

ECOLOGICAL SUCCESSION IN INTRAFORMATIONAL HARDGROUND FORMATION

by R. GOLDRING and J. KAŻMIERCZAK

ABSTRACT. A review of discontinuity hardgrounds shows that an ecological succession can be recognized accompanying the gradual increase in lithification. The burrowing, boring, and encrusting biota is divided into five groups: soft to firm substrate burrowers, animals that penetrate firm or cemented substrates, borers restricted to cemented substrates, non-restricted encrusters on firm to cemented substrates, and encrusters restricted to cemented substrates. The type of ecological succession present depends on the lithology, and four types of hardground are recognized reflecting differences in lithification potential: calcarenite, calcirudite, calcilitite with very low clay content, and calcilitite with about 2% clay.

THE principal factor influencing marine organisms in colonizing the substrate is the degree of consolidation, which depends on grain size and shape distribution, and mineralogy, together with external factors such as temperature, turbulence, and salinity. Much is known about the ecology of rocky shorelines and also, though to a lesser extent, of submarine rocky surfaces, submarine canyon walls, and the extensive submarine lithified pavements that have been described from the Persian Gulf and elsewhere (Shinn 1969; Taft *et al.* 1968). The latter type have received particular attention from geologists because they appear to be the modern analogues of fossil intraformational hardgrounds (see Bathurst 1971 for summary). Such hardgrounds represent stratigraphical discontinuities in calcareous sediment where the substrate became lithified before a permanent cover was established. Their recognition is chiefly by the boring and encrusting fauna. In North America the term hardground has only recently been applied to such discontinuities (Halleck 1973). Other geologists have used hardground synonymously with hard substrate, regardless of its stratigraphical and sedimentological context, e.g. Krantz (1972). This is quite valid biologically and it may be useful to distinguish intraformational hardgrounds from other types.

Intraformational hardgrounds must have formed from unlithified sediment. Since benthonic organisms have a limited range of tolerance to degree of consolidation an ecological succession of organisms able to cope with the different stages of surface consolidation is to be expected. That such successions in fossil hardgrounds are found confirms that these discontinuity horizons did pass through various stages of consolidation. By comparison with the tolerance ranges of modern taxa, we can infer the degree of consolidation attained.

Kaźmierczak and Pszczółkowski (1968, 1969) and, independently, Bromley (1968) recognized that a succession of biocoenoses had occurred when hardgrounds could be shown to have passed through earlier softer stages. Fürsich (1971) and Palmer and Fürsich (1974) have described successions from Middle Jurassic hardgrounds.

The many interacting factors which influence substrate colonization, in addition

to the degree of consolidation, means that community successions are likely to be complex. Any discontinuity surface which is being colonized and is undergoing change in degree of consolidation must also be undergoing a sere. Further, interruption of the ecological succession is possible, at any stage of consolidation, by deposition of a permanent sedimentary cover. Recognition of an interrupted sere is difficult. Frequently, lithification appears to have taken place over a period of discontinuous sedimentation and erosion. Kaźmierczak and Pszczółkowski (1968, 1969) recognized that discontinuity surfaces in the Polish Trias and Jurassic must have reached different stages of consolidation before being permanently smothered.

