HIATELLA—A JURASSIC BIVALVE SQUATTER?

by SIMON R. A. KELLY

ABSTRACT. English late Jurassic (Middle Volgian) *Hiatella* occur in two habitats; firstly, as simple byssal nestlers on local hard substrates and, secondly, within *Gastrochaenolites*-type borings penetrating hard substrates. Most *Hiatella* occupy borings that they did not originally construct themselves, although ancestors as well as other bivalve genera could have been responsible. The morphology of the Mesozoic *Hiatella* is compared briefly with modern species which occur around the British Isles and which include both boring and nestling forms. A sequence of events is postulated for the formation of the Basal phosphatized Nodule Bed of the Spilsby Sandstone in Lincolnshire, and a palaeoenvironmental model is suggested for the East Midlands Shelf in Middle Volgian times.

THE borings made by bivalves into hard substrates have been the subject of considerable attention from both zoologists and palaeontologists and there are many important articles in the publications edited by Clapp and Kenk (1963), Crimes and Harper (1970, 1977), and Frey (1975). Unlike most trace fossils, borings of bivalves may commonly contain the skeletal remains of their occupants. However, caution is necessary in recognizing whether the occupant is primary, i.e. the organism which originally constructed the boring, or whether it is secondary and is effectively a squatter in the vacated domicile. There is ample evidence of modern bivalves reoccupying vacant borings, largely those of pholads, but including (updated names) *Tresus, Petricola, Macoma,* and *Irus* (Evans 1967); *Kellia* and *Notirus* (Stevenson 1946); *Tapes, Cumingia, Kellia, Diplodonta, Endodesma,* and *Mytilus* (Barrows 1917); *Modiola, Scaphula,* and *Corbula* in *Martesia* borings in brickwork (Annandale 1923); *Idasola* in borings of *Teredo* in wood (Jensen 1912). Kühnelt (1933, 1951) recorded *Ungulina, Montacuta, Lepton, Coralliophaga, Trapezium, Venerupis, Sphenia, Perna, Lyonsia, Petricola,* and *Hiatella,* all of which are deformed to some degree to fit the borings in which they occur. Some bivalves like *Hiatella* and *Petricola* (Yonge 1958; Hunter 1949) may either bore into hard substrates or nestle epibyssally. Bivalve borings in turn may be reinfested by other phyla, e.g. hydroids and bryozoa described by Evans (1949), surviving in the wet microenvironments of the vacant borings in the intertidal zone. Warme (1970) noted that abandoned borings may be modified and deepened by nestling bivalves, gastropods, polychaetes, arthropods, etc.

Records of fossil bivalves reoccupying vacant borings are much less common. Masuda (1968) noted *Barbatia, Irus,* and *Phlyctiderma* in partially eroded Miocene borings. Itoigawa (1963) recorded the borings of Miocene *Parapholas* which were subsequently infilled by sediment, and then burrowed by *Lutraria* before consolidation. Kennedy and Klinger (1972) discussed a number of encrusting and nestling organisms occupying borings constructed by a Cretaceous mytilid; these include serpulids, a bryozoan, ostreids, and *Barbatia.* Jurassic *Hiatella* has been recognized only rarely. Eudes-Deslonchamps (1838) ascribed two species from the Middle Jurassic of Normandy to *Saxicava* (a junior synonym of *Hiatella*), and Chavan (1952) introduced the genus *Pseudosaxicava* for a Lower Kimmeridgian species from the same area, and this name is placed as a subgenus of *Hiatella* by Keen (*in* Moore 1969). From England, Cox (1929) described '*Arca*' *foetida* from the Portland Sand and Hartwell Clay (Middle Volgian). This latter species is conspecific with other material described here from the Middle Volgian. The updated name of this species is *Hiatella (Pseudosaxicava) foetida* (Cox 1929).

There has been little ecological information associated with these early records, though Eudes-Deslongchamps noted that his Middle Jurassic examples were associated with borings into corals and bivalve shells. The description here of specimens from the English Middle Volgian adds significantly

to the paleoecology of *Hiatella*. There is evidence that the shell shape is strongly controlled by the substrate to which it is attached. There is little positive evidence for English Upper Jurassic *Hiatella* having been capable of boring, while there is plenty of evidence which indicates that vacant bivalve borings were commonly infested by *Hiatella* spat. Modern British *Hiatella* have been studied by Hunter (1949), who described considerable variation in shell shape which is closely paralleled by the late Jurassic forms, depending largely on whether they are boring or nestling. Strauch (1968) suggested that the shell length of Recent *Hiatella* was inversely related to the winter minimum water temperature and consequently was useful in estimation of Cenozoic palaeotemperatures. However, this is partially doubted by Rowland and Hopkins (1971) who believe that there is a more complex situation and that size is controlled more by mode of life in each population.

