological scenario (see Rieppel et al. 1999).

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