

THE FIRST RECORDED TRIGONIOIDOIDEAN BIVALVE FROM EUROPE

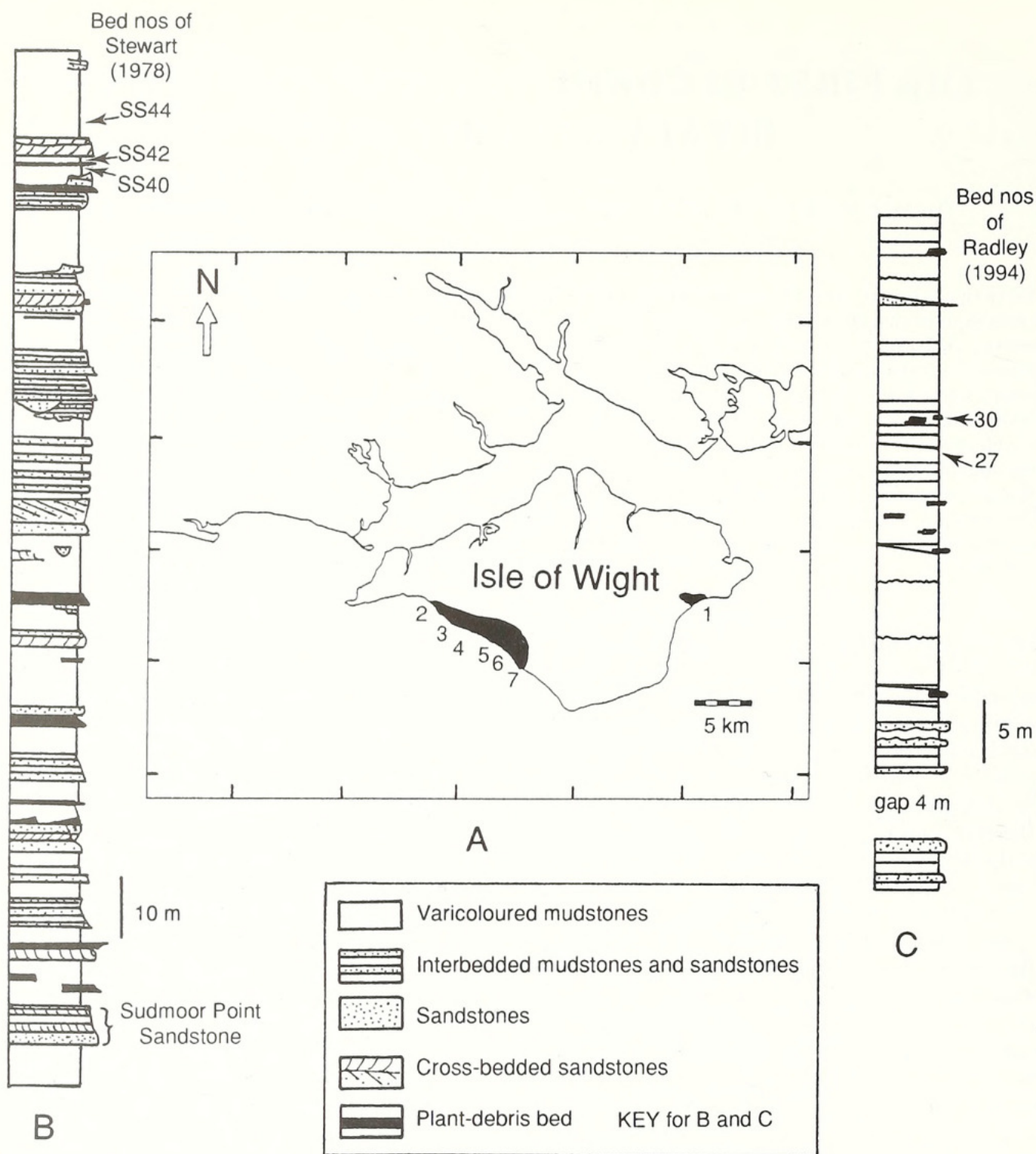
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ABSTRACT. The non-marine bivalve superfamily Trigonioideoidea has been considered to be restricted to the Cretaceous of east Asia. It is a distinctive taxon of unionoids, characterized by separated anterior adductor and anterior pedal retractor muscle scars, and an ornament which typically comprises chevron-forming ribs. Well preserved bivalves (with chevron-forming ribs) from the Wealden Group (Barremian and ? Upper Hauterivian, Lower Cretaceous) of the Isle of Wight (southern England), which had previously been assigned to the unionacean unionoids, were re-examined and separated anterior adductor and anterior pedal musculature recognized. The combined character states of musculature, ornament and hinge teeth indicate affinity to the trigoniodid genus *Nippononaia*. However, placement in the established subgenera *N.* (*Nippononaia*) and *N.* (*Eonippononaia*) is precluded by the distinctively larger angle produced by the specimens' chevron ornament. Therefore, a new subgenus, *N.* (*Subnippononaia*), and a new species, *N.* (*S.*) *fordi*, are proposed to accommodate them. This constitutes the first confirmed record of the superfamily Trigonioideoidea outside of east Asia.