STRATIGRAPHY

The specimens used in this study are all from the Middle Volgian (equivalent to the upper part of the Upper Kimmeridgian and the lower part of the Portlandian of England). Extensive collecting was carried out in the Basal Spilsby Nodule Bed in a sand pit, now bulldozed, on Nettleton Hill, Lincolnshire (TF 108989) (see text-fig. 1 for localities). Although *in situ* collecting is no longer possible at this site, the hillside about 200 m to the north provides much weathered-out loose material from the same horizon. The collections made from this horizon have been deposited with the Institute of Geological Sciences, London (IGS). Casey (1973) referred this bed to the *Titanites giganteus* Zone. The status of this zone in Lincolnshire is not clear since Wimbledon and Cope (1978) have completely revised the zonal sequence in southern England. However, it is possible that the fauna of this bed may represent several zones as repeated phases of phosphatization can be recognized and the ammonites (all phosphatized) belong to the genera *Crendonites*, *Epilaugeites*, *Kerberites*, and *Pavlovia* (R. Casey pers. comm.). The Basal Spilsby Nodule Bed rests upon eroded, plastic blue-grey Kimmeridge Clay with occasional cementstones up to 0·2 m thick and containing *Pectinatites* of Lower Volgian age. The nodule bed itself is about 0·2 m thick and is composed of brown and blackened phosphatized concretions up to 0·2 m in diameter, but commonly 10–30 mm, together with small lyditic pebbles set in a dark, glauconitic silty sand. Many of the concretions show compound structure and are commonly abraded, showing signs of bioerosion, e.g. flask-shaped borings attributable to bivalves

TEXT-FIG. 1. Sketch map of the distribution of Middle Volgian strata in England, with locations of sites where *Hiatella* has been obtained.

and grazing trails probably caused by gastropods. A rich fauna, especially of bivalves, has been obtained from this bed (Kelly 1977). The preservation of the fauna is normally as hollow phosphatized moulds, with internal moulds of bivalves and of parts of ammonites making up a high proportion of the nodules of the bed. Above the nodule bed lies 0·6 m of poorly consolidated glauconitic silty sand, the base of which is pale coloured, becoming brown (ferruginous) near the centre and grey at the top, and which contains unidentified, partly phosphatized, ammonites.

Similar phosphatized material with *Hiatella* occurs in the base of the Lower Greensand at Upware, Potton, and Brickhill, and is preserved in the Sedgwick Museum, Cambridge. Although these specimens are mixed with other phosphatized material ranging from Oxfordian to Aptian in age, they occur with ammonites, a large proportion of which are of Middle Volgian age and they are undoubtedly of the same age. Unphosphatized *Hiatella* occur in the Hartwell Clay of Buckinghamshire and the Swindon Clay of Wiltshire (both of *Pavlovia pallasioides* Zone) and are preserved in the British Museum (Natural History), the Institute of Geological Sciences, and the Sedgwick Museum, Cambridge (e.g. Pl. 96, figs. 15, 16). From an unspecified horizon in the Portland Sand of Hounstout, Dorset (Waddington Collection, untraced), two specimens were figured as '*Arca*' *foetida* sp. nov. by Cox (1929, pl. 1, figs. 2, 3). These specimens are likely to have come from the horizons recorded by Arkell (1935, p. 310), who listed *Parallelodon* (*Beshausenia*) *foetidum* from the White Cementstone and Bed 11 of the Emmit Hill Marls. In the latter horizon Arkell noted that another more elongate species of the genus was also present. *Hiatella* has also been collected recently from borings in the upper part of the Portland Limestone on the Isle of Portland. It is interesting to note that Woodward (1851–1856) recorded modern *Hiatella* actively attacking the Portland Stone breakwater at Plymouth, which perhaps even makes possible the reoccupation of Jurassic borings after some 135 million years.

DESCRIPTION OF BORINGS AND THE *HIATELLA*

In the Basal Spilsby Nodule Bed, *Hiatella* was collected both from within flask-shaped borings and independently of the borings. These two types appear to be morphologically distinct and are therefore described separately, although it is possible to find intermediate forms. As much of the discussion in this paper centres around the occurrence of *Hiatella* in the borings, these structures are described first, followed by details of the shell shape in both the boring and the non-boring habitat.

