

The identity of the Middle Jurassic Ostracoda *Fastigatocythere juglandica* (Jones) and *Lophocythere fulgurata* (Jones & Sherborn): a solution to an old enigma

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ABSTRACT – The Upper Bathonian and Lower Callovian ostracod species *Fastigatocythere juglandica* (Jones, 1884) is shown to comprise a total of five subspecies. Of these, *F. juglandica juglandica*, *F. juglandica major* (Jones & Sherborn, 1888) and *F. juglandica postrotunda* subsp. nov., described as new herein, are all confined to the Upper Bathonian. *Lophocythere fulgurata* (Jones & Sherborn, 1888) is demonstrated to be an instar of *F. juglandica major*. *Fastigatocythere juglandica degenerata* subsp. nov., described as new herein and *F. juglandica rugosa* Weinholz comb. nov., both confined to the Lower Callovian, extend the known range of the species into that stage for the first time. *J. Micropalaeontol.* 21(2): 155–166, December 2002.

INTRODUCTION

Two pioneer studies of British Bathonian Ostracoda were those of T. R. Jones (1884) and his subsequent joint study with C. D. Sherborn (1888). This material was from a deep boring at Richmond, Surrey, and from localities near Bath, Avon, respectively. The collections on which these two works were based were revised by Bate (1969), who re-described and re-illustrated the faunas and, where necessary, designated type specimens. In revising Jones & Sherborn (1888), Bate also drew upon a third collection, that of the Rev. H. H. Winwood, who had made his material available to Jones and to Sherborn for their 1888 monograph, and whose own collection was of duplicate specimens.

Among the taxa Bate revised were *Cythere juglandica* Jones, 1884, *Cythere juglandica* var. *major* Jones & Sherborn, 1888 and *Cytheridea fulgurata* Jones & Sherborn, 1888. Bate followed Sylvester-Bradley (1948, p. 193) in considering *C. juglandica* and *C. juglandica* var. *major* to be conspecific, whilst assigning the species *juglandica* to the genus *Fastigatocythere* Weinholz (1967, pp. 389, 412). Bate (1969, p. 419), on the other hand, placed *Cytheridea fulgurata* in the genus *Lophocythere* Sylvester-Bradley, 1948. An element of uncertainty, however, surrounded this last assignment, Bate himself recognizing (p. 420) that ‘... the strongly tapering outline and the [?] antimerodont] hinge suggest that the material is of a pre-adult instar’. Nevertheless, he added, ‘... it is doubtful whether the adult ornament would be different ...’.

Malz (1975, pp. 132, 133) also considered the type material of *Lophocythere fulgurata* to be juvenile, and extended this comment to all other material of the species known to him. He also remarked that the only likely candidate for the adult in his

samples was *Fastigatocythere juglandica*. However, because his largest *L. fulgurata* specimen was longer than his smallest *F. juglandica*, and despite the fact that the specimens came from different samples, he was unwilling to consider them as conspecific. He conceded, however, that if sufficiently distinct local variants of *F. juglandica* existed, this might account for the overlap in size. The question of *fulgurata* belonging to a genus other than *Lophocythere*, was difficult for any of these authors to consider since it conforms exactly to Whatley’s (1970, p. 333) emended diagnosis of the genus.

TYPE AND FIGURED MATERIAL

Most of the confusion surrounding these two species seems to stem from two causes. First, the type and figured material of *Fastigatocythere juglandica* (Jones, 1884) comes from different localities and, even when the locality is the same, the stratigraphical level from which the specimens came may differ. Secondly, little or no attention has been paid to the juveniles of these populations, which as we will show below, is an important omission.

Details of the origins and nature of the type and figured material are given in the text and in the captions to the plates of those specimens illustrated in the present study.

ONTOGENETIC CONSIDERATIONS

In a number of previous studies (e.g., Ware & Whatley, 1983, in which the authors used serial counts of Ostracoda in a Bathonian clay to elucidate their palaeoecology and its depositional history), it has been of great importance to correctly relate young instars to their appropriate adults. This is a cardinal requirement when applying population age statistics (Whatley & Wall, 1969; Whatley, 1983, 1988). Unfortunately, in the case of *Fastigatocythere juglandica* (Jones), dominant in some of the samples we have studied from Tarlton, Gloucestershire, two suites of instars are in contention. These are an abundant ovate form with a rounded posterior outline in the left valve, and a less frequent, more posteriorly acuminate form. The larger of these more acuminate juveniles resemble the published illustrations of *Lophocythere fulgurata* (Jones & Sherborn).

[†]In Memoriam. Dr Martin Ware, a distinguished physician and former editor of *The British Medical Journal*, died in 1998. The research embodied in this paper was carried out while he was a doctoral student in micropalaeontology in Aberystwyth during the late 1970s and early 1980s. From a series of Ware’s copious notes and some of his own, from memories of numerous discussions and using plates which resurfaced when he was revising the Ware collections prior to their being donated to The Natural History Museum, the junior author has put together the following paper, which he dedicates to the memory of Martin to whom this research was such ‘great fun’. *Ars longa, vita brevis!*

Ware (1978 MS, pp. 154–156) noted in an adult population of *F. juglandica* from the Kirtlington Mammal Bed, Oxfordshire (see below), the presence of a minority of specimens with a notably rounded posterior margin in the left valve. These specimens were shorter than those without such a rounded posterior which constituted the majority of the population, but like them, exhibited strong sexual dimorphism. At the time, the relationship between the two forms was unresolved, but it now seems that this may have some relevance to the problem posed by the juveniles from Tarlton.

Whatley & Stephens (1977, p. 83) in their study of precocious sexual dimorphism noted that *L. fulgurata* 'also seems to exhibit precocious sexual dimorphism in its ontogeny. Unfortunately, this species is too rare in the material studied for the authors to demonstrate this adequately and, therefore, no diagrams are included.'

SAMPLED SITES

In this revision extensive use is made of the original material of Jones (1884), and of Jones & Sherborn (1888), preserved in The Natural History Museum, London (BMNH), supplemented with new washings (1975) made from the original Richmond Borehole material preserved in the British Geological Survey, Keyworth, Nottingham (BGS).

In addition, in order to better elucidate the problem, much new material was also analysed. Samples of Bathonian age were taken from two notable UK sites: the Old Cement Works Quarry [Grid Reference: SP 494 199] at Kirtlington, near Oxford, and from a clay pit [Grid Reference: SO 970 001], originally described by Upton (1909), and the adjacent Severn Canal, near Tarlton, Gloucestershire.

The beds sampled at Kirtlington were the Mammal Bed (Freeman, 1979, p. 136) and a clay bed which underlies it and is separated from it by a 0.33 m massive limestone, the Coral-*Epithyris* Limestone of McKerrrow *et al.* (1969, p. 56). We refer to this clay level as the Sub Coral-*Epithyris* Clay.

The Mammal Bed is a lens of marly clay which, when collected in the late 1970s, cropped out for some 22 m at the NE corner of the quarry and was nowhere thicker than 0.25 m. It corresponds to Bed 3p of McKerrrow *et al.* (1969, p. 58, text-fig. 1; pl. 9). Freeman (1979, p. 136, text-fig. 1) correlates the Mammal Bed with part of the Kemble Beds shown in Arkell's (1931, p. 571) section of the east face of the quarry. The Coral-*Epithyris* Limestone is bed 3o of McKerrrow *et al.*, who correlate it with the Upper *Epithyris* Bed of Arkell, at the base of his bed 11 (1931, p. 571). McKerrrow (pers. comm. to Ware, 1975) confirms that our Sub Coral-*Epithyris* clay is their bed 3n.