THE non-marine bivalve superfamily Trigonioideoidea (?Mid Jurassic to Late Cretaceous) is a distinctive group of unionoids. Representatives of the superfamily are characterized by separated anterior adductor and anterior pedal retractor muscle scars; their distinctive ornament of chevron-forming ribs and (usually) crenulated hinge teeth. The classification used herein follows that of Sha and Fürsich (1993) except that the ending -oidea is used in the superfamilial name. Previous records indicate a distribution restricted mainly to Asia (i.e. the eastern seaboard of the Panthalassan Ocean). Several authors have recorded isolated occurrences of the superfamily from America (Reeside 1957), North Africa (Mongin 1963) and northern South Australia (Ludbrook 1985) but in the absence of the diagnostic musculature, Sha and Fürsich (1993) placed all of these records from outside of Asia in Unionoidea rather than Trigonioideoidea.

Sha (1989) and Sha and Fürsich (1993) recorded bivalves from the Wealden Group (Lower Cretaceous) of the Isle of Wight, off the south coast of England, which have characteristic trigonioideoidean V-shaped ribs on the mid-flank area and reversed V-shaped ribs on both the anterior and posterior areas. The latter authors commented upon the similarity of the hinge structure to that of the Asiatic trigoniodid *Nippononaia* but, since the muscle scars in the Isle of Wight specimens were considered to be feeble and no separation of the anterior pedal retractor scar was observed, they were likewise placed within the superfamily Unionoidea although a similarity to the ancestral trigoniodid *Danlengiconcha* Liu, 1978 (?Mid Jurassic to Early Cretaceous) was noted. Sha and Fürsich (1993) further suggested that all non-Asiatic records of Trigonioideoidea should be re-assigned to Unionoidea because, contrary to the diagnostic character state of Trigonioideoidea, all the non-Asiatic taxa which they reviewed showed coalescence of the anterior pedal retractor muscle scar with the anterior adductor muscle scar. Moreover, they suggested that the morphological similarity and contemporaneity of the non-Asiatic forms with the Asiatic trigoniodids *sensu stricto* indicated a common ancestry and parallel evolution, rather than morphological convergence.

We describe here well-preserved material from the Isle of Wight, amongst which an internal mould clearly shows separate anterior pedal and adductor muscle scars, thereby warranting placement in Trigonioideoidea. Using the character states proposed by Sha and Fürsich (1993) for



TEXT-FIG. 1. A, outcrop of the Wealden Group (coloured black) on the Isle of Wight, and localities. Key: 1, Yaverland; 2, Compton Bay; 3, Sudmoor Point; 4, Chilton Chine; 5, Brighstone Bay; 6, Cowleaze Chine; 7, Atherfield. B, composite lithological log of the Wessex Formation (Wealden Group) from the south-west coast of the Isle of Wight, after Stewart (1978). C, lithological log of the Wessex Formation (Wealden Group) at Yaverland, Isle of Wight, after Radley (1994).

the classification of this superfamily, we propose the new subgenus *Nippononaia* (*Subnippononaia*), described below, to accommodate this new material.