The borings. The Basal Spilsby nodules contain several types of borings of which the most conspicuous are flask-shaped cavities or their phosphatized infillings, commonly up to 30 mm in length (text-fig. 2a–c). The flask is circular in cross-section (text-fig. 3c) with a maximum diameter of 13 mm. The constricted neck reaches 5 mm diameter and is circular except near the aperture, where it becomes slightly oval and weakly flared (Pl. 96, fig. 23). Oblique sections through the flask may be
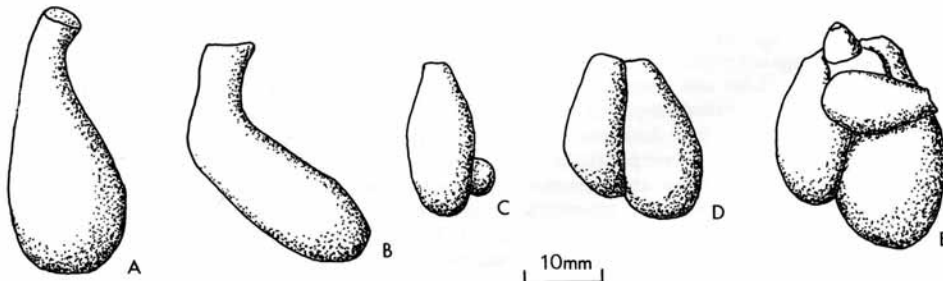
TEXT-FIG. 2. Camera lucida drawings of phosphatized infillings of *Gastrochaenolites* borings in Basal Spilsby Nodule Bed, Nettleton, Lincolnshire, S. R. A. Kelly Collection IGS: A, Zu2229; B, Zu2230; C, Zu2228; D, Zu2231; E, Zu2232.
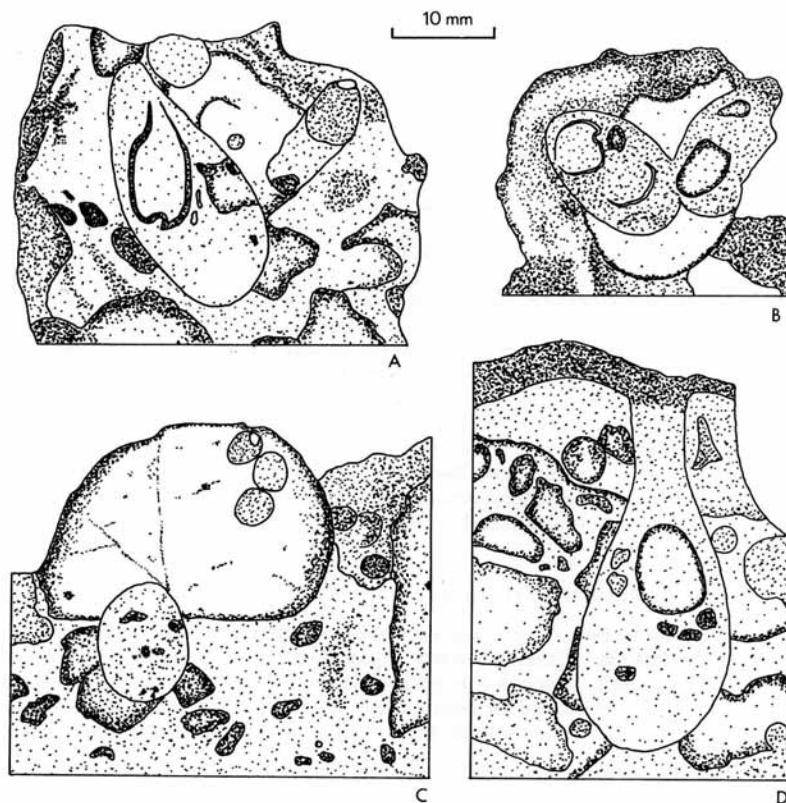
TEXT-FIG. 3. Camera lucida drawings of polished sections through phosphatized compound nodules of the Basal Spilsby Nodule Bed showing *Gastrochaenolites* borings; some (figs. A and B) show *Hiatella* in sites within the borings. Nettleton, Lincolnshire. S. R. A. Kelly Collection, IGS: A, Zu2237; B, Zu2223; C, Zu2238; D, Zu2236.

pear-shaped (text-fig. 3a). A complete longitudinal section through an infilled boring is shown in text-fig. 3d. The borings are preserved as hollows penetrating the already phosphatized nodules. They may penetrate both nodules and phosphatized matrix alike without break, which indicates that the substrate was evenly lithified despite an apparent heterogeneous nature. Each phase of phosphatization can be distinguished by a darkened outer margin. Absence of crushed or distorted borings also shows that the substrate was completely lithified. Borings may not be perfectly straight but may have bent necks (text-fig. 2b). These are presumably due to the original boring organism modifying the direction of boring because of unsuitable substrate or of crowding by other individuals. Interpenetrating borings also occur (text-figs. 2c, e). The first-formed boring appears to be infilled and phosphatized before being cut across by a second boring.

Although the substrate of these borings is normally a phosphatized nodule, one particular example shows a large piece of reptilian bone which has been attacked. The upper surface of the bone (Pl. 96, fig. 23) shows that little erosion has taken place since the original construction of the borings as the openings are still oval. The whole flasks can be seen in Plate 96, fig. 24, together with a specimen of

Hiatella in situ in one of them. The bone must have been buried before abrasion destroyed the oval necks of the borings. Another specimen, not figured, shows a boring penetrating an icthyosaurian vertebra. In contrast, Plate 96, fig. 18 shows part of a phosphatized nodule that has been bored and subsequently abraded so deeply prior to final burial that only rounded bases of the deepest part of the borings remain visible. The borings are normally found penetrating nodules; however, during phases of reworking the nodules may become broken and the lithified boring infillings become loose. Such infillings may be found reworked into the sediment as clasts in the manner described by Radwanski (1977).

These borings correspond closely to the ichnogenus *Gastrochaenolites* Leymerie (1842), originally described from the Calcaire à Spatangues, Neocomian, Aube, France. This name was not included in the *Treatise* (Häntzschel 1975). Leymerie clearly described *Gastrochaenolites* as a boring in rock which was found in association with *Gastrochaena dilatata* Deshayes. It is distinguished from *Teredolites* Leymerie (1842) which penetrated wood and is more evenly tapered along its length. Bromley (1972) placed both *Gastrochaenolites* and *Teredolites* with the more recent ichnotaxon *Trypanites* Magdefrau (1932), which Häntzschel (1975) restricted to straight-sided tunnels of 1–2 mm width. The ichnogenus *Gastrochaenolites* is retained here for the Basal Spilsby Nodule Bed borings until the taxonomy of these ichnogenera is clarified.

Evans (1970) showed that with increasing rock hardness the ratio of the valve length to valve depth decreased for *Penitella*, and the weight of a valve of given size increased. As a consequence, the shape of the boring also changed, becoming shorter and broader with increased hardness. It has not yet been possible to compare in detail the borings containing *Hiatella* from the Portland Stone in southern England, and therefore varied substrates cannot be compared to show whether the hardness of the substrate affected the shape of the boring. There is also the problem of establishing without doubt the original constructor of the boring and if several different bivalves are constructing the borings they may each have distinctive sized and shaped borings.