All those who have studied the stratigraphy at Kirtlington this century (e.g., Odling, 1913, p. 493; Arkell, 1931, p. 571; 1947, p. 46; McKerrrow, *et al.*, 1969, p. 57; and Palmer, 1973, p. 61) agree in assigning what is now called the Mammal Bed to the Upper Bathonian Forest Marble. Depending on where the White Limestone–Forest Marble boundary is drawn, the Sub Coral-*Epithyris* Clay is held to lie at (Arkell, 1947) or near the top of (Odling, 1913; Palmer, 1973) the White Limestone, or the base of the Forest Marble (McKerrrow *et al.*, 1969).

Zonal ammonites have not been found at Kirtlington and, elsewhere in Oxfordshire, are exceedingly rare (Torrens, 1969),

so that assignments of strata to ammonite zones are necessarily indirect. Bate & Mayes (1977, p. 37), on the basis of finding there the index ostracod *Glyptocythere penni* Bate & Mayes 1977, in the *fimbriata-waltoni* Clay, a bed which lies below both the Mammal bed and the Sub Coral-*Epithyris* Clay, give a *discus* Zone age for both these beds. However, Torrens (in Cope *et al.*, 1980, p. 36), while acknowledging that the age of the Mammal Bed is uncertain, suggests that it belongs to the *aspidoides* Zone.

As shown by Ware (1978 MS, pp. 320–325), the ostracods of the Mammal Bed indicate its inclusion within Ostracod Zone 6 of Bate (in Bate & Robinson, 1978, pp. 221–223) and as revised by Sheppard (in Bate & Robinson, 1978, pp. 474, 475). Species such as the very abundant *Theriosynoecum kirtlingtonense* Bate, 1965 and *Timiriasevia mckerrrowi* Bate, 1965 typify the Mammal Bed fauna, although Ware (1978 MS) records a total of 18 species as being autochthonous to it.

The Sub Coral-*Epithyris* Clay is dominated by the autochthonous (using the population age criteria of Whatley, 1988) species *Glyptocythere penni* Bate & Mayes, 1977, *Lophocythere propinqua* Malz, 1975, *Schuleridea* (*Eoschuleridea*) *trigonalis* (Jones, 1884) and *Micropneumatocythere falcata* Sheppard, 1978. These all support assignment to Bate's (revised) Ostracod Zone 6.

Tarlton is situated about 3 km south of Cirencester, from where three sets of samples were collected. Before Upton's (1909) original clay pit had been located, two samples were taken from a dried-out section of the Thames and Severn Canal. The first (T1) came from below the floor of the canal, some 145 m NW of the railway bridge that crosses it near the disused clay pit. The second (T2) was from the canal bank opposite that clay pit. Although the exact stratigraphical position of samples T1 and T2 is not known, their ostracod fauna, which comprised a well-preserved and diverse Bathonian assemblage, is identical with that of the clay pit.

The other two sets of samples, both from the clay pit, are well documented elsewhere (Ware & Windle, 1981, p. 416; Ware & Whatley, 1983). T3 is a bulk clay sample from the top 0.9 m of clay immediately underlying the Lower Cornbrash. From the numerous Ostracoda this contained, this sample was shown (Ware & Windle, 1981, p. 417) to be within Bate's (revised) Ostracod Zone 6, the equivalent to the *Clydoniceras discus* Zone, which Torrens (in Cope *et al.* 1980, fig. 6a, opposite p. 24) relates to the upper part of the Forest Marble and the Lower Cornbrash. The T5 series of samples was taken 18 m SW of sample T3, from a newly dug section exposing some 7 feet (2.06 m) of fresh clay immediately below the Lower Cornbrash, from which 27 samples were taken (see Ware & Whatley, 1983, fig. 2, p. 135). Although the clay is macroscopically uniform, Ware & Whatley (1983) demonstrated, on the basis of its contained Ostracoda, five distinct depositional phases.

The Callovian samples were collected in early 1962 from the Putton Lane Brick Pit, about 1 km SE of Chickerell Church, near Weymouth, Dorset [NGR 649 799]. This section is described by Arkell *et al.* (1947, p. 27) and two samples were taken from the *Proplanulites koenigi* Zone of the Kellaways Beds, one (sample Kell-PI-1) at the base of the exposure and the other (sample Kell-PI-2) some 5 feet (1.52 m) above. The sediments are of soft blue clay with lines of cementstones and each sample of clay weighed approximately 2 kg.

SYSTEMATIC DESCRIPTIONS

The following conventions are employed: RV, right valve; LV, left valve; C, articulated carapace; A-1, A-2, A-3, A-4, juvenile specimens with respective pre-adult instar stages with A-1 being the penultimate instar; npc, normal pore canal; rpc, radial pore canal. All dimensions are given in mm and relative size refers to the following scheme: very small, <0.40; small, 0.40–0.50; medium, 0.50–0.70; large, 0.70–1.00; very large, >1.00. In the captions to the plates, dimensions for the specimens in each figure are given in round brackets in the following order: length, height and width.

All the specimens used in this paper, which were not originally loaned from the British Geological Survey, Keyworth, Nottingham (BGS), and referred to under their catalogue and slide numbers, are housed in the collections of the Department of Palaeontology, The Natural History Museum, London, (BMNH) to which the catalogue numbers prefixed OS apply. Some earlier BMNH numbers are prefixed In, Io, or I. Some specimens from the Ware Collection (e.g., M/4/8) illustrated in the plates were unfortunately subsequently lost or broken on the stubs following scanning electron microscopy and/or their long period of storage. This is indicated in the various plate descriptions and under the dimensions of the various taxa.

Phylum **Crustacea** Pennant, 1777

Class **Ostracoda** Latreille, 1806

Order **Podocopida** Müller, 1894

Suborder **Podocopina** Sars, 1866

Superfamily **Cytheracea** Baird, 1850

Family **Progonocytheridae** Sylvester-Bradley, 1948

Subfamily **Progonocytherinae** Sylvester-Bradley, 1948

Genus *Fastigatocythere* Wienholz, 1967

For an emended generic diagnosis, see Whatley & Ballent, 1996.

Fastigatocythere juglandica (Jones, 1884)

Remarks. This species was named by Jones (1884) for its resemblance to a walnut. In the present study, by careful consideration of size, the shape and outline and ornament of the adults and the ornament of the instars, we are able to distinguish five distinct subspecies of *F. juglandica*. Two of these were isolated by Jones & Sherborn (1888) but subsumed by subsequent authors in *F. juglandica*. We have resurrected *F. juglandica* (Jones) var. *major* (Jones & Sherborn) as a subspecies and, as revising authors, have synonymized within it *Lophocythere fulgurata* (Jones & Sherborn), described in the same paper, which we demonstrate to be its juvenile. *Fastigatocythere juglandica postrotunda* subsp. nov. is a new late Bathonian subspecies, while *Fastigatocythere juglandica degenerata* subsp. nov. is from the early Callovian. Lastly, we consider *Fastigatocythere rugosa* Weinholz, 1967, which is quite closely related to the latter subspecies, to be yet another subspecies of *F. juglandica*. To avoid repetition, while the nominative subspecies is described in full, other subspecies are merely given extended diagnoses and the differences between the five subspecies are further outlined in the remarks sections.

Fastigatocythere juglandica juglandica (Jones, 1884)

(Pl. 1, figs 1–23; Pl. 2, figs 1–4)

1884 *Cythere juglandica* sp. nov. Jones: 766–768, pl. 34, figs 36, 37.