The Wealden Group of the Isle of Wight (see Text-fig. 1A) comprises the Wessex Formation

(formerly known as the Wealden Marls; Daley and Stewart 1979) and the overlying Vectis Formation. The specimens described herein all come from the Wessex Formation which, where exposed, comprises up to 180 m of varicoloured mudstones and sandstones interleaved with plant-debris beds, all of fluvial/overbank origin and deposited in a mosaic of subtropical coastal alluvial environments (Stewart 1978; Stewart *et al.* 1991; Text-fig 1B–C). The formation probably dates wholly from the Barremian (Early Cretaceous) but, based on palynomorphs, possibly also the Late Hauterivian (Allen and Wimbledon 1991). The trigonioidid bivalves occur in both varicoloured overbank mudstones and plant-debris beds throughout the formation. They are preserved as either internal and external moulds (often the internal moulds have smooth listric surfaces along which some internal shear has taken place) or as neomorphic calcite shell replacements. No trigonioidid specimens have been recovered from the Vectis Formation which, for the most part, was deposited under brackish lagoonal conditions and consequently contains a depleted unionoid fauna.

SYSTEMATIC PALAEOLOGY

Order UNIONOIDA Stoliczka, 1871

Superfamily TRIGONIOIDOIDEA Cox, 1952 [nom. corr. Kolesnikov, 1977]

Family TRIGONIOIDIDAE Cox, 1952

Subfamily TRIGONIOIDINAE Cox, 1952

Genus NIPPONONAIYA Suzuki, 1941

Subgenus SUBNIPPONONAIYA subgen. nov.

Derivation of name. From *Nippononaiya* Suzuki, 1941, the east Asian genus to which the new subgenus is allied.

Type species. *Nippononaiya* (*Subnippononaiya*) *fordi* sp. nov.

Diagnosis. Medium-sized bivalve, rectangular/oval in outline, with submedian chevron-forming V-shaped ribs. Both anterior and posterior reversed chevron-forming ribs flank submedian sets. Submedian chevron sets of V-shaped ribs (VA) meet at 30–35°. Distinct and separate anterior pedal muscle scar present.

Remarks. *N.* (*Subnippononaiya*) subgen. nov. is distinguished from other subgenera of *Nippononaiya* by the larger angle (VA) between the limbs of the submedian V-shaped ribs on the valve flanks. Other recorded subgenera of *Nippononaiya* are *N.* (*Nippononaiya*) Suzuki, 1941 (VA < 20°) and *N.* (*Eonippononaiya*) Guo, 1981 (VA 20–25°); see discussion below.

Nippononaiya (*Subnippononaiya*) *fordi* sp. nov.