SEDIMENTOLOGICAL ASPECTS

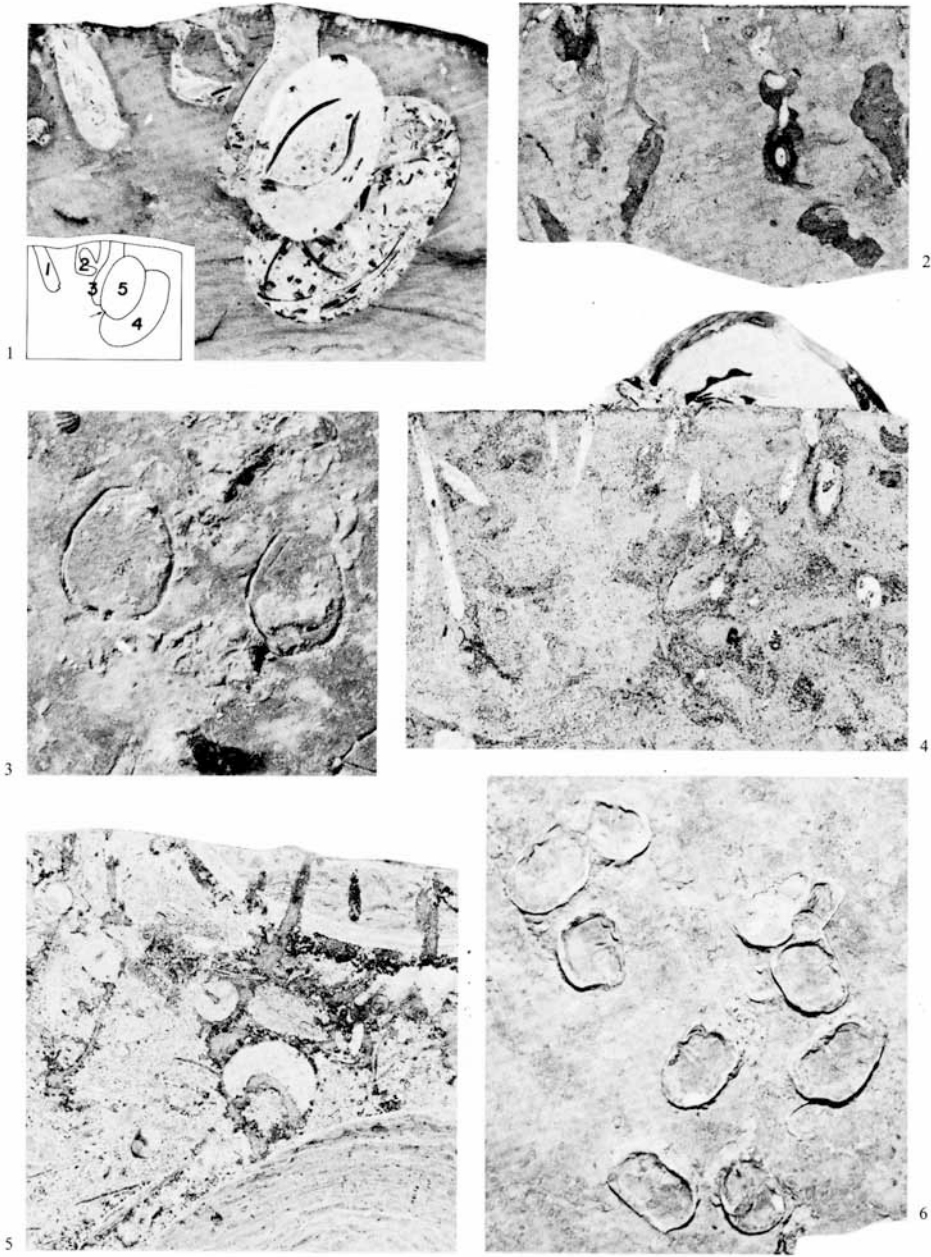
Little work has yet been done on several important sedimentological aspects of hardgrounds, but it is not the purpose of this paper to investigate the processes of submarine consolidation. Whilst corrosion and bioerosion were undoubtedly active on the substrate, the smoothness of many truncated surfaces, especially those on calcilutites, suggests that degradation by corrosion was often dominant. Likely corrosion agents were the coarse sediment seen infilling burrows and borings (Pl. 125, fig. 1) and evidently derived from temporary mobile covers. Occasionally such covers were themselves lithified (Pl. 126, fig. 3; text-fig. 1) as in the re-bored borings of Rose (1970), suggesting that consolidation and lithification proceeded very quickly. In the example figured (Pl. 125, fig. 1) the coarse crypt fill lithified more quickly than the micritic host sediment. Similar examples have been observed in Canadian Ordovician hardgrounds (M. E. Brookfield pers. comm.). Hardgrounds in pelagic facies (Fabricius 1968; Wendt 1970; Jenkyns 1971; Tucker 1973) are often more irregular, probably reflecting the greater role played by corrosion in their formation.

BIOLOGICAL ASPECTS

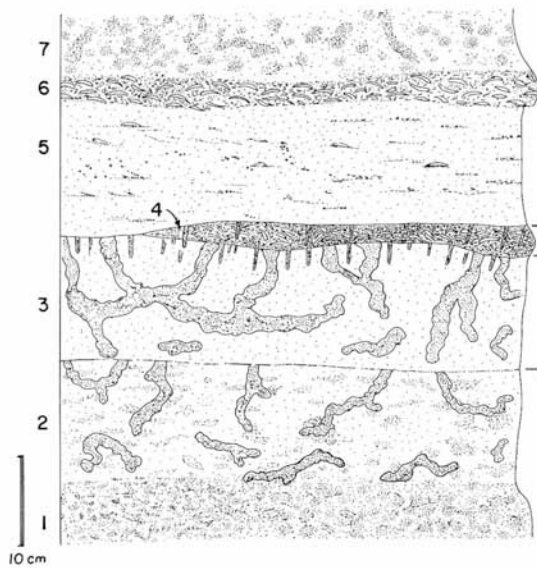
There is relatively little information on the way infaunal and sedentary taxa are affected by different substrates. Ekman (1947), Trueman *et al.* (1966), and Evans (1968) have discussed bivalve penetration into different types of soft and hard