1948 *Progonocythere juglandica* (Jones); Sylvester-Bradley: 193, pl. 12, figs 5, 6; pl. 13, fig. 8.

1957 *Progonocythere* cf. *juglandica* (Jones); Oertli: 281, fig. 2 (1); fig. 3 (1).

1967 *Glyptocythere juglandica* (Jones); Bate: 51, pl. 14, fig. 9.

1969 *Fastigatocythere juglandica* (Jones); Bate: 389, pl. 3, figs 4, 7, 8.

Non 1990 *Fastigatocythere juglandica* (Jones); Brand: 207, pl. 14, fig. 4.

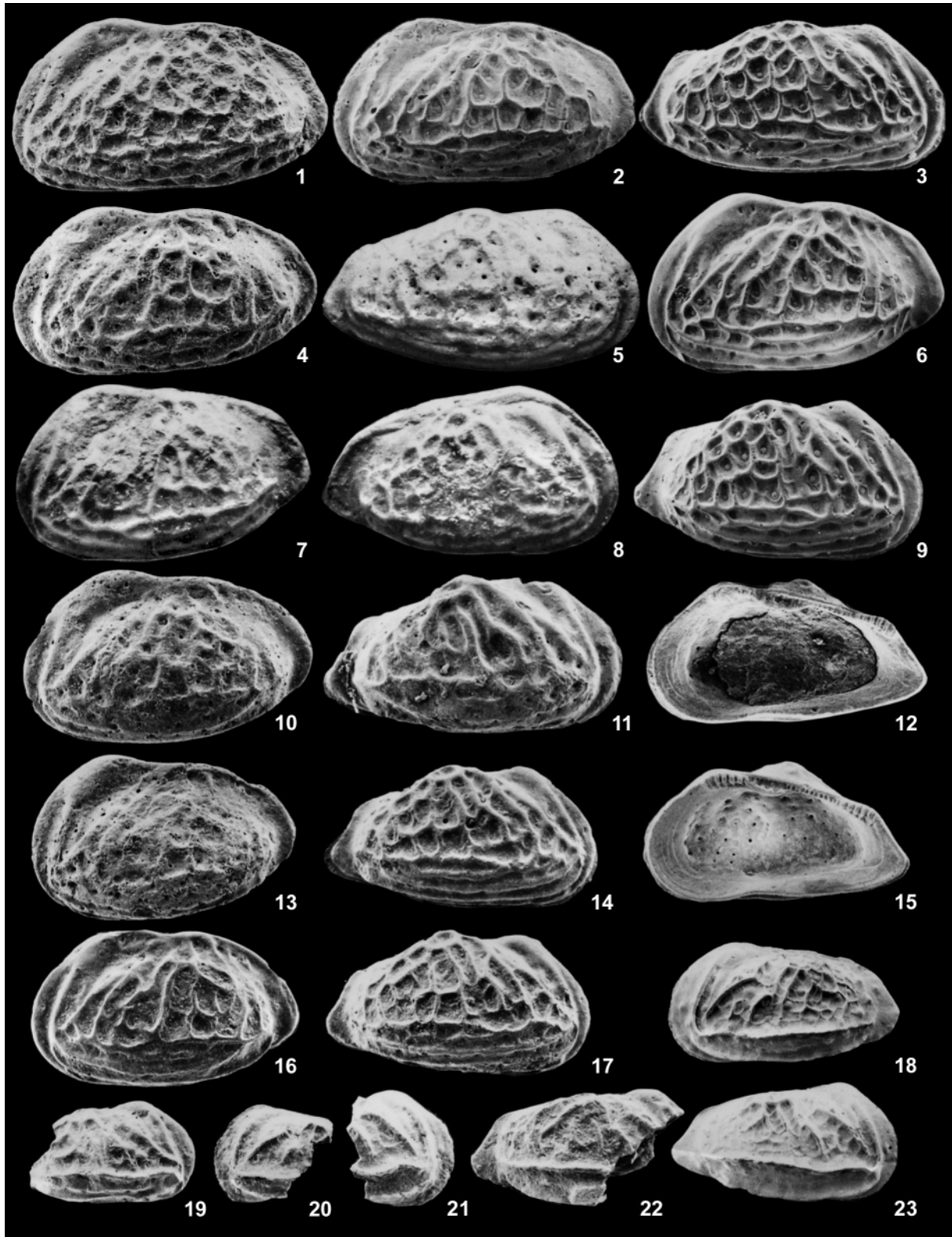
Type locality. Originally recorded (Jones, 1884) from the Richmond Borehole, Surrey. Late Bathonian.

Type specimens. The lectotype (BMNH no. In 41947) and paralectotype (BMNH no. In 41948) are refigured in Pl. 1, figs 5, 7, respectively.

Material. Some 250 specimens in various collections.

Diagnosis. The nominative subspecies of *F. juglandica* (Jones) is characterized by its fairly strong reticulate/costate ornament in which the former dominates. With numerous, relatively small reticulae, bluntly pointed posterior margin in LV, strongly radiating ribs originating from umbonate mid-dorsal region in RV. Vento-lateral and ventral horizontal ribs well defined. Ribs and muri relatively sharp and narrow. Normal pores fairly large, openings slightly elevated, mostly in solae. Juveniles with well-developed median and ventro-lateral ribs and pronounced anterior rib; median and dorso-lateral surfaces densely reticulate.

Description. Large. Thick-shelled. Strongly sexually dimorphic; males notably more elongate and less inflated than females, this dimorphism detectable in late instars. Valves of different shape; RV more subtriangular than LV which is larger and more subrectangular, especially in males. LV notably larger than RV with strong overlap. Mid-laterally inflated, especially in females. Anterior margin broadly but asymmetrically rounded; antero-dorsal slope long and almost straight in RV; apex at mid-height in RV, below mid-height in LV. Posterior margin subcaudate with concave postero-dorsal slope in RV. In LV the posterior margin is bluntly pointed, more sharply in females than in males. In RV, the dorsal margin is medianly umbonate due to the projection of the dorso-lateral surface; in LV this does not project beyond margin. In both valves the dorsal cardinal angles are well marked and the dorsal margin is enhanced by a marginal rim. Ventral margin with a shallow oral incurvature which is obscured in lateral view. Greatest length at or just below mid-height; greatest height at mid-length in RV, at anterior cardinal angle in LV. Ornament of coarse reticulae dorso-laterally, where a series of ribs radiate obliquely downwards from a mid-dorsal position which is above the dorsal margin in the RV but below it in the LV. These ribs are linked by sub-horizontal ribs of almost equal strength, thereby imparting a reticulate pattern. At the ventro-lateral change of slope, the oblique vertical ribs are terminated at the most dorsal of a series of parallel horizontal ribs which extend across the



ventro-lateral and ventral surfaces. The horizontal ribs are linked by a series of much weaker vertical riblets. Eye tubercle and post ocular sulcus prominent (especially in the LV), the former passing into an ocular rib which parallels the rimmed anterior margin and is separated from it by a parallel sulcus. The large sieve-type normal pores occur in the solae of the reticulae, with fewer simple pores exiting on the muri. Calcified inner lamella wide, with prominent striae. Hinge entomodont, robustly developed with, in RV, strongly dentate terminal elements bearing seven teeth anteriorly and five posteriorly and a median element with five deep antero-median locules and a strongly locellate postero-median element. The adductor scars are a closely adjacent, slightly oblique row of four oval scars with a circular to heart-shaped frontal scar. Juvenile specimens are characteristically densely and delicately reticulate, especially dorsal to the ventro-lateral rib.