Hiatella in the borings. Specimens of *Hiatella* found inside *Gastrochaenolites* borings in the Basal Spilsby Nodule Bed range up to 12 mm in length. They are preserved as internal and external moulds in phosphorite. The specimens illustrated on Plate 96 are largely casts made from silicone rubber. The distinctive features of these specimens are: the tendency of the two carinae bounding the dorsal and
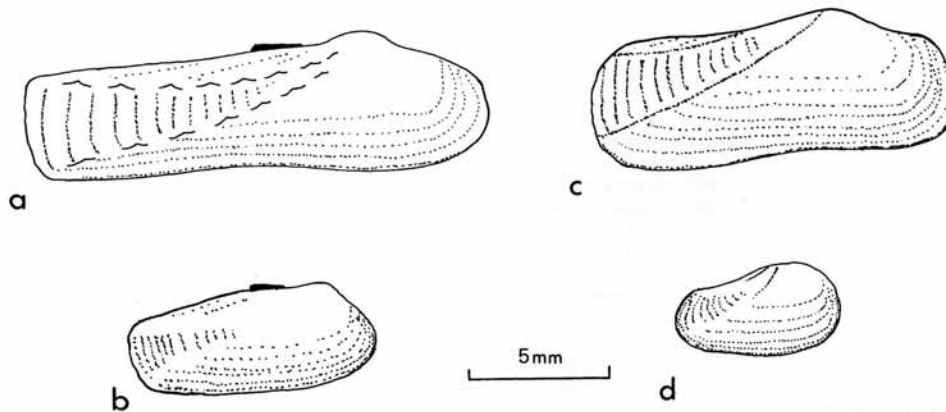
TEXT-FIG. 4. Sketches of Recent and Jurassic *Hiatella* valves to illustrate shell form in boring and non-boring habit. *a, Hiatella (Hiatella) arctica* (Linné), non-boring habitat, Recent (after Hunter 1949); *b, H. (H.) gallicana* (Lamarck), boring habitat, Recent (after Hunter 1949); *c, H. (Pseudosaxicava) foetida* (Cox), non-boring habitat, Middle Volgian; *d, H. (P.) foetida* (Cox), boring habitat, Middle Volgian.
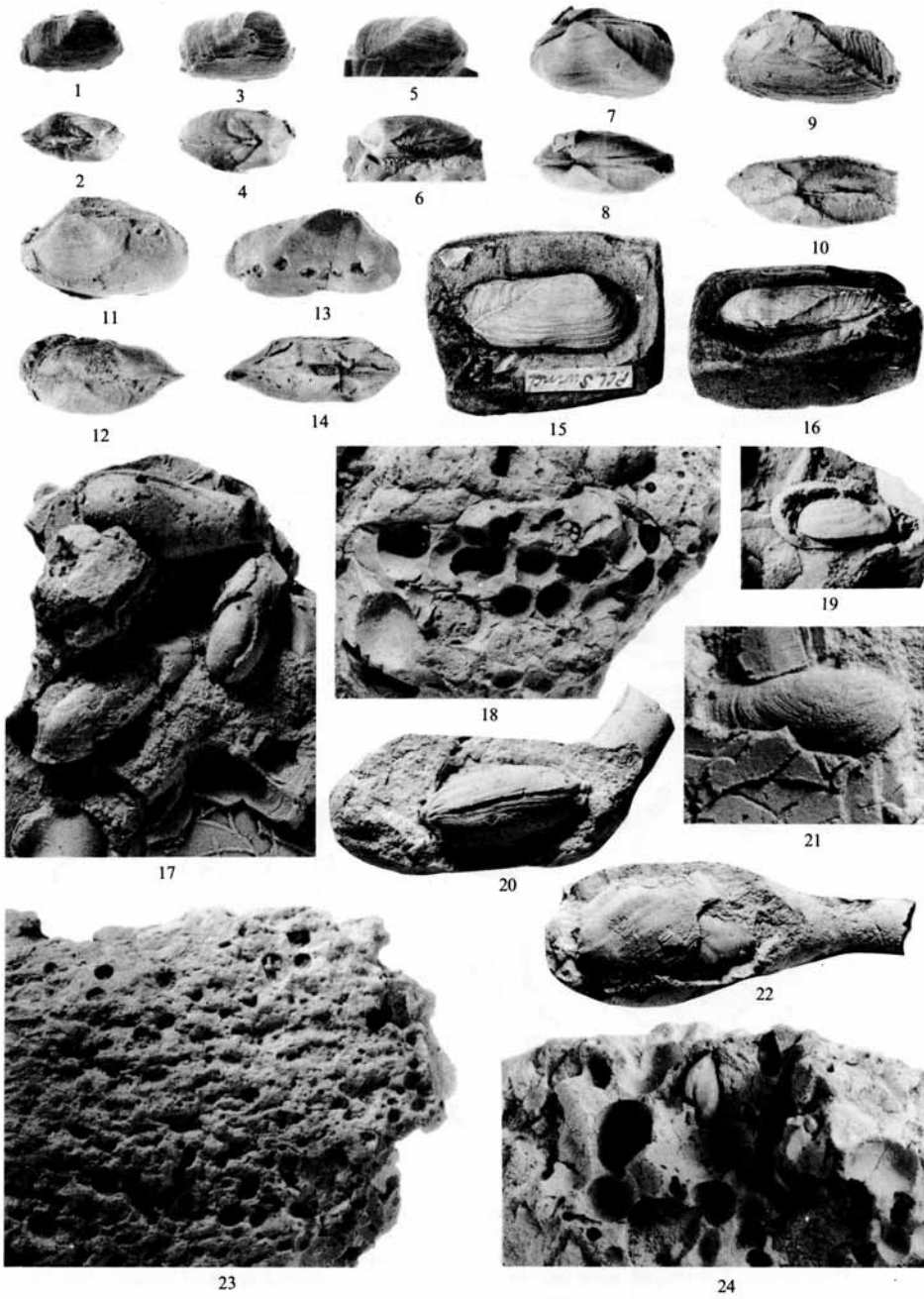
ventral margins of the posterior area to be distinct only close to the umbo and to disappear gradually towards the posterior margin (Pl. 96, figs. 1–6, 19; text-fig. 4d); the posterior area tends to be weakly inflated and the comarginal ornament is normally suppressed; the umbones are usually low; the growth-lines may become crowded towards the commissure and there is little trace of median sulcus on the ventral margin. All these features suggest that the shell may be becoming confined by the shape of the boring in which it lived. Some specimens, however, are clearly too small to have constructed the boring (text-fig. 3a, b; Plate 96, fig. 20) and also two individuals have been found in the same boring (Pl. 96, fig. 22); such specimens lack features which indicate confining by the boring and tend to have fully developed ornament. These features in general indicate that the *Hiatella* is infesting borings which are not of its own making.