EXPLANATION OF PLATE 125

- Fig. 1. Successive generations of borings in micritic, slightly clayey limestone in Lower Kimmeridgian, top of unit 13 in Kaźmierczak and Pszczółkowski (1968), Bolmin village, south-western Holy Cross Mountains, Poland, $\times 3$. Inset, 1, 2, 3 first generation of borings, deformed by compaction and in 2, possibly with injection of soft sediment; 4, boring of second generation less deformed; 5, boring of third generation also slightly deformed at point indicated. When boring 5 was formed the infilling of 4 was probably fully cemented (shells truncated) although the surrounding sediment was only firm.
- Fig. 2. Successive generations of burrows and borings into low clay calcilutite, Pskov Formation, Upper Devonian, River Velikaya at Vybuty village (Porogi Vybutskiye), Pskov district, U.S.S.R., $\times 1$.
- Figs. 3, 4. Impressions of atrypid valves in low clay calcilutite. Same horizon and locality as fig. 2. 3, bedding surface with impressions of two valves, $\times 0.85$. 4, section normal to bedding cutting atrypid valve and showing early generations of burrows and later *Trypanites* borings, $\times 3$.
- Fig. 5. *Trypanites* borings cutting oolitic calcirudite of Snetogorsk Formation, Upper Devonian, at River Velikaya section near Snetogorsk Monastery, Pskov district, U.S.S.R., $\times 2$.
- Fig. 6. *Irboskites* encrusting shelly low clay calcarenite. Pskov Formation, Upper Devonian, at Pskov quarry (east side of River Velikaya), Pskov district, U.S.S.R., $\times 1$.



GOLDRING and KAŻMIERCZAK, hardground ecology



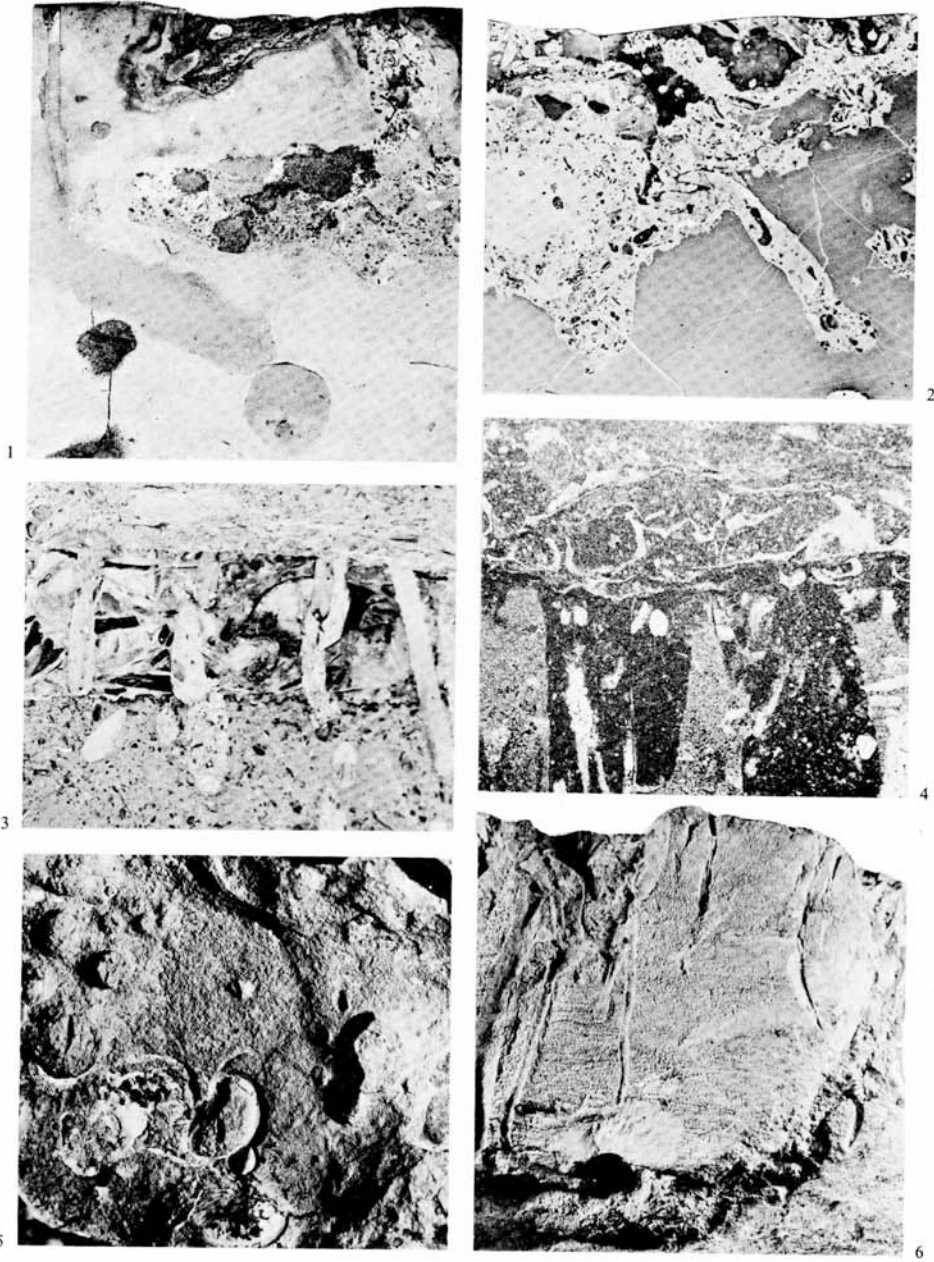
TEXT-FIG. 1. Different types of hardground in the Upper Devonian, Pskov Formation, River Velikaya section at Vybuty village, Pskov district, U.S.S.R. At A a hardground state was not attained. Hardground was attained at B and C.