Distribution. Late Bathonian of southern England and France.

Dimensions	Length (mm)	Height (mm)
^a Male LV, RB/51/5	0.93	0.51
^b , ^c Male LV, L/1/1	0.93	0.50
^b Male RV, OS 15744	0.91	0.45
^a Male LV, RB/45/6	0.92	0.53
^a Male RV, In 41947 (lectotype)	0.93	0.47
^b Female LV, OS 15745	0.87	0.53
^a Female C, In 41948 (metatype)	0.87	0.51
^b Female RV, OS 15746	0.85	0.46
^a Female LV, RB/45/5	0.86	0.53
^a Male RV, RB/47/5	0.90	0.47
^a Female RV, RB/51/4	0.83	0.44
^a Female LV, RB/45/1	0.80	0.50
^a Female RV, RB/51/1	0.81	0.42
^b Female RV, OS 15747	0.84	0.43
^a Female LV, RB/45/8	0.80	0.47
^a Female RV, RB/51/6	0.79	0.43
^b Male A-1 juv. LV, OS 15748	0.73	0.39
^b Male A-1 juv. RV, OS 15749	0.73	0.39

Dimensions	Length (mm)	Height (mm)
^b Male A-1 juv. RV, M/4/3	0.72	0.37
^b Male A-1 juv. RV, M/4/5	0.69	0.37
^b Female A-2 juv. LV, M/4/7	0.64	0.36
^b Female A-2 juv. RV, M/4/8	0.62	0.33

Specimens prefixed RB/ are deposited in the collections of the British Geological Survey, Keyworth, Nottingham; specimens prefixed by L/ or M/ are in the Ware Collection, but many are unfortunately now lost.

^aRichmond Borehole, Surrey.

^bKirtlington, Oxfordshire, Sub Coral-*Epithyris* Clay.

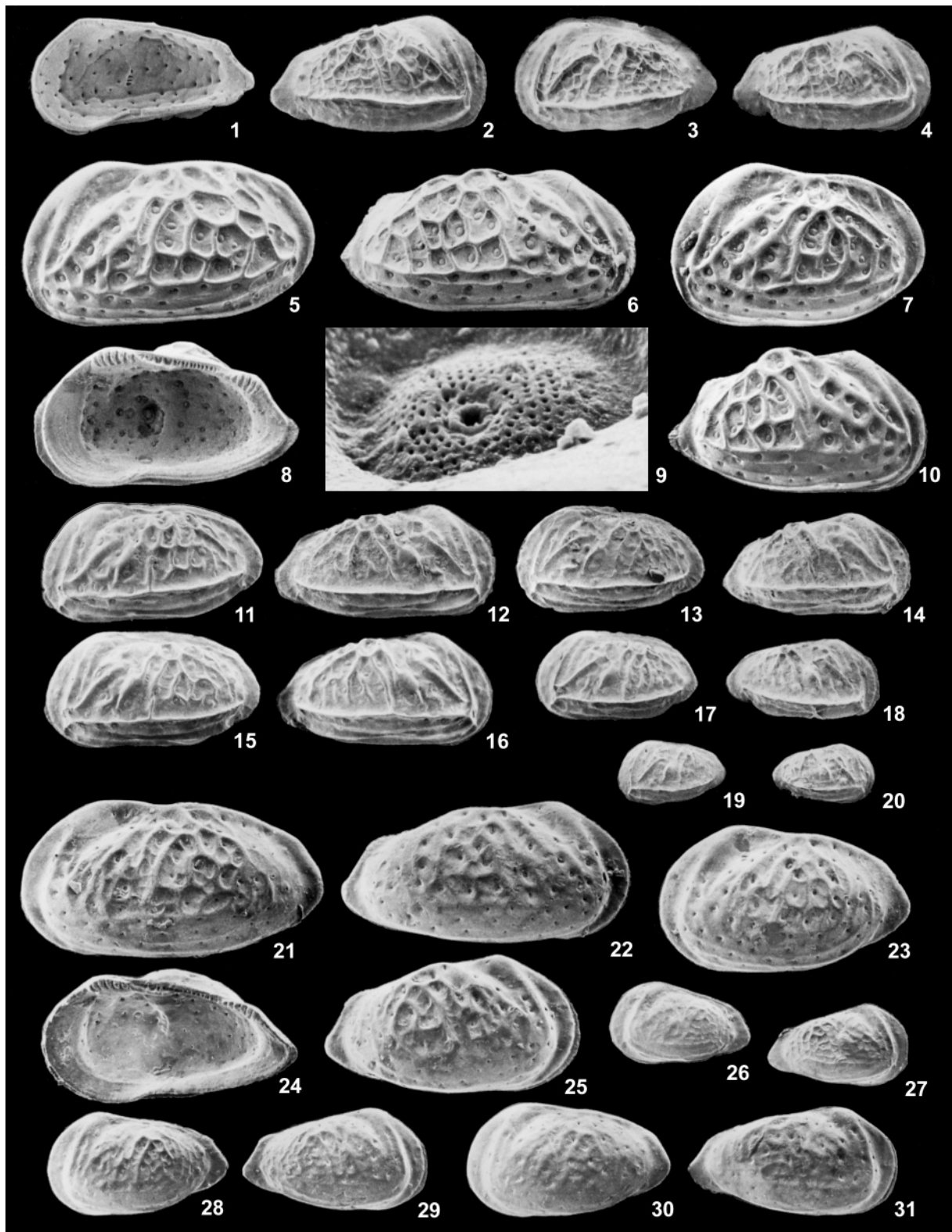
^cspecimen lost.

Range of adult dimensions	Length (mm)	Height (mm)
Female LV + C.	0.80–0.86	0.47–0.53
Female RV	0.79–0.85	0.42–0.46
Male LV	0.92–0.93	0.50–0.53
Male RV	0.90–0.93	0.45–0.47

Remarks. The major distinctions between this subspecies and *F. juglandica* (Jones) *major* (Jones & Sherborn) are in their respective ornament. The present subspecies has less coarse dorso-lateral reticulation with a higher number of reticulae per unit area and much weaker radial muri. It is also considerably larger and its instars, with their strong reticulation do not resemble the '*Lophocythere fulgurata*' instars of *F. juglandica major*. The subspecies *F. juglandica postrotunda* subsp. nov. also has coarser dorso-lateral reticulation (but less so than *F. juglandica major*) but is mainly distinguished by its subrounded posterior margin in the LV and a characteristic median swelling in its instars of the second radial rib on the antero-median lateral surface in about the position of the adductor scars. *Fastigatocythere juglandica degenerata* subsp. nov. differs from the present subspecies in its much more subdued ornament and *F. juglandica rugosa* (Weinholz, 1967) has only the radial components of the ornament strongly developed antero-dorsally. The specimen illustrated by Brand (1990), which he considers to

Explanation of Plate 1.