Gastrochaena *in borings*. About 150 specimens of *Hiatella* have been found in *Gastrochaenolites* borings in the Basal Spilsby Nodule Bed. However, one rock specimen has two *Gastrochaenolites* borings containing the bivalve *Gastrochaena* itself (Pl. 96, fig. 17) and a single external mould of a right valve of *Gastrochaena* shown as a cast in Plate 96, fig. 21. Recent *Gastrochaena sensu stricto* is well known as a borer into calcareous substrates in temperate and tropical regions. It is distinguished from *Hiatella* by its large anterior pedal gape and its lack of external ornament like carinae and lamellae. The borings associated with the Spilsby *Gastrochaena* fit tightly around the shells and show weak traces of the calcareous extension tubes, which are not actually seen on any borings associated with *Hiatella*. It is not clear whether *Gastrochaena* was a precursor to the *Hiatella* in the borings of the Basal Spilsby Nodule Bed, or whether the two were contemporaneous.

Hiatella *independent of borings*. The best-preserved examples of *Hiatella* found independently of the borings are the aragonitic examples from the Hartwell and Swindon Clays (Pl. 96, figs. 15, 16). Such specimens are normally found as disarticulated valves, while those from the Basal Spilsby Nodule Bed are normally complete internal phosphatized moulds with valves in occlusion (steinkerns) (Pl. 96, figs. 7, 8, 11–14). The independent shells commonly range up to a larger size (30 mm) than those from the borings. Although the upper length limit of 30 mm is identical to the maximum length of the borings, the maximum expected size of a *Hiatella* in a boring would be about 20 mm, because of the constricted neck area. Presumably the destruction of further large *Gastrochaenolites* specimens would provide larger *Hiatella* than the 12 mm recorded above. The shell is more oval in cross-section;


EXPLANATION OF PLATE 96

Figs. 1–14, 19, 20, 22. *Hiatella (Pseudosaxicava) foetida* (Cox). 1, 2, cast of complete individual, IGS Zu2216, 2217, × 1. 3, 4, cast of complete individual, IGS Zu2219, × 1. 5, 6, cast of incomplete individual, IGS Zu2222, × 1. 7, 8, phosphatized steinkern, IGS Zu2241, × 1. 9, 10, cast of complete individual, IGS Zu2218, 2219, 2220, × 1. 11, 12, phosphatized steinkern with cast of some adhering shell, IGS Zu2242, × 1. 13, 14, phosphatized steinkern, IGS Zu2243, × 1. 19, phosphatized internal mould completely fitting within boring, IGS Zu2225, × 1. 20, cast within boring that is too small to have been made by this occupant, IGS Zu2234, 2235, × 1·5. 22, two phosphatized internal moulds of right valves representing two individuals within the same boring; Basal Spilsby Nodule Bed, Middle Volgian, Nettleton, Lincolnshire.

Figs. 15, 16. *H. (P.) foetida* (Cox). Right valve exterior, IGS Y709, Hudleston Collection, × 1; Upper Kimmeridge Clay, *Pavlovia pallasioides* Zone, Middle Volgian, Swindon, Wiltshire.

Figs. 17, 21. *Gastrochaena* sp. 17, individuals with *Gastrochaenolites*-type borings, × 1·5. 21, cast (seen as mould on fig. 17) of left valve, × 2. IGS Zu2224. Basal Spilsby Nodule Bed, Middle Volgian, Nettleton, Lincolnshire.

Figs. 18, 23, 24. *Gastrochaenolites* ichnosp. 18, eroded flask bases, IGS Zu2226, × 1·5. 23, reptilian bone showing oval apertures to flask-shaped borings. 24, same specimen in broken section showing opened flasks and an individual *Hiatella* steinkern *in situ* in one, IGS Zu2227, × 2. Basal Spilsby Nodule Bed, Middle Volgian, Nettleton, Lincolnshire.