1, fine calcarenite, slightly mottled. 2, marly, high clay calcilutite with burrows of *Balanoglossites*-type somewhat deformed by compaction. Top of unit truncated and burrows infiltrated by limonite. 3, slightly marly calcilutite (type 3b) with burrows (undeformed) of *Balanoglossites*-type. Top of unit truncated and densely bored by *Trypanites* (Pl. 126, figs. 3, 4). 4, brachiopod-crinoidal calcirudite (type 2) with truncated top bored by *Trypanites*. 5, very fine calcarenite with inclusions of coarser material. 6, brachiopod coquina, calcirudite, without hardground. 7, bioturbated marls.

sediment and Wilson (1952) has reviewed aspects of larval settlement. Rhoads (1970) distinguished between bioturbation structures made in thixotropic sediment from those made in plastic sediment and recognized both types in fossil sediments. In thixotropic sediment the structures have an indistinct outline whereas in plastic sediment the outline is sharp and well-defined. Changes in burrow morphology, reflecting the change from thixotropic to plastic state can be seen in calcilutites from the Devonian of the Pskov area, U.S.S.R. On polished surfaces and peels the successive burrow generations have increasingly sharp outlines and increasingly circular cross-sections (Pl. 125, fig. 2; Pl. 126, fig. 1).

EXPLANATION OF PLATE 126

- Fig. 1. Successive generation of burrows and borings into low clay calcilutite. Same locality and horizon as Plate 125, fig. 2, $\times 1.8$.
- Fig. 2. Burrows, probably of crustacean origin and later *Trypanites* borings (white spots) in pure calcilutite. Lower Kimmeridgian (top of unit 11 in Kaźmierczak and Pszczółkowski 1968, text-fig. 2), locality as for Plate 125, fig. 1, $\times 1.5$.
- Figs. 3, 4. Two hardgrounds, shown diagrammatically in text-fig. 1; levels B, C truncating lithologies 3 and 4 respectively. Locality and horizon given in explanation to text-fig. 3, $\times 5$. 4, part of hardground encrusted by nebecularid-like foraminifera, $\times 20$.
- Fig. 5. *Exogyra* sp. encrusting surface with abraded boring of *Gastrochena* sp. Banded oolitic calcilutite with chert. Lower Kimmeridgian (top of unit 8 in Kaźmierczak and Pszczółkowski 1968, text-fig. 2), Skorkow village, south-western Holy Cross Mountains, Poland, $\times 1$.
- Fig. 6. *Trypanites* borings into banded, fine calcarenite (oolite), from upper surface and from within earlier formed burrows (lower right). Same locality and horizon as fig. 5, $\times 0.8$. (= Kaźmierczak and Pszczółkowski 1968, pl. 4, fig. 3.)



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Schäfer (1962, 1972), Trueman (1968), and others have described how animals move into and through non-lithified sediment. Undulatory movement (Schlängelbewegung) and 'swimming' is probably confined to thixotropic and liquid sediment whilst several other modes of burrowing occur in thixotropic and plastic sediment, e.g. peristaltic movement and the movement of burrowing scaphopods, gastropods, and bivalves. (Animals employing certain types of movement, of course, change the physical state of the sediment during penetration.) The polychaete *Polydora ciliata* is capable of penetrating a wide range of sediments from mud to limestone, boring into the latter chemically. The trace fossil *Trypanites* (generally restricted to a straight tunnel, but more widely interpreted by Bromley 1972) seems to have been made in a similarly wide range of sediment.

Many bivalves that penetrate the substrate mechanically, using the armed shell, are relatively tolerant: burrowing into firm substrates and thereby displacing particles, and boring into cemented substrates by cutting the fabric. Boring and burrowing have been used more or less synonymously by authors but it is useful to define them more narrowly (following Shinn 1969; Bromley 1970, 1974 in press; Perkins 1971).

Organisms that bore or drill have been reviewed by Yonge (1963) and Bromley (1970). Boring may be difficult to prove in fine-grained sediment but deformed crypts indicate a somewhat plastic substrate. Borings may enter from open galleries, older burrows (Pl. 126, fig. 6) and crevice roofs as well as from the upper sedimentary surface. In Plate 125, fig. 1 (at 5) the substrate was partly burrowed and partly bored. Similar situations have been observed where a bivalve, having bored through a cemented crust, continues penetration into firm sediment. The bored margin to the crypt is sharp whilst the burrowed margin is ragged.

A more restricted group of boring organisms only penetrates sediment where the grains are cemented together. This includes boring sponges, algae, fungi, bivalves which bore by chemical means, boring bryozoans, and the barnacle *Lithotrya*. Warne (1970) has pointed out that rocks with only 5% carbonate may be chemically bored.