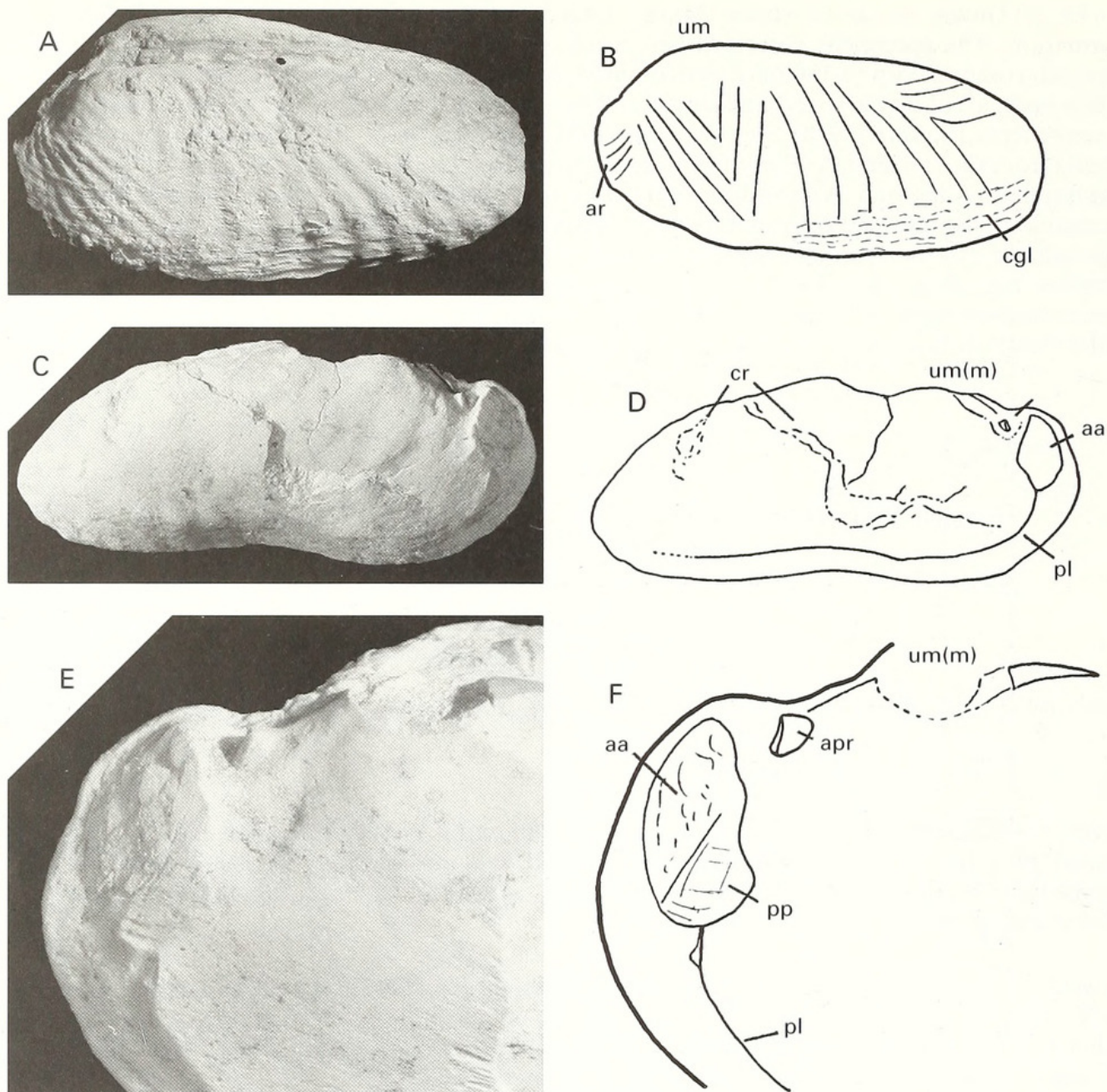
Text-figure 2A–F

1993 *Nippononaiya* sp. nov., Barker and Munt, p. 44.

Derivation of name. The late Richard Ford, of Yarmouth, Isle of Wight, in recognition of his contribution to the collective knowledge of that island's palaeontology.

Diagnosis. As for subgenus.

Holotype. Museum of Isle of Wight Geology, Sandown, Isle of Wight, IWCMS: 1995.68 (Text-fig. 2A–B). Neomorphosed calcitic shell showing the external morphology of the two valves but with some slight distortion. From plant debris bed 27 or 30 of Radley (1994), Wessex Formation, Wealden Group, Yaverland foreshore, Isle of Wight.



TEXT-FIG. 2. *Nippononaia* (*Subnippononaia*) *fordi* sp. nov.; Barremian, Wessex Formation, Isle of Wight, England. A–B, IWCMS: 1995.68, holotype, Yaverland. A, left valve, (oblique view). B, left valve, (perpendicular view), indicating the opposed sets of chevron-forming ribs. C–F, IWCMS: 1995.214, paratype, Brighstone Bay. C–D, internal mould of right valve showing musculature. E–F, anterior musculature of left valve. Abbreviations: aa, anterior adductor scar; apr, anterior pedal retractor scar; ar, anterior ribs; cgl, crenulated growth lamellae; cr, areas of crushing; pl, pallial line; pp, pedal protractor scar; um, umbo; um(m), umbonal infill missing. A whitened with ammonium chloride; all photographs taken with an Olympus SZ-PT. A–D, $\times 2.3$; E–F, $\times 6.5$.

Paratypes. IWCMS: 1995.214 (Text-fig. 2C–F). Internal mould showing muscle scars. From plant-debris bed SS40 or SS42 of Stewart (1978), Wessex Formation, Wealden Group, Brighstone Bay, Isle of Wight; MIWG 7321 from a plant-debris bed above the Sudmoor Point Sandstone, c. 600 m north-west of Chilton Chine; MIWG 6962 from a shell bed on the foreshore south-east of Chilton Chine; MIWG 21, 7001 and 7342 from plant-debris beds 27 and/or 30 of Radley (1994), Yaverland foreshore and cliff, and MIWG 5816 from a lenticular plant-debris horizon near the top of bed SS44

of Stewart (1978), west of Cowleaze Chine. All specimens are housed in the Museum of Isle of Wight Geology, Sandown, Isle of Wight.