PLATE 96

KELLY, Jurassic boring bivalves

the posterior carinae are distinct throughout their length; the posterior area is gently concave; comarginal lamellae are well developed on the posterior area, and the ventral margin is usually gently sulcate, the latter feature giving the byssate shell greater stability in currents (Pl. 96, figs. 9, 10; text-fig. 4c). Unfortunately Oates (1974), in his palaeoecological study of the Hartwell Clay, did not recognize *Hiatella*, although the collections he examined do contain them, but they tend to be confused with species of *Grammatodon*. I believe that in the Hartwell and Swindon clays both the *Hiatella* and *Grammatodon* are byssate nestlers and not shallow infauna as Oates suggested. Both these taxa may show a weak byssal gape.

The non-boring *Hiatella* are believed to have been byssally attached to the exterior of local hard substrates such as shells of ammonites and phosphatized nodules. Uninhibited growth allowed the shells to grow to a greater size than in the borings. The large number of complete internal moulds in the Basal Spilsby Nodule Bed, as opposed to isolated valves, probably reflects rapid burial, with the shells still attached to the substrate. Early diagenetic phosphatization took place within the reduced zone defined by the valves. Subsequent winnowing and destruction of the shell concentrated the internal moulds together with other phosphatized debris. A reconstruction of a Basal Spilsby Nodule infested with boring and non-boring *Hiatella* is shown in text-fig. 5.

10mm
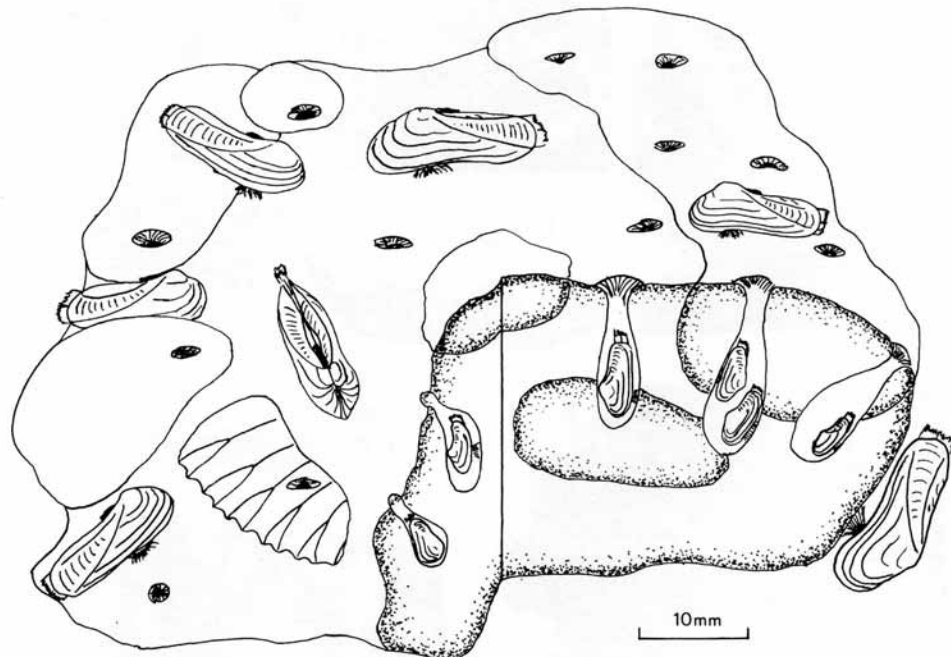
TEXT-FIG. 5. Reconstruction of a Basal Spilsby Sandstone phosphatized nodule, partially cut away to illustrate *Hiatella* (*Pseudosaxicava*) *foetida* (Cox) in its two ecological niches. The smaller, more constricted shelled specimens occupy the borings, while the larger, more fully developed examples are epibyssally attached to the exterior of the nodule. For simplification the abundant and varied associated fauna of bivalves, gastropods, brachiopods, serpulids, etc. are omitted.

DISCUSSION

Recent *Hiatella* are byssally attached to the substrate of their choice, whether living epifaunally on hard substrates or infaunally in borings. The range in shape of the Jurassic shells is very similar to that of the recent British species (discussed by Hunter 1949), and there is little reason to suspect that they lived in different ways.

Hunter (1949) recognized two recent species; the first, *H. gallicana* (Lamarck) (text-fig. 4*b*) is normally found inhabiting borings in calcareous substrates. The shell shows features akin to *Hiatella* from borings in the Basal Spilsby Nodule Bed, in particular the suppression of the umbo, posterior carinae, and lamellae. The species is accepted as a rock borer and is believed to bore with the foot using sand grains and mucus as an abrasive. There is as yet no positive evidence for any chemical secretion being used as in the calcium complexing compound discovered in *Lithophaga* by Jaccarini, Bannister, and Micallef (1968). There is, however, one significant difference between the Jurassic and recent species. The Jurassic species had no posterior gape, while the modern species does. *H. gallicana* may frequently start its byssal life attached in the opening of an annelid boring (Parfitt 1871), which is then enlarged and deepened into the substrate. The second species, *H. arctica* (Linné) (text-fig. 4*a*) is a byssal nestler which is not normally associated with borings, but which may fortuitously occur there. It is commonly found single in association with masses of byssate bivalves like *Mytilus*, although Ockelmann (1958) records it occurring as monotypic clusters in Greenland. This species is similar to the non-boring Jurassic forms described above, but is slightly more elongate and the posterior carinae have more lamellose tuberculate ornament. *H. arctica* and *H. gallicana* are readily distinguished in the larval stage, but the adult morphologies intergrade because of overlap in habitat, and it is not always possible to separate them perfectly on features of the hard-part anatomy. There is therefore little reason to attempt to separate the Volgian ecomorphs into different species.