Some encrusting organisms can also cope with a considerable range of substrate consolidation and cementation. In part this depends not only on the degree of consolidation and cementation but also on the distribution and size of clasts sufficiently attractive for larval settlement. The roughness and erodability of a substrate and the presence of an organic film are also important factors. Today, algae, encrusting serpulids and encrusting bryozoa attach to weed, shells, or to smooth and cemented surfaces. From geological observations (fig. 3) the tabulate coral *Aulopora* and encrusting foraminifera such as *Tolypammina* and *Bdelloidina* also required a cemented surface.

In contrast, animals less specialized in attachment, such as oysters, may only require a small area of hard substrate such as a shell fragment to attach to on an otherwise firm but uncemented substrate. The Devonian brachiopod *Irboskites* (Pl. 125, fig. 6) apparently attached in a manner similar to oysters (Pl. 126, fig. 5), though with most of its ventral valve attached.

Crinoids, and other pelmatozoans known from some hardgrounds were probably able to attach themselves to firm as well as to hard surfaces. In attaching to hard surfaces 'roots' or discs of attachment were usually covered by stereomal secretion (Ehrenberg 1929). Organism encrustations and bivalve crypts are not, in themselves, conclusive evidence for full lithification.

Classifications of organisms in relation to hardgrounds

From the above, five groups of living and fossil organisms may be distinguished:

Group 1. Burrowers in loose to firm substrates.

(a) Animals moving by swimming and undulatory movement into very soft or thixotropic sediment and making impermanent burrows include many polychaetes, oligochaetes, echinoderms, enteropneusts, certain holothurians, and certain arthropods together with nuculid bivalves. Fossil forms include the branching burrow *Balanoglossites* (Ord.-Trias).

(b) Firm substrate burrowers include many burrowing bivalves (e.g. *Mya*, *Ensis*), echinoderms, arthropods, burrowing coelenterates, and burrowing polychaetes producing permanent burrows. Fossil forms include the trace fossils *Thalassinoides*, unlined *Ophiomorpha*, *Arenicolites*, *Diplocraterion*, and *Corophioides*. In incohesive sediment *Ophiomorpha* is lined by pellets.

Group 2. Animals that penetrate firm or cemented substrates (burrowers or borers) include those bivalves using mechanical means (e.g. *Pholas*), and the polychaete *Polydora*. The trace fossil *Trypanites* seems to have been similarly unrestricted.

Group 3. Borers restricted to hard substrates. Bivalves which bore by chemical means (e.g. *Hiatella*) together with boring sponges, algae, fungi, and boring phoronids. Fossil forms include the boring *Entobia* attributed to clionid sponges.

Group 4. Encrusters on firm or cemented substrates (non-restricted encrusters) include some oysters, byssally attached bivalves, and crinoids. Fossil forms include the productid brachiopod *Irboskites*, *Exogyra*, *Apiocrinus*, some edrioasteroids, and other primitive echinoderms.

Group 5. Encrusters restricted to hard substrates. Serpulid polychaetes (e.g. *Spirorbis*), encrusting calcareous algae, bryozoans, cirripedes, foraminifera, thecideidid and craniid brachiopods. Fossil forms include encrusting tabulate corals, encrusting foraminifera such as *Tolypammina*, *Bdelloidina*, encrusting serpulids, and bryozoans.

STRATONOMICAL CRITERIA

There are several stratonomical criteria for determining the degree of consolidation achieved.

1. Burrow-in-burrow structure (Pl. 125, fig. 2; Pl. 126, fig. 1), where successive generations of burrow show progressively sharper margins, less distortion, and increasingly circular cross-sections, indicating that the sediment was undergoing an increase in degree of consolidation.

2. Deformed crypts (Pl. 125, fig. 1) indicate that the organism penetrated firm but not lithified sediment and deformation occurred with subsequent compaction of the sediment.

3. Borings truncating evenly across shells, ooids, oncoids, and older crypt fills (Pl. 126, fig. 3, also Purser 1969, figs. 4, 12) indicate that the matrix was as hard as the shells and other clasts.

4. Discontinuity surfaces evenly truncating clasts, shells, and matrix, likewise indicate full lithification of the surface (Pl. 125, fig. 5).

5. The hardness of the substrate at the time of penetration may be estimated from the form of the shell and borings of pholads (Evans 1968, 1970).

6. The absence from a sedimentary unit of burrows penetrating down from the overlying unit may indicate that an increase in consolidation had occurred before the overlying unit was deposited, if it can be shown that non-penetration was unlikely to have been because of other factors (e.g. depth of penetration required); text-fig. 1, horizon A.

7. Shells and other objects of known hardness introduced above the discontinuity surface in the smothering layer and pressed into the surface (Pl. 125, figs. 3, 4) show that the discontinuity surface was sufficiently plastic to take an impression.