Additional material. Four further specimens (UOP 18/9–12) are housed in the Department of Geology, University of Portsmouth. These were collected from overbank deposits during the excavation of a brachiosaurid dinosaur, *c.* 10 m below the top of the Wessex Formation, north-west of Cowleaze Chine. It has not been possible to locate material reportedly held in the collections of The Natural History Museum, London (Sha 1989 pp. 78–79; Sha and Fürsich 1993, p. 155).

Measurements. Holotype IWCMS 1995.68 (external shell): H (maximum height) = 16.1 mm; L (maximum length) = 30.4 mm; D (anterior end to umbo) = *c.* 8.0 mm; I (inflation of valves) > 8.5 mm (specimen slightly crushed). Paratype IWCMS 1995.214 (internal mould): H = 11.3 mm; L = 26.2 mm; D – not measurable; I > 5.9 mm (specimen slightly crushed).

Description. Medium-sized bivalve, rectangular/oval in shape, with only moderate inflation of the valves. The hinge details are imperfectly known, but a simple pair of corresponding teeth (RV) and sockets (LV) are indicated from silicone-rubber casts taken from an internal mould. Sha and Fürsich (1993) noted that specimens in The Natural History Museum (London) had smooth or very weakly crenulated teeth. There are no submedian teeth. Anterior muscle scars comprise a large anterior adductor conjoined to a large pedal protractor scar. A separate small anterior pedal retractor muscle scar is sited above and behind the adductor scar (see Text-fig. 2E–F). The posterior adductor scar is very weak. The pallial line is strong, but there is no pallial sinus. A high degree of variability occurs in the detail of the valve margins. The following description is based upon the more common morphs. The antero-dorsal margin is initially straight but becomes convex distally. The margin then forms a continuous convexity through the anterior to the antero-ventral margin. The ventral margin may be flat, concave or convex but is always crenulated. The postero-ventral margin is tightly convex. The posterior margin may be flat, shallowly concave or shallowly convex. However, it is distinctively angled to the postero-ventral extremity at *c.* 53°. The posterior margin terminates abruptly at its meeting with the postero-dorsal margin, which is flattened and slopes gently up to the umbo. The postero-dorsal margin forms a slight claustra (i.e. one or two lamellar ridges), carrying an opisthodetic external ligament.

The exterior ornament of the flank comprises five or six sets of chevron-forming ribs. The limbs of the inner sets are straight but the outer sets are arched. These inner (submedian) sets of ribs are centred directly below the umbones and close ventrally. Both the anterior and posterior sets of chevron-forming ribs close dorsally. The main submedian sets have a VA of 30 and 35°. The ornament becomes diffuse and less prominent in mature specimens.

The umbones are slight and set between one-third and one-quarter of the shell length from the anterior margin. A rounded carina is generated behind the umbones and extends to the postero-ventral extremity. The postero-ventral area is concave from behind the umbones to the postero-ventral extreme. The flanks of the shell at the confluence of the chevron sets are also shallowly concave, rising to a gently convex anterior area. The flanks are at best only moderately inflated.

Remarks. *N. (Subnippononaia) fordi* displays the clear separation of the anterior adductor and the anterior pedal muscle scars, which is diagnostic of the superfamily Trigonioidoidea (Cox 1952; Sha and Fürsich 1993). This is contrary to the observations of Sha and Fürsich (1993), who considered that separate anterior pedal retractor, and anterior adductor scars could not be detected in this taxon or other non-Asiatic bivalves previously attributed to Trigonioidoidea. The earliest description of the superfamily Trigonioidoidea (= Trigonoidacea) was apparently that given by Kolesnikov (1977) but application of Article 36 of the ICZN ascribes the nominal status to Cox, 1952. The distinctive ornament of the shell exterior, comprising submedian and reversed posterior and anterior V-shaped ribs, suggests an affinity with the Asiatic trigonioidid genus *Nippononaia*.

Sha (1989) considered that trigonioidoidean genera can be distinguished by the angle produced by the submedian chevron ribs (VA). With the exception of the genus *Trigonioides* (*Wakinoa*) Ota, 1963, none of the Asiatic genera has VA ranges that coincide with that of the specimens described herein. However, affinity with *Trigonioides* is precluded by the absence of submedian teeth in the new species.