figs 1–23. *Fastigatocythere juglandica juglandica* (Jones, 1884): **1**, male LV, (0.93, 0.51), Richmond Borehole, Surrey, 1152 ft, from BGS slide MPA 21953, RB/51/5, × 57; **2**, male LV, (0.93, 0.50), Kirtlington, Oxfordshire, Sub Coral-*Epithyris* Clay, L/1/1 of Ware collection (specimen lost), × 56; **3**, male RV, (0.91, 0.45), Kirtlington, Sub Coral-*Epithyris* Clay, BMNH no. OS 15744, × 58; **4**, male LV, (0.92, 0.53), Richmond Borehole, 1145 ft 9 in., from BGS slide MPA 21952, RB/45/6, × 55; **5**, male RV, (0.93, 0.47), Richmond Borehole, Surrey, 1146 ft 6 in., Sylvester-Bradley's (1948) lectotype of *Progonocythere juglandica*, refigured by Bate (1969) as *Fastigatocythere juglandica*, original material presented by Professor Judd (1885) to the BMNH (no. In 41947), micrograph of uncoated specimen taken in SEM Environmental Chamber, × 57; **6**, female LV, (0.87, 0.53), Kirtlington, Sub Coral-*Epithyris* Clay, BMNH no. OS 15745, × 58; **7**, female carapace, seen from the left (0.87, 0.51, 0.49), Richmond Borehole, 1151 ft 6 in., Sylvester-Bradley's (1948) metatype of *Progonocythere juglandica* and Bate's (1969) paralectotype of *F. juglandica*, original material presented by Professor Judd (1885) to the BMNH (no. In 41948), micrograph of uncoated specimen taken in SEM Environmental Chamber, × 57; **8**, same specimen seen from the right, × 57; **9**, female RV, (0.85, 0.46), Kirtlington, Sub Coral-*Epithyris* Clay, BMNH no. OS 15746, × 58; **10**, female LV, (0.86, 0.53), Richmond Borehole, 1145 ft 9 in., from BGS slide MPA 21952, RB/45/5, × 56; **11**, male RV, (0.90, 0.47), Richmond Borehole, 1145 ft 9 in., from BGS slide MPA 21952, RB/47/5, × 55; **12**, female RV, (0.83, 0.44), internal view, Richmond Borehole, 1151 ft, from BGS slide MPA 21952, RB/51/4, × 56; **13**, female LV, (0.80, 0.50), Richmond Borehole, 1145 ft 9 in., from BGS slide MPA 21952, RB/45/1, × 55; **14**, female RV, (0.81, 0.42), Richmond Borehole, 1151 ft, from BGS slide MPA 21953, RB/51/1, × 57; **15**, female RV, (0.84, 0.43), internal view, Kirtlington, Sub Coral-*Epithyris* Clay, BMNH no. OS 15747, × 57; **16**, female LV, (0.80, 0.47), Richmond Borehole, 1145 ft 9 in., from BGS slide MPA 21952, RB/45/8, × 56; **17**, female RV, (0.79, 0.43), Richmond Borehole, 1151 ft, from BGS slide MPA 21953, RB/51/6, × 56; **18**, male A-1 juvenile LV, (0.73, 0.39), Kirtlington, Sub Coral-*Epithyris* Clay, BMNH no. OS 15748, × 53; **19**, A-2 juvenile RV, anterior fragment, Richmond Borehole, from BGS split sample BS 4638, RB/51/10, × 57; **20**, A-2 juvenile LV, anterior fragment, Richmond Borehole, 1151 ft, from BGS split sample BS 4638, RB/51/13, × 57; **21**, A-2 juvenile RV, anterior fragment, Richmond Borehole, 1151 ft, from BGS split sample BS 4638, RB/51/12, × 57; **22**, ?female A-1 juvenile RV, posterior fragment, Richmond Borehole, 1151 ft, from BGS split sample 4638, RB/51/11, × 57; **23**, male A-1 juvenile RV, (0.73, 0.39), Kirtlington, Sub Coral-*Epithyris* Clay, BMNH no. OS 15749, × 53. All specimens are late Bathonian in age. External lateral views unless otherwise stated. Dimensions (in brackets) are of length, height and width, respectively, in mm. BMNH, The Natural History Museum, London. BGS, British Geological Survey, Keyworth, Nottingham; their Richmond borehole samples are from new washings of original material made in 1975.



be a possible female of *F. juglandica s.l.* does not belong to any of the subspecies described here. It seems to have adult ornament but measures only 0.42 mm, only about half the mean length of adults of the species. The specimen illustrated on our Pl. 1, fig. 11 more closely resembles *F. juglandica major* in its ornamentation. However, the specimen, a male RV from the BGS Richmond Borehole, at 0.90 mm in length, is considerably larger than the largest known male RV of this particular subspecies (0.84 mm) and conforms in size to the present subspecies.

Fastigatocythere juglandica (Jones) *major* (Jones & Sherborn),
1888
(Pl. 3, figs 1–26)

1888 *Cythere juglandica* Jones var. *major* var. nov. Jones & Sherborn: 255, pl. 4, fig. 2a,b.

1888 *Cytheridea fulgurata* sp. nov. Jones & Sherborn: 273, pl. 4, fig. 12a, b, c [juveniles].

1948 *Progonocythere juglandica* (Jones); Sylvester-Bradley: 193, 194.

1969 *Lophocythere fulgurata* (Jones & Sherborn); Bate: 419, pl. 12, fig. 7.

1975 '*Lophocythere fulgurata*' (Jones & Sherborn); Malz: 132, pl. 3, figs 21, 22.

1977 *Lophocythere* (*Lophocythere*) *fulgurata* (Jones & Sherborn); Whatley & Stephens: 83.

1978 *Fastigatocythere juglandica* (Jones); Bate: 238, pl. 7, fig. 16.

1978 *Lophocythere fulgurata* (Jones & Sherborn); Bate: 236, pl. 6, figs 14, 15.

1984 *Fastigatocythere juglandica* (Jones); Dépêche: 246, pl. 9, figs 7, 9.

1985 *Lophocythere fulgurata* (Jones & Sherborn); Dépêche: pl. 30, fig. 10.

1985 *Fastigatocythere juglandica* (Jones); Dépêche: pl. 30, fig. 22.

Type locality. Bradford Clay, Bradford-on-Avon. '*C. fulgurata*' originally came from the Blue Fuller's Earth Clay, Midford.

Both localities are near Bath, Avon, and are late Bathonian in age.

Type specimens. The holotype of *Cythere juglandica* var. *major* is refigured in Pl. 3, fig. 1. The lectotype and paralectotypes of '*Cytheridea fulgurata*' are refigured in Pl. 3, figs 10–13.

Diagnosis. A subspecies of *F. juglandica* characterized by its strong, coarse reticulate/costate ornament in which the costae dominate. With relatively few, large, irregular reticulae and with strongly radiating ribs originating in umbonate mid-dorsal region in RV. Ventro-lateral and ventral ribs only moderately well defined. Ribs broad and rounded. Posterior margin bluntly pointed in LV with apex at mid-height; more acute, slightly upturned, caudate and with apex rather below mid-height in RV. Normal pores sieve-type, openings depressed. Juveniles corresponding to *Lophocythere fulgurata*, with very strongly developed median and ventro-lateral ribs and median and dorso-lateral surfaces sparsely reticulate to almost smooth.