8. Toolmarks scratched on the discontinuity surface provide information, especially if the tool can be identified. A. Pszczółkowski (pers. comm. to J. K.) has observed, on the top of a Lower Kimmeridgian discontinuity surface penetrated by bivalves, prod or impact marks made probably by the small calcareous algae *Marinella*.

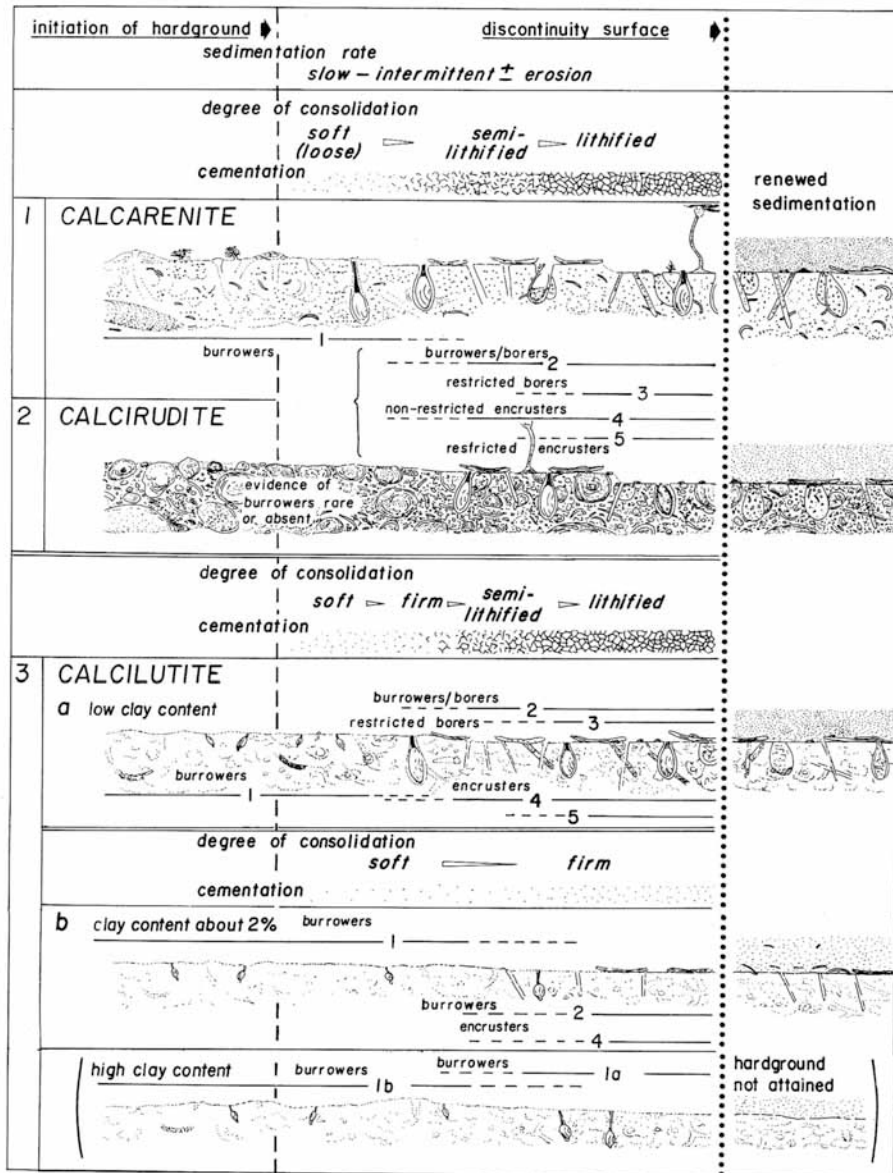
TYPES OF INTRAFORMATIONAL HARDGROUND

Direct measurement of the physical state of a fossil intraformational hardground at the time of penetration or encrustation is not possible. Resort has to be made to biological and sedimentological criteria. However, intraformational hardgrounds are known only from calcareous sediments whose diagenetic history is to a large degree dependent on grain size and sedimentation rate (Shinn 1969) and the proportion of clay minerals. Some indication of the rate of lithification may be shown by the frequency and stratigraphical spacing of hardgrounds. Sugden and McKerrow (1962) recognized that a carbonate to clay ratio of four to one was critical in separating limestone and marly limestone from marl. Subsequently, the work of Bausch (1968) and Zankl (1969) has indicated that where clay exceeds 2% in calcilutites early recrystallization is inhibited and compaction will occur on subsequent loading.

The proportion of clay must have influenced the maximum degree of consolidation attained and consequently the ecological succession. In the literature authors have, unfortunately, only infrequently identified the lithology associated with hardgrounds and whether or not earlier bioturbation preceded the actual hardground colonization. This limits our ability to interpret previously described hardgrounds. Four types of ecological succession can be recognized (text-fig. 2) on palaeontological evidence and, whilst we have not, at this stage, made extensive determinations of the clay content of various hardgrounds we have attempted a correlation with lithological type.