Based upon differences in the angle VA, the genus *Nippononaia* has been subdivided into two subgenera, *N.* (*Nippononaia*) and *N.* (*Eonippononaia*) (see Guo 1981). In *N.* (*Nippononaia*) (type species *N. ryosekiana* Suzuki, 1941, from the Aptian of Japan), the VA is less than 20°, with an ornament consisting of fine, tight chevron ribs. The hinge teeth are also feebly crenulated. *N.* (*Eonippononaia*) Guo, 1981 has a VA of 20–25° and almost smooth hinge teeth.

Recorded non-Asiatic occurrences of bivalves of similar exterior ornament and age include *Nippononaia asinaria* Reeside, 1957 from the Aptian of Colorado. This species is broadly oval in outline, the chevron ribs are stronger than on *N. ryosekiana*, with posterior ribs sub-horizontal. Sha (1989) considered *N. asinaria* to be distinct and he created a new, monospecific genus, *Asinarianaia*, to accommodate it. Additional records noted by Sha (1989) are from Africa (*Subplicatounio flatterensis* Mongin, 1963 – Lower Cretaceous) and from South Australia (*Pledgia eyrensis* Ludbrook, 1985 – Upper Albian or Cenomanian), both with similarities to the trigonioidid genus *Plicatounio*. Sha (1989) and Sha and Fürsich (1993) in referring to these non-Asiatic occurrences of the 'so-called Trigonioididae' were not convinced as to their affinities. However, they considered that their similarity to, and contemporaneity with, the true Asiatic trigonioidids implied the existence of a common ancestor for all these taxa.

Stratigraphical distribution. Wessex Formation, Wealden Group, Barremian and ?Upper Hauterivian, Lower Cretaceous.

FUNCTIONAL MORPHOLOGY OF *SUBNIPPONONAI*A

Within Palaeoheterodonta, chevron ornament is found in the orders Unionoida (all members of Trigonioididae and some members of Unionoidae) and Trigonioida (some members of Trigoniidae). Within Unionoidae, such ornament is commonly found on juvenile specimens and subsequently on the umbonal region of adult specimens which have not suffered dissolution. However, there is a number of genera in which the ornament is continued on mature shells. Amongst these, the Recent African genus *Nyassunio* has tight 'W'-shaped ribs on the posterior of the shell; these become more diffuse and shallower anteriorly. Functional comparison can be made with the trigoniids, notably the Early to Late Jurassic *Vaugonia* (see Stanley 1977) which was adapted to life in mobile substrates, and also the Early Jurassic to Eocene myoid *Goniomya*. Complex ribbing increases the shell surface area which in turn increases the organism's hold in the substrate, thereby reducing the risk of exhumation. Analogy can also be made with the divaricate ornament of the extant lucinid genus *Divaricella* (Stanley 1970) which is used in a saw-like motion during burial. However, this is a disc-like taxon unlike the more elongate *N.* (*Subnippononaia*).

In extant unionoids, the outer shell layer is protected by a periostracum, one of the primary functions of which is to protect the outer shell layers from dissolution, a major problem for molluscs inhabiting calcium carbonate-depleted fresh water. Dissolution pitting can be seen around the umbonal region of the holotype of *N.* (*Subnippononaia*) *fordi*. This indicates that although a periostracum was probably present, the umbonal regions were typically exposed through either microbial degradation, ageing of the proteins of the periostracum (as in extant unionoids) or abrasion, thereby allowing dissolution in the oldest parts of the shell.

As *Subnippononaia* lacks a pallial sinus, short siphons are indicated and only shallow burrowing could have been achieved. We can infer that the mode of life of *N.* (*Subnippononaia*) *fordi* was similar to that of trigoniids and unionoideans, namely infaunal and mobile, but lying largely concealed in the substrate. However, sedimentological and biostratigraphic settings indicate that *N.* (*Subnippononaia*) *fordi* mainly, or exclusively, inhabited floodplain lakes and ponds. It was never very abundant, and occurs as both articulated specimens and as isolated valves.