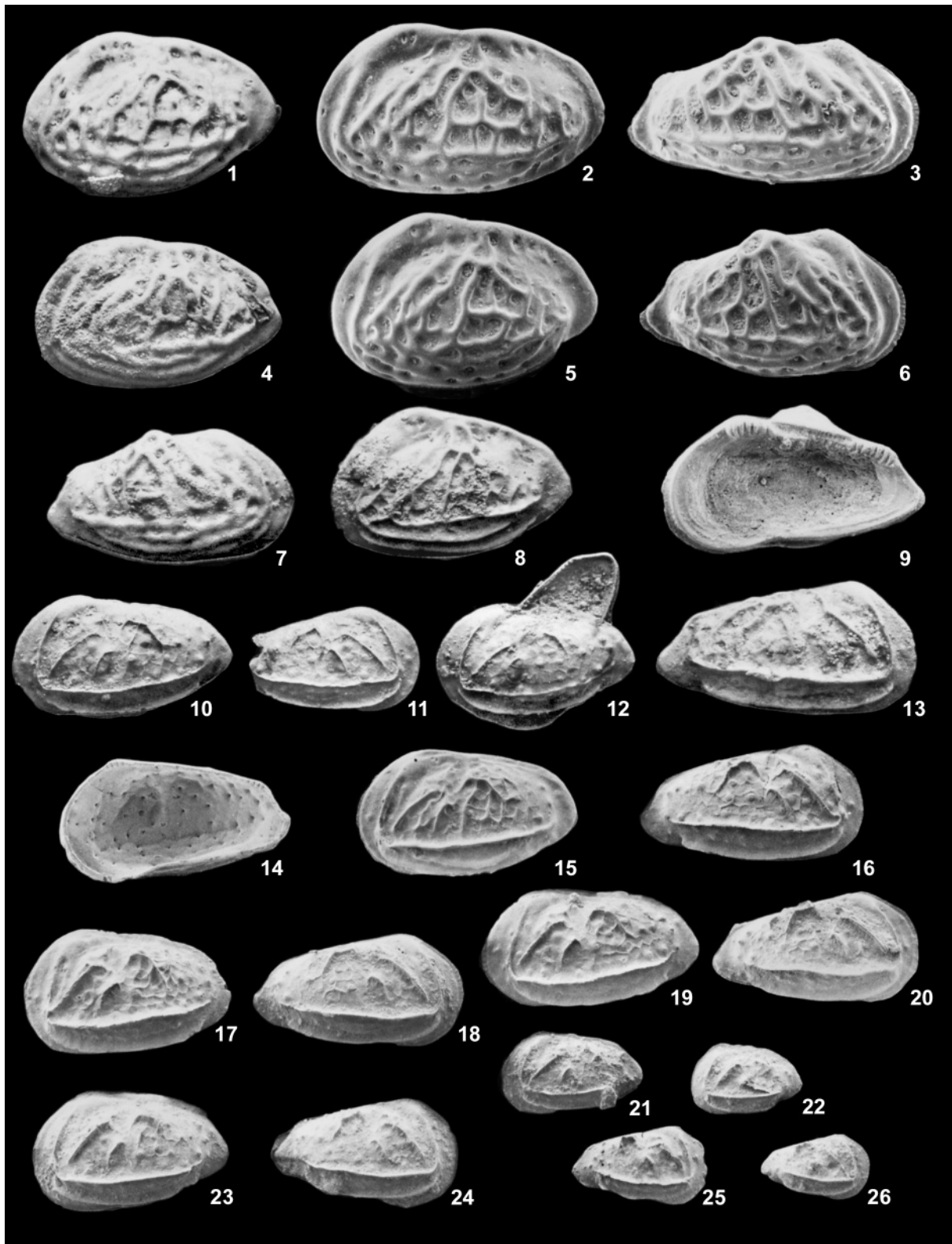
Distribution. Late Bathonian of southern England and France.

Dimensions	Length (mm)	Height (mm)
^a Female LV, I 1872 (holotype)	0.74	0.49
^b Male LV, OS 15774	0.85	0.49
^b Male RV, OS 15775	0.84	0.42
^c Female LV, In 41910 (plesiotype)	0.72	0.43
^b Female LV, OS 15776	0.78	0.50
^b Female RV, OS 15777	0.77	0.42
^c Female RV, In 41911 (plesiotype)	0.72	0.39
^d Female LV, Io. 2513	0.70	0.38

Remarks. This subspecies differs from the nominative subspecies in its coarser, more irregular reticulation, smaller size and in its instars which are much less reticulate, to the point of being almost intercostally smooth and which conform to '*Lophocythere fulgurata*'. Although *Cythere juglandica* var. *major* and

Explanation of Plate 2.

figs 1–4. *Fastigatocythere juglandica juglandica* (Jones 1884). **1**, male A-1 juvenile RV, (0.72, 0.37), internal view, Kirtlington, Oxfordshire, Sub Coral-*Epithyris* Clay, BMNH no. OS 15750, × 57; **2**, male A-1 juvenile RV, (0.69, 0.37), Kirtlington, Sub Coral-*Epithyris* Clay, BMNH no. OS 15751, × 52; **3**, female A-2 juvenile LV, (0.64, 0.36), Kirtlington, Sub Coral-*Epithyris* Clay, M/4/7 of Ware collection (specimen broken), × 52; **4**, female A-2 juvenile RV, (0.62, 0.33), Kirtlington, Sub Coral-*Epithyris* Clay, M/4/8 of Ware collection (specimen broken), × 51. All specimens are late Bathonian in age. **figs 5–20.** *Fastigatocythere juglandica* (Jones) *postrotunda* subsp. nov. All specimens from sample T3, Tarlton, Gloucestershire: **5**, male LV (0.85, 0.48), holotype, BMNH no. OS 15752, × 57; **6**, male RV, (0.85, 0.42), paratype, BMNH no. OS 15753, × 57; **7**, female LV, (0.74, 0.48), paratype, BMNH no. OS 15754, × 57; **8**, female RV, (0.77, 0.42), paratype, internal view, BMNH no. OS 15755, × 57; **9**, holotype, sieve pore from ventro-lateral surface, × 3000. **10**, female RV, (0.75, 0.42), paratype, BMNH no. OS 15756, × 58; **11**, male A-1 juvenile LV, (0.71, 0.38), paratype, BMNH no. OS 15757, × 53; **12**, male A-1 juvenile RV, (0.70, 0.36), paratype, BMNH no. OS 15758 (fragments), × 53; **13**, A-2 juvenile LV, (0.61, 0.35), paratype, BMNH no. OS 15759, × 52; **14**, A-2 juvenile RV, (0.61, 0.35), paratype, BMNH no. OS 15760 × 52; **15**, female A-1 juvenile LV, (0.69, 0.37), paratype, M/1/4 of Ware Collection (specimen lost), × 52; **16**, female A-1 juvenile RV, (0.70, 0.37), paratype, M/1/5 of Ware Collection (specimen broken), × 52; **17**, A-3 juvenile LV, (0.52, 0.28), paratype, M/2/6 of Ware Collection (specimen broken), × 53; **18**, A-3 juvenile RV, (0.49, 0.25), paratype, M/2/7 of Ware Collection (specimen broken), × 53; **19**, A-4 juvenile LV, (0.34, 0.20), paratype, BMNH no. OS 15761, × 54; **20**, A-4 juvenile RV, (0.32, 0.19), paratype, BMNH no. OS 15762, × 54. All specimens are Late Bathonian in age. **figs 21–31.** *Fastigatocythere juglandica* (Jones) *degenerata* subsp. nov.: all specimens from Putton Lane Brick Pit, Chickerell, Dorset, *koenigi* Zone: **21**, male LV, (0.90, 0.47), holotype, BMNH no. OS 15763, × 56; **22**, male LV, (0.86, 0.41), paratype, BMNH no. OS 15764, × 57; **23**, female LV, (0.76, 0.45), paratype, BMNH no. OS 15765, × 56; **24**, female RV, (0.79, 0.42), paratype, internal view, BMNH no. OS 15766, × 55; **25**, female RV, (0.78, 0.42), paratype, BMNH no. OS 15767, × 55; **26**, A-3 juvenile LV, (0.46, 0.27), paratype, BMNH no. OS 15768, × 52; **27**, A-3 juvenile RV, (0.47, 0.26), paratype, BMNH no. OS 15769, × 52; **28**, female A-2 juvenile LV (0.59, 0.33), paratype, BMNH no. OS 15770, × 51; **29**, female A-2 juvenile RV (0.61, 0.34), paratype, BMNH no. OS 15771, × 50; **30**, female A-1 juvenile LV (0.68, 0.33), paratype, BMNH no. OS 15772, × 50; **31**, female A-1 juvenile RV (0.67, 0.35), paratype, BMNH no. OS 15773, × 53. All specimens are late Bathonian or early Callovian in age. External lateral views unless otherwise stated. Dimensions (in brackets) are of length and height, respectively, in mm. BMNH, The Natural History Museum, London.