Type 1. The most common type of fossil hardground is formed of calcarenite (oosparite, biosparite) with low clay content (e.g. Voigt 1959, 1970; Purser 1969; Halleck 1973; Palmer and Fürsich 1974), similar to that of modern hardgrounds in the Persian Gulf (Shinn 1969). Prior to lithification the sandy loose sediment was burrowed and on lithification the discontinuity crust was bored and encrusted.

Type 2 (Pl. 125, fig. 5). Less commonly hardgrounds are formed in calcirudites. Burrowing in a coarse substrate leaves little evidence, but where truncation, consolidation, and cementation have led to a lithified surface, this surface may become encrusted and bored.



TEXT-FIG. 2. Schematic diagram to illustrate relationships between hardground formation in different lithologies (sedimentation rate, degree of consolidation, and cementation) and ecological succession.

Type 3. It is clear that hardgrounds of types 1 and 2 cemented relatively quickly compared with calcilititic hardgrounds. Where the proportion of clay minerals was sufficient to prevent early diagenetic recrystallization an actual hardground state could not be attained and the discontinuity surface must have remained no firmer than plastic, akin to discontinuity and bedding surfaces in clastic sediments. Where, however, clay was largely absent calcilitites were able to attain the hardground state.

Type 3a (Pl. 125, figs. 1, 2; Pl. 126, figs. 1, 2). Discontinuity hardgrounds in low clay calcilitites show a similar ecological succession to those in calcarenites. The principal difference is that more extensive burrowing took place during the thixotropic and plastic stages. Several examples of such hardgrounds have been figured in the literature.

1. Upper Devonian, U.S.S.R. (Hecker 1960, pl. 4, fig. 11; also figured in Hecker 1965, pl. 7, fig. 2), with *Aulopora*, *Irboskites*, and *Trypanites*. Although Hecker does not describe the lithology, from our observations of the Pskov Formation with Professor Hecker we consider it to be a calcilitite of this type.

2. Upper Devonian, U.S.A. (Koch and Strimple 1968) with *Aulopora*, *Spirorbis*, edrioasteroids and cystids, *Trypanites*. Although Koch and Strimple considered that lithification had probably taken place subaerially, submarine lithification is more likely. A specimen collected and donated by Dr. C. R. C. Paul (University of Liverpool) has an insoluble residue of about 3%. The mottling in Koch and Strimple's fig. 2 suggests that an ecological succession may be determinable.

3. Upper Jurassic, Poland (Kaźmierczak and Pszczółkowski 1968, fig. 2, tops of horizons 11 and 13 and pl. 3, fig. 4) with serpulids on walls of *Rhizocorallium* burrows near to their apertures.

Type 3b (Pl. 125, figs. 3, 4; text-fig. 1, level B). Where the percentage of clay in calcilitites was intermediate consolidation was somewhat hindered so that the climax fauna included only members of groups 2 and 4 (e.g. *Trypanites*, *Irboskites*, and crinoids). In the example figured (insoluble residue 5%) the critical evidence for the final hardness of the discontinuity surface prior to a permanent cover being established is that *Atrypa* valves, introduced with the covering sediment, were impressed into the discontinuity surface. Earlier stages of burrowing can be recognized as in type 3a. Deformed crypts may also demonstrate that the substrate was still incompletely lithified. Some examples are listed below.

1. Triassic, Poland (Kaźmierczak and Pszczółkowski 1969, pl. 4, fig. 1) with *Trypanites*.

2. Upper Jurassic, Poland (Kaźmierczak and Pszczółkowski 1968, pl. 4, fig. 3).

3. Upper Cretaceous, Europe (Voigt, 1959, p. 134, types 2 and 3). Certain of the hardgrounds described by Bromley (1968) probably fall into this group, e.g. those from the Chalk Rock showing vermiform and sponge borings and occasional bivalve borings but not polyzoan or polychaete encrustations.

Type 3c. In clayey calcilitites (text-fig. 1, level A; text-fig. 2) only two stages of substrate colonization can be recognized and the fauna shows no evidence that hardening and lithification proceeded beyond that required for firm substrate burrowing; no hardground state was attained. The form of the early mottling suggests that the sediment was thixotropic at that stage and the sediment was virtually completely destratified. Increasing firmness of the substrate (probably reflecting the change to a firm stage of consolidation) can be seen by the later, more distinct burrow system. *Thalassinoides* is a common burrow system below many hardgrounds and Kaźmierczak and Pszczółkowski (1969) also recognized the importance of enteropneusts. On no occasion, in their examples, have encrusters or structures attributable to boring organisms been observed, indicating that insufficient time for the state of lithification

required to be attained was not a reason for their absence. It may be significant that bioturbation from overlying units did not penetrate below the discontinuity surface (above—stratonomical criterion 6). Similar surfaces are common in shallow-water clastic facies (e.g. Goldring 1964; Farrow 1966).

1. Middle Triassic, Poland (Kaźmierczak and Pszczółkowski 1969), where most of the discontinuity surfaces are of this type.