Bivalve borings in phosphatized hardgrounds. Although bivalves are commonly found associated with calcareous substrates, there appear to be relatively few recorded examples of them penetrating phosphatized hardgrounds. It is clear that the Spilsby nodules were already phosphatized at the time of attack; any doubts that could be raised can be dispelled by the occurrence of the borings into fossil bone, which is a primary phosphate. Carcelles (1944) recorded *Lithophaga* (*Diberus*) penetrating the plates of *Glyptodon* and Boreske, Goldberg, and Cameron (1972) reported the occurrence of Miocene bivalve borings in the bone of *Squalodon* and attributed them to *Parapholas*. They also recorded the occurrence of such borings in mammoth tusks. If these borings in phosphatized substrates are constructed by mechanical processes there are no problems. However, if chemical techniques are to be invoked, further research along the lines of Jaccarini *et al.* (1968) should be investigated.

Environment of deposition of Basal Spilsby Nodule Bed. The Basal Spilsby Nodule Bed formed a hardground not of a continuous type (e.g. type 2 of Goldring and Kazmierczak (1974, p. 957)), but of isolated nodules surrounded by glauconitic silty matrix. The nodules show a complex depositional history and correspond partly to the hiatus concretions of Voigt (1968), whose observations were based on Liassic calcareous concretions. These calcareous concretions were formed by coalescence of concretions of different age. The younger concretions envelope the older, the concretions themselves being of early diagenetic origin. Voigt recognized the following cyclic sequence of events: 1, formation of concretion; 2, washout; 3, corrosion, boring, and encrustation; 4, burial. The Cenomanian phosphatized nodules described by Kennedy and Garrison (1975) correspond more closely to the Spilsby nodules. For discussion of earlier studies on phosphatized horizons of condensation see Brückner (1977). Kennedy and Garrison (1975) propose the following sequence for the formation of nodules that are largely composed of fossil moulds: 1, infilling of shell by sediment; 2, burial; 3, mould cementation (probably by high-magnesian calcite); 4, dissolution of aragonitic shell; 5, disinterment; and 6, phosphatization, boring, and encrusting. The Basal Spilsby Nodules appear to have formed under similar conditions, although it is believed here that phosphatization probably took place at depth in the sediment and not on the surface of the sea floor as Kennedy and Garrison (1975, p. 357) suggest. It is not possible to see deep burrowing bivalves like *Pleuromya* and

Lucina in life position in the Basal Spilsby Nodule Bed, although they are particularly common as heavily darkened phosphatized internal moulds. However, in the Speeton Clay of the Yorkshire coast (Lower Cretaceous), deep burrowers such as *Thracia* and *Pleuromya* are commonly preserved in life position as weakly phosphatized, pink or pale-brown internal moulds with some original shell attached. These have clearly never been exposed on the sea floor; those that have become exposed and occur in the reworked nodule beds are usually blackened on the exterior and may show signs of erosion.
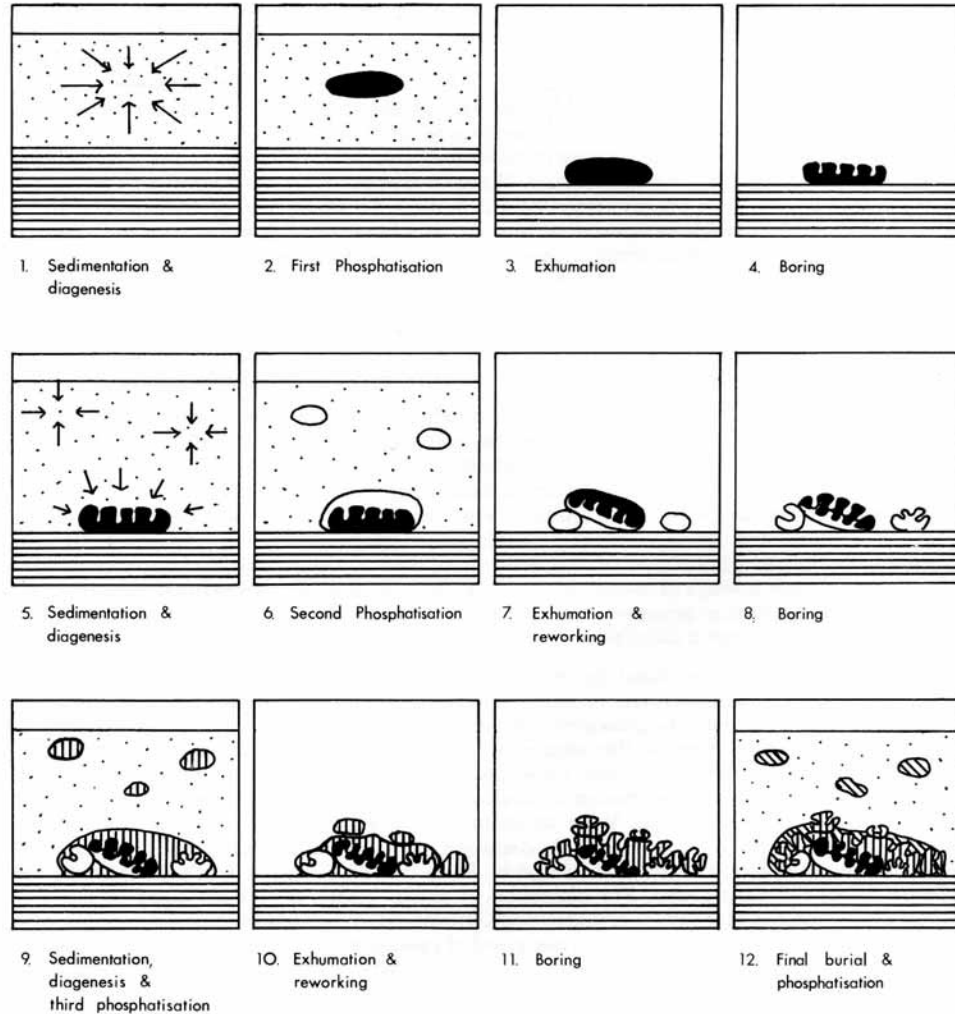
TEXT-FIG. 6. Simplified diagrammatic representation of the sequence of events leading to the formation of the Basal Spilsby Nodule Bed.