ASSOCIATED WEALDEN FAUNA

Amongst the Mollusca, only viviparid and physid gastropods, and unionid bivalves have been recorded from the Wessex Formation (Radley 1994). Mörter (1978) suggested that the British Barremian unionids may be conspecific with those described by Cornuel (1874) from the Wassay region of France. Ancestry from stratigraphically lower horizons is unlikely since there is only limited faunal continuity between the pre-Barremian Weald Clay and Hastings Beds of the Weald Sub-basin, and the stratigraphically higher and geographically separated Wessex Formation. The 'gull-wing' ornamented unionid *Protelliptio gualteri* (J. de C. Sowerby, 1836) which ranges from the Weald Clay into the Wessex Formation may be the only species to do so, although *Unio compressus* (J. de C. Sowerby, 1828), found in the Hastings Beds, reoccurs as a Lazarus taxon in the Vectis Formation (late Barremian–early Aptian). *Unio elongata* Cornuel, 1874 and *U. cornueliana* (d'Orbigny, 1850) can be confirmed as 'Wassay' species which are found in the Wessex Formation. *Unio valdensis* (Mantell, 1844) was re-examined by Mongin (1961) and placed in the genus *Margaritifera* but later returned to *Unio* (Mongin 1963). *Unio valdensis* is distributed throughout the Barremian of Europe and into North Africa.

PALAEOBIOGEOGRAPHY

Trigonioidoidea as recognized by Sha and Fürsich (1993) comprises 17 genera whose present day distribution encompasses Japan, South Korea, Mongolia, China, Laos, Thailand and the central Asian part of the former USSR. The oldest records (Middle to Upper Jurassic) are from China and belong to the subfamily Martinsonelliinae. The earliest record for the subfamily Trigonioidinae (which includes the genus *Nippononaia*) is from the Upper Jurassic of Japan (Matsukawa and Ido 1993). To judge by the recorded occurrences, the superfamily Trigonioidoidea attained a wider geographical distribution (mainly southward) during the Early Cretaceous. For example, in south-west China, *N. (Eonippononaia)* occurs in the Berriasian to Barremian; during the Aptian and Albian, *N. (Nippononaia)* occurs as part of the *Trigonoides-Plicatunio-Nippononaia* fauna (Ma 1994). The superfamily is also found in the Early Cretaceous (undivided) Middle Khorat Subgroup of eastern Thailand (Kobayashi 1984). Given the morphological similarity of *N. (Subnippononaia)* to *N. (Eonippononaia)* and their relationship in time, the documented southward migration of the group must also include a rapid westward migration and subsequent isolation of the stock in Europe giving rise to *N. (Subnippononaia)* by the Barremian. If *Nippononaia asinaria* Reeside, 1957 can be demonstrated to be trigonioidoidean (as yet, its musculature is unknown), a continued westward migration with subsequent allopatric speciation could have produced the Aptian taxon in Colorado.

During the Early Cretaceous, southern England comprised two sedimentary sub-basins, the Wessex and the Weald, both of which were sites of essentially non-marine 'Purbeck–Wealden' deposition from the Berriasian to the Barremian or Early Aptian (Allen and Wimbledon 1991). *Nippononaia (Subnippononaia) fordii* is recorded solely from the Wessex Sub-basin, within the higher (Barremian and ?Late Hauterivian) part of the alluvial Wessex Formation. The new taxon is found associated with other geographically more widespread unionoid species, mainly found in France but in one case (*Unio valdensis*) into North Africa (Mongin 1961). Like most freshwater bivalves, unionoids would have been restricted to long-standing and permanent bodies of water. Such bodies of water suitable for the migration of freshwater bivalves must have existed between at least Europe, North Africa and South-east Asia and possibly North America. It is unknown whether fossil unionoids reproduced in a similar manner to extant representatives, namely via glochid larvae requiring obligate fish hosts.

CONCLUSIONS

By the early Cretaceous, a wider distribution than previously recognized had been achieved within the superfamily Trigonioidacea. *Nippononaia (Subnippononaia) fordii* subgen. et sp. nov., described herein, represents the first record of the superfamily Trigonioidoidea from Europe. *Nippononaia*

(*Subnippononaia*) *fordi* from the Barremian (and ?Late Hauterivian) Wessex Formation of the Isle of Wight is found associated with other unionoid species which extend into France and North Africa. This confirmation of the existence of trigonioidid bivalves outside of east Asia clearly necessitates the re-examination of previous non-Asiatic records from North America, Africa and Australia.

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