Dimensions	Length (mm)	Height (mm)
^b Female RV, OS 15778	0.76	0.41
^c A-1 juv. LV, Io 3648 (paralectotype)	0.66	0.36

All specimens housed in The Natural History Museum, London.

^aBradford-on-Avon.

^bTarlton, Gloucestershire, sample T1.

^cBoueti Bed, Herbury, Dorset.

^dKingscliffe, Northamptonshire.

^eMidford, near Bath, Blue Fuller's Earth Clay.

Range of adult dimensions	Length (mm)	Height (mm)
Female LV	0.70–0.78	0.38–0.50
Female RV	0.72–0.77	0.39–0.42
Male LV	0.85	0.49
Male RV	0.84	0.42

Cytheridea fulgurata were described in the same paper by Jones & Sherborn (1888) we, as revising authors, formally subsume the latter (as its instars) into *F. juglandica major*. *Fastigatocythere juglandica postrotunda* subsp. nov. is of similar size but differs in that the posterior margin of the LV is rounded, its dorso-lateral surface is more regularly reticulate, its sieve-type pores are generally larger and more pronounced and its juveniles more reticulate (but less so than those of *F. juglandica juglandica*). *Fastigatocythere juglandica degenerata* subsp. nov. has much more subdued ornament and is larger, while *F. juglandica rugosa* has strong but distinct ornament antero-dorsally and lacks the ventro-lateral rib. The juveniles of the latter two subspecies are very different in lacking the ventro-lateral rib.

Fastigatocythere juglandica (Jones) *postrotunda* subsp. nov.
(Pl. 2, figs 5–20)

1996 *Fastigatocythere juglandica* (Jones); Whatley & Ballent: pl. 1, figs 10–14.

Holotype. Male LV, OS 15752. Housed in The Natural History Museum, London.

Derivation of name. Refers to the well-rounded posterior margin in the left valve.

Type locality and type level. Tarlton, Gloucestershire. Sample T3. Late Bathonian, *Clydoniceras discus* Zone.

Material. More than 100 specimens.

Diagnosis. A new subspecies of *F. juglandica* characterized by its fairly strong to strong reticulate/costate ornament in which both vertical and horizontal elements are of more or less equal importance. With relatively numerous, medium-sized reticulae and with ribs of medium width and strength radiating from dorsal margin, which is strongly umbonate in RV. Ventro-lateral and ventral ribs fairly well defined. Normal pores very large and prominent, sieve type, openings strongly elevated and almost all situated in solae. Posterior margin of LV rounded. Juveniles with ribs radiating from mid-dorsal and dominating the ornament; these ribs terminate ventrally against a strongly developed ventro-lateral rib. Several strong parallel ribs traverse the ventral surface. Instars with distinct bulbous swelling of the second radial rib on the antero-median lateral surface in about the position of the adductor scars.

Explanation of Plate 3.

figs 1–26. *Fastigatocythere juglandica* (Jones) *major* (Jones & Sherborn, 1888): **1**, female left valve, (0.74, 0.49), Bradford Clay, Bradford-on-Avon, near Bath, Sherborn (1888) Collection, figured as *Cythere juglandica* var. *major* by Jones & Sherborn (1888), as plesiotype of *Progonocythere juglandica* (Jones & Sherborn) by Sylvester-Bradley (1948), and re-figured as *Fastigatocythere juglandica* by Bate (1969), BMNH no. I 1872. × 57; **2**, male LV, (0.85, 0.49), sample T1, Tarlton, Gloucestershire, BMNH no. OS 15774, × 57; **3**, male RV, (0.84, 0.42), sample T1, Tarlton, BMNH no. OS 15775, × 58; **4**, female LV, (0.72, 0.43), Herbury, Dorset, *boueti* Bed, plesiotype of *Progonocythere juglandica* by Sylvester-Bradley (1948), BMNH no. In 41910, × 56; **5**, female LV, (0.78, 0.50), sample T1, Tarlton, BMNH no. OS 15776, × 57; **6**, female RV, (0.77, 0.42), sample T1, Tarlton, BMNH no. OS 15777, × 57; **7**, female RV, (0.72, 0.39), Herbury, Dorset, *boueti* Bed, figured as plesiotype of *Progonocythere juglandica* by Sylvester-Bradley (1948), BMNH no. In 41911, × 56; **8**, female LV, (0.70, 0.38), Kingscliffe, Northamptonshire, figured by Bate (1967) as *Glyptocythere juglandica*, BMNH no. Io 2513, × 57; **9**, female RV, (0.76, 0.41), internal view, sample T1, Tarlton, BMNH no. OS 15778, × 58; **10**, LV, (0.66, 0.36), Midford, near Bath, Blue Fuller's Earth Clay, Winwood (1888) Collection, designated as paralectotype of *Lophocythere fulgurata* by Bate (1969), BMNH no. Io 3648, (=A-2 juvenile of *Fastigatocythere juglandica major*), × 55; **11**, broken RV, Midford, Blue Fuller's Earth Clay, Winwood (1888) Collection, designated paralectotype of *Lophocythere fulgurata* by Bate (1969), BMNH no. Io 3646, (=A-2 juvenile of *Fastigatocythere juglandica major*), × 55; **12**, LV (with attached RV), (l=0.60), Midford, Blue Fuller's Earth Clay, Winwood (1888) Collection, designated paralectotype of *Lophocythere fulgurata* by Bate (1969), BMNH no. I 1832, (=paedomorphic adult of *Fastigatocythere juglandica major*), × 56; **13**, RV, (0.77, 0.42), Midford, Blue Fuller's Earth Clay, Sherborn (1888) Collection, figured as *Cytheridea fulgurata* by Jones & Sherborn (1888), and designated lectotype of *Lophocythere fulgurata* by Bate (1969), BMNH no. I 1832, (=paedomorphic adult of *Fastigatocythere juglandica major*), × 56; **14**, male A-1 juvenile RV, (0.68, 0.37), internal view, sample T5, Tarlton, Phase 1, M/6/5 of Ware Collection (specimen broken), × 56; **15**, male A-1 juvenile LV, (0.69, 0.39), sample T1, Tarlton, BMNH no. OS 15779, × 54; **16**, male A-1 juvenile RV, (0.71, 0.36), sample T5, Tarlton, Phase 1, M/6/4 of Ware Collection (specimen broken), × 53; **17**, female A-1 juvenile LV, (0.66, 0.40), sample T5, Tarlton, T5, M/6/6 of Ware Collection (specimen broken), × 53; **18**, female A-1 juvenile RV, (0.66, 0.34), sample T1, Tarlton, BMNH no. OS 15780, × 52; **19**, male A-1 juvenile LV, (0.68, 0.37), sample T5, Tarlton, Phase 1, BMNH no. OS 15781, × 53; **20**, male A-1 juvenile RV, (0.64, 0.35), sample T1, Tarlton, BMNH no. OS 15782, × 54; **21**, female A-3 juvenile, LV, (0.45, 0.26), sample T1, Tarlton, M/5/8 of Ware Collection (specimen broken), × 51; **22**, female A-4 juvenile, LV, (0.35, 0.23), sample T1, Tarlton, BMNH no. OS 15783, × 53; **23**, female A-1 juvenile LV, (0.63, 0.38), sample T1, Tarlton, BMNH no. OS 15784, × 51; **24**, female A-2 juvenile RV, (0.58, 0.34), sample T1, Tarlton, BMNH no. OS 15785, × 54; **25**, female A-3 juvenile RV, (0.43, 0.24), sample T5, Tarlton, Phase 1, M/7/4 of Ware Collection (specimen broken), × 53; **26**, A-4 juvenile RV, (0.35, 0.21), sample T1, Tarlton, BMNH no. OS 15786, × 53. All specimens are late Bathonian in age. External lateral views unless otherwise stated. Dimensions (in brackets) are of length and height (respectively), in mm. BMNH, The Natural History Museum, London.