The preservation of many fossils in the Basal Spilsby Nodule Bed as phosphatized internal moulds suggests that the confining shell walls have provided a reduced zone within the sediment. The phosphatization occurred within this zone and appears first in deep recesses such as the umbonal infilling in bivalves, and may appear weaker towards the commissure, especially so in forms with commissural gapes. During a phase of winnowing these moulds would have been condensed and concentrated in the manner described by Fürsich (1978, p. 247). Once the nodules were exposed on the sea floor they would have been open to attack by boring bivalves and grazing gastropods, etc., and available for encrustation by ostreids and *Plicatula*. During the next phase of burial, the first-formed concretions would have been bound together by further phosphatization. Repetition of this sequence would have increased the complexity of formation of these hiatus concretions. So far at least three phases of phosphatization have been recognized in the Basal Spilsby Nodule Bed, as illustrated in text-fig. 3*a–d*. All these figures show light-coloured but phosphatized areas with blackened exteriors. These are surrounded by glauconitic sand which in turn is phosphatized. Both these earlier phases of phosphatization are cut across by borings which have then been filled with sediment and phosphatized again. The number of phases of boring and phosphatization are likely to be a conservative estimate, as the largest pieces of the nodule bed are small, with a maximum diameter of 20 cm. The reconstructed series of events leading to the formation of the Basal Spilsby Nodule Bed is shown diagrammatically in text-fig. 6.

In modern sediments phosphate formation has been described by Parker (1975) and Mannheim, Rowe, and Jipa (1975). Parker, working on the Agulas Bank on the south coast of South Africa, concluded that the area of phosphate formation was estuarine and undergoing regression. Phosphatization was replacing lime mud matrix of packestones and wackestones, and sometimes cementing conglomerates of similar reworked sediments. Deeper-water phosphate appeared to be redeposited from shallow areas. Mannheim *et al.*, working on Holocene sediments from the coast of Peru, recognized that the calcareous tests of foraminifera were being replaced by phosphate. The sediments were rich in organic debris, but occurred in an area with a low rate of terrigenous sedimentation which allowed concentration of the phosphate. The depth at which high-concentration phosphate occurred is between the shelf break and 1000 m. But the highest concentration was recorded from a submarine hillock at 144 m.

The Basal Spilsby Nodule Bed is a shelf deposit; although it would be dangerous to suggest an absolute depth, it appears to be a shallower-water deposit than the preceding Kimmeridge Clay, and contains a much more diverse benthic macrofauna. There is no evidence for the environment being estuarine, although it would appear that it occurs in a marine strait that crossed the East Midlands Shelf in Middle Volgian times. To the south-east it was bounded by the Anglo-Brabant Massif, and to the north-west by the Pennine Anticline. Despite penecontemporaneous uplift the land must have had low water runoff and therefore low sedimentation rates in the adjacent sea. Cold currents from the northern connection to Boreal seas could have provided the high organic content and source of phosphate. Uplift has probably been caused by movements of axes such as the Market Weighton structure. The Basal Spilsby Nodule Bed, which is well developed in the north of Lincolnshire, probably represents a winnowed local topographic high on the East Midlands Shelf. Contemporaneous sediments like the glauconitic Hartwell Clay in Buckinghamshire probably represent what the Basal Spilsby sediment would have been like during a phase of deposition. The Hartwell Clay-type sediment was probably originally widespread over most of the East Midlands Shelf and central England, from Swindon to Lincolnshire, at least in early Middle Volgian times. The bulk of it was destroyed during phases of condensation, leaving only the phosphatized nodules.

CONCLUSIONS

Although it is clear that *Hiatella* is largely a squatter, reoccupying vacant *Gastrochaenolites*-type borings in the Basal Spilsby Nodule Bed, it is still not established that the original borings were made by *Hiatella* itself. *Gastrochaena* was responsible at least for some of the borings, but it seems unlikely that these were the ones subsequently occupied by *Hiatella*. Certainly the necks of borings containing

Hiatella do not show traces of a calcareous extension tube, nor do they have figure-of-eight apertures which are both features of *Gastrochaena* borings.

British Middle Volgian *Hiatella* has two distinctive morphological varieties. One occurs in borings where shell features are suppressed due to the enclosure of the boring, which it was possibly unable to modify. A larger, more elongate and fully ornamented form occurs which is not associated with borings and was probably a simple byssate nestler. As both forms intergrade they probably represent the same species.

The Basal Spilsby Nodule Bed represents a highly condensed and phosphatized unit once composed of a Hartwell Clay-type sediment. It probably formed on a topographic high on the East Midlands Shelf from which fine unlithified sediment was winnowed.

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