2. Upper Jurassic, Poland (Kaźmierczak and Pszczółkowski 1968, text-fig 3).

HIATUS CONCRETIONS, CONCRETION HORIZONS, AND CREVICES

Concretions and concretion horizons exhumed on the sea-floor differ from the hardgrounds discussed in that the surface was generally already lithified before being exposed to organic colonization. Even in those described by Voigt (1968), Hallam (1969), and Kennedy and Klinger (1972) the repeated borings record subsequent burial and re-exhumation rather than diagenetic change whilst the concretions were actually forming the substrate.

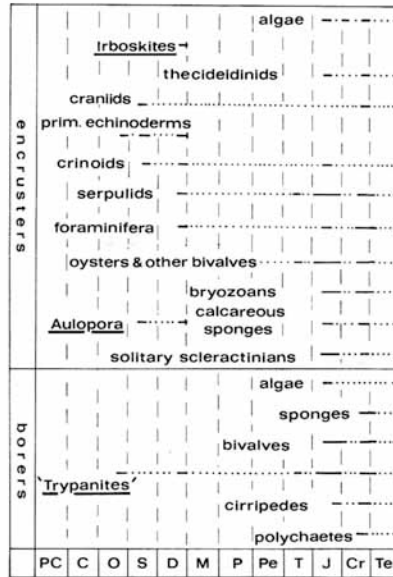
Hardgrounds lithified subaerially at an earlier stage should also be distinguished from intraformational hardgrounds formed below low-water mark since they too will not show biotal succession relative to gradual lithification. This criterion may be added to those given by Rose (1970) for distinguishing between submarine and subaerial discontinuity surfaces.

The formation of crevices on the sea-floor emphasizes how thin the hardground crust may be. Purser (1969) and Palmer and Fürsich (1974) have described crevices below Jurassic hardgrounds and others have been described from pelagic facies (Tucker 1973). The latter were never colonized although they may contain a hydraulically introduced fauna. Palmer and Fürsich describe the ecological distinction between the biota colonizing the upper surface and the crevice roof, analogous to the distribution in modern crevices.

EVOLUTION OF THE HARDGROUND BIOTA

The number of hardgrounds described in the literature is still small and narrowly distributed through the stratigraphic column. An attempt has been made to show the geological range of organisms having colonized hardgrounds (text-fig. 3). Information on encrusting organisms is not easy to assemble and although borers have been reviewed by Boekschoten (1965) and Bromley (1970) it is not always clear whether the borings are into the actual hardground surface or into shells which may or may not be associated with a hardground. The trace fossil assemblage of hardgrounds, like that of any trace fossil facies, essentially reflects certain behavioural patterns and shows little change with time, although the organisms responsible for particular traces certainly changed.

Hecker (1935) has suggested that the productid brachiopod *Irboškites* is paralleled in younger environments by encrusting barnacles. A major feature of Mesozoic and younger shallow-water hardgrounds is encrustation by oysters which also act as a site for other encrusters and borers. Pelagic hardgrounds encrusted by



TEXT-FIG. 3. Distribution of disconformity hard-ground biota. (Borers and encrusters presently known to be associated only with mineralized skeletons and shells are excluded.)

the foraminifera *Tolypammina* and *Bdelloidina* show no change from the Devonian to the Mesozoic.

There is a notable absence of any described intraformational hardgrounds from the Cambrian, and only sparse records from the Carboniferous and Permian. As Hecker (1970) has mentioned, this is an enigma. The most likely explanation, outside the Carboniferous and Permian of the Russian platform where hardgrounds have been searched for, is that they have not yet been fully recognized in these systems. Hardgrounds have not yet been recognized in the Precambrian. This is almost certainly because of the difficulty of recognizing such surfaces in the absence of biological evidence.

The Cretaceous-Tertiary unconformity. It is pertinent to note that the unconformity surface between the Cretaceous (Chalk) and Tertiary in south-east England and Germany was sufficiently soft for arthropods to leave distinctive scratch marks on the burrow walls (see Kennedy 1967). For the Chalk to have remained as soft as this at the unconformity, the surface must have been cut below low-water mark, since it does not seem possible for Chalk to have remained sufficiently soft intertidally.

Acknowledgements. The evidence on which this contribution is based comes to a large extent from the Upper Devonian of the Main Devonian Field in the Pskov area of Russia. The palaeoecology of this area has been documented by Hecker (1935, 1960, 1970) and we were privileged in having been shown several sections by Professor R. F. Hecker. One of us (J. K.) has investigated Mesozoic hardgrounds in Poland (Kaźmierczak and Pszczółkowski 1968, 1969) and Dr. A. Kendall (Department of Mineral Resources, Regina, Canada) demonstrated Middle Jurassic hardgrounds in England to R. G. We have also benefited from discussion with Messrs. F. Fürsich and T. Palmer (Oxford), Dr. R. G. Bromley (Copenhagen), and Dr. G. Warner (Reading).

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