Distribution. Late Bathonian. So far, confined to the type locality.

Remarks. This subspecies can be distinguished from all other subspecies of *F. juglandica* in the well-rounded posterior margin

Dimensions	Length (mm)	Height (mm)
Male LV, OS 15752 (holotype)	0.85	0.48
Male RV, OS 15753 (paratype)	0.85	0.42
Female LV, OS 15754 (paratype)	0.74	0.48
Female RV, OS 15755 (paratype)	0.77	0.42
Female RV, OS 15756 (paratype)	0.75	0.42
Male A-1 juv. LV, OS 15757 (paratype)	0.71	0.38
Male A-1 juv. RV, OS 15758 (paratype)	0.70	0.36
A-2 juv. LV, OS 15759 (paratype)	0.61	0.35
A-2 juv. RV, OS 15760 (paratype)	0.61	0.35
^a Female A-1 juv. LV, M/1/4 (paratype)	0.69	0.37
Female A-1 juv. RV, M/1/5 (paratype)	0.70	0.37
A-3 juv. LV, M/2/6 (paratype)	0.52	0.28
A-3 juv. RV, M/2/7 (paratype)	0.49	0.25
A-4 juv. LV, OS 15761 (paratype)	0.34	0.20
A-4 juv. RV, OS 15762 (paratype)	0.32	0.19

All specimens from sample T3, Tarlton, Gloucestershire. Housed in The Natural History Museum, London.

^aspecimen lost.

Range of adult dimensions	Length (mm)	Height (mm)
Female LV	0.74	0.48
Female RV	0.75–0.77	0.42
Male LV	0.85	0.48
Male RV	0.85	0.42

of the LV, in its particular reticulation, the very large and prominent sieve-type normal pore canal openings and in the ornament of its instars, especially the bulbous swelling approximately above the adductor scars.

Fastigatocythere juglandica (Jones) *degenerata* subsp. nov.
(Pl. 2, figs 21–31)

1965 MS *Glyptocythere juglandica* (Jones) *calloviana* Whatley: 350, pl. 38, figs 1–13; pl. 39, figs 1–8 [*nomen nudum*].

Holotype. Male LV OS 15763. Housed in The Natural History Museum, London.

Derivation of name. Latin, *degener*, departing from its kind, degenerate. With reference to the reduction and weakening of the adult ornamentation of this Callovian subspecies, compared to that of its Bathonian progenitors.

Type locality and level. Sample Kell-Pl-1, Putton Lane Brick Pit, 1 km SE of Chickerell Church, near Weymouth, Dorset [NGR 649 799]. *Proplanulites koenigi* Zone of the Kellaways Beds, soft blue clay at base of section. Lower Callovian.

Material. 210 valves and carapaces.

Diagnosis. A subspecies of *F. juglandica* characterized by its subdued ornament, which is a weak reticulum based on very poorly defined ribs radiating from mid-dorsal. End margins relatively smooth. Posterior margin of LV strongly pointed. Ventro-lateral and ventral ribs very poorly defined. Sieve type normal pores rather small for the species, with recessed openings. Late stage instars without strongly developed ventro-lateral or ventral ribs; A-1 with ornament similar to adult, earlier instars with better-developed anterior, ventro-lateral and ventral ribs and with dense, delicate reticulum on lateral surface.

Distribution. Lower Callovian (Kellaways Beds). So far, confined to the type locality.

Dimensions	Length (mm)	Height (mm)
Male LV, OS 15763 (holotype)	0.90	0.47
Male RV, OS 15764 (paratype)	0.86	0.41
Female LV, OS 15765 (paratype)	0.76	0.45
Female RV, OS 15766 (paratype)	0.79	0.42
Female RV, OS 15767 (paratype)	0.78	0.42
Female A-1 juv. LV, OS 15772 (paratype)	0.68	0.33
Female A-1 juv. RV, OS 15773 (paratype)	0.67	0.35
Female A-2 juv. LV, OS 15770 (paratype)	0.59	0.33
Female A-2 juv. RV, OS 15771 (paratype)	0.61	0.34
A-3 juv. LV, OS 15768 (paratype)	0.46	0.27

All specimens from Putton Lane Brick Pit, Chickerell, Dorset. Housed in The Natural History Museum, London.

Range of adult dimensions	Length (mm)	Height (mm)
Female LV+C.	0.76–0.83	0.41–0.48
Female RV	0.78–0.80	0.42–0.48
Male LV+C.	0.86–0.96	0.41–0.48
Male RV	0.93	0.43

Including data from Whatley (1965 MS)

Remarks. Its very subdued ornament and the absence of a ventro-lateral rib serve to distinguish this subspecies from *F. juglandica juglandica*, *F. juglandica major* and *F. juglandica postrotunda*, both at adult and instar stages. From *F. juglandica rugosa* it differs in lacking the strong diagonal components of the ornament dorso-laterally, although the two subspecies are clearly closely related.

Fastigatocythere juglandica (Jones) *rugosa* Weinholz, 1967
comb. nov.
(not figured)

1967 *Fastigatocythere rugosa* sp. nov. Weinholz: 25, pl. 1, figs 5–12, pl. 2, figs 10b, 15.

Diagnosis. A subspecies of *F. juglandica* characterized by an ornament of very strong, smooth diagonal ribs dorso-laterally, especially anterior of mid-length. Ventro-lateral area largely smooth except for radial pore canals, with horizontal ribs absent there, but present on ventral surface. Lateral surface adjacent to end margins largely smooth. Posterior margin of LV strongly pointed. Juveniles not known.

Dimensions	Length (mm)	Height (mm)	Width (mm)
Female LV+C.	0.77–0.85	0.45–0.50	0.45–0.47
Female RV	0.77–0.82	0.42–0.43	
Male LV+C.	0.92–0.96	0.50–0.53	0.50–0.52
Male RV	0.91–0.93	0.44–0.45	

From Wienholz (1967)

Distribution. Wienholz (1967) records this species from the Lower Callovian (Upper *calloviense* Zone) of northern Germany.

Remarks. Although Wienholz (1967) used *Fastigatocythere rugosa* as the type species of her new genus, the present authors consider it to represent a late stage in the evolution of *F. juglandica* (Jones). It is obviously closely related to *F. juglandica degenerata* subsp. nov., from which it differs in its much more strongly developed and coarser dorso-lateral ornament, and the absence of horizontal ribs ventro-laterally. It also seems to have lost almost all trace of the reticulate ornament of the nominate subspecies.

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