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BORING AND NESTLING ORGANISMS FROM UPPER JURASSIC
CORAL COLONIES FROM NORTHERN POLAND

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The Upper Jurassic coral colonies collected from glacial deposits in northern Poland reveal abundant boring and nestling organisms. The most common borers were bivalves, among which 4 gastrochaenid species (*Gastrochaena* s. s. and *Spengleria*) and 2 lithophagid species are described. Other borers included sipunculid worms and sponges (?). The nestling fauna consists of the bivalves *Hiatella* (probably also a facultative borer), *Plicatula*, and oysters, as well as serpulids. The assemblage of borers is surprisingly similar to Recent assemblages from coral reefs. The excellent preservation of aragonitic bivalve structures allowed for a detailed examination of the internal structure of shells and boreholes. Basing on these features, new diagnostic characters are here proposed and a partial revision is undertaken.

Key words: Boring organisms, bivalves, taxonomy, Upper Jurassic, Poland.

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INTRODUCTION

The coral colonies of Oxfordian-Kimmeridgian age (see Roniewicz 1984) gathered from glacial deposits of northern Poland show the presence of rich and diversified borings. The majority were executed by bivalves but other taxonomic groups were also responsible for some borings. In many cases, the boreholes contain their original inhabitants and/or secondary dwellers.

Boring and nestling bivalves of Jurassic age are known since long ago (see Phillips 1829, Eudes-Deslongchamps 1838, Buvignier 1843, 1852, Loriol 1888, 1892, 1893, Boehm 1893, Borissjak 1906) and numerous species have been described. The majority, however, are poorly, if at all, illustrated and only inadequately described. Often, they are preserved as moulds or impressions only, which do not allow for a detailed examination of the shell. Moreover, they are oversplitted at the species level; Rollier (1914), for example, listed 47 specific names of the Jurassic lithophagid bivalves.

The excellent preservation of the currently investigated material permits, for the first time, to examine the interior of the shell and to classify these organism according to more recent standards.

Carter (1978) and Freneix and Roman (1979) dealt recently with different aspects of gastrochaenid taxonomy, evolution, and ecology. They examined, however, mostly a Recent material. In the present paper I am trying to relate the results of these extremely important papers to an Upper Jurassic material.¹⁾

The investigated material is housed in the Institute of Paleobiology, Polish Academy of Sciences, Warsaw, (ZPAL).

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INVESTIGATED MATERIAL

The original collection of coral colonies consists of 1023 specimens, most of them however are only small fragments. Nearly 26% of specimens show traces of different boring organisms; over 24% were bored by bivalves. Epifauna occurs on only 2% of specimens. In fact, the percentage of originally bored colonies had to be much higher, for the collection contains mostly fragments of larger colonies. More than 100 bivalves (boring and nestling) have been found and make up the basis for the present study.

The collection consists mostly of *Thamnasteria concinna*; much less common is *Actinaraeopsis exilis* Roniewicz, while other species are represented each by a single or few specimens (Roniewicz 1984). The richest collection of corals was gathered in the gravel pit at Ostromice (Wustermitz or Wusterwitz of German authors: Roniewicz 1984). Both the corals and the bivalves are exceptionally well preserved, in form of the original aragonite.

AGE OF BORINGS

As all the material comes from glacial deposits, there is no direct indication of the age of borings in coral colonies. Indirect evidence, however, points to the same age of corals and borings. In some natural cavities,

¹⁾ Note added in proof: The results of the important paper by Kleemann (1983) were not discussed here, as I was not aware that it was already published.

for example, ferruginous sandy to sandy carbonate rock occurs between coral colonies (Roniewicz 1984), and the same type of sediment fills up some of the borings which still contain intact bivalve shells; this indicates syndepositional origin of the borings. Undamaged apertures of bivalve boreholes are preserved only on the original, and not on eroded, coral surfaces. If the corals were drilled only after deposition and redeposition, in a secondary environment, one could expect preservation of the original apertures also on the eroded coral surfaces, which is not the case. This observation also points to the same age of the corals and the borings. The most important evidence supporting such hypothesis, however, comes from the rare cases when a borehole, still containing its primary inhabitant, is completely overgrown by coral (pl. 39: 3) without any traces of disruption in the coral growth. More precisely, these cases indicate that the bivalves bored coral colonies still alive.

BIVALVE BORERS

In the investigated material, the majority of borings were made by bivalves, among which the most common were gastrochaenids (pl. 33: 3, 5—6) accompanied also by the genus *Lithophaga*. For a detailed description of these bivalves see the systematic part of this paper.

NON-BIVALVE BORERS AND BIVALVE SQUATTERS

The most common non-bivalve borings are very small, tubular in shape (one to two millimetres in cross section), very irregular and interconnected in a chainlike pattern, sometimes bifurcated. They penetrate shallow below the surface and have only a single small, rounded opening (pl. 33: 1—4). They are similar to the Cretaceous trace fossil *Entobia* as well as to the Recent excavations of boring sponges. They are preserved on many investigated coral colonies but mainly on somewhat eroded surfaces, which does not allow to recognise the taxonomic position of the animal responsible for their origin.

Other common boreholes are much larger, up to 5 centimetres long and up to 3 mm in diameter. They usually are gently curved and circular in cross section, and may penetrate deep into the coral substrate (pl. 33: 1—2, 5). Similar borings are produced in Recent corals by sipunculid worms (Warme 1975, 1977, MacGeachy and Stearn 1976). Basing on this morphological similarity and the ecological context, I am attributing these Jurassic borings to sipunculid worms.

Many boreholes as well as some natural coral growth cavities in my material were inhabited by secondary dwellers (squatters). The most common among them was the bivalve *Hiatella* (*Pseudosaxicava*) *phaseolus*

(Deslongchamps), which is described in detail in the systematic part. Where this species is found in a gastrochaenid or lithophagid borehole which still contains its primary inhabitant, this suggests that *Hiatella* was a squatter rather than borer. In some cases, however, it occurs alone in a borehole (pl. 37: 5) which differs from the gastrochaenid and lithophagid borings; this suggests that the Upper Jurassic hiatellids already had some boring ability, at least the ability to reshape a primary borehole. Sometimes, three generations of inhabitants of the same borehole existed; a gastrochaenid borehole (with the shell inside) was colonized by *Hiatella*, which was finally succeeded by a young *Lithophaga*.

Other common inhabitants of empty boreholes, as well as growth cavities of coral colonies, were serpulids (probably *Glomerula gordialis* (Schlotheim) (pl. 34: 5—6) and small spinose *Plicatula* sp. (resembling *Plicatula spinosa* Sowerby) (pl. 34: 1—2, 4). A few oysters colonized large natural coral growth cavities and mimicked their shape (pl. 34: 3).

ECOLOGICAL REMARKS

Roniewicz (1984) considered the lithology of the matrix and the growth forms of the corals, and postulated a low energy environment with high influx of detrital material from crystalline rocks as the original setting for these corals. According to her, the bottom was unstable sand or sandy mud with admixture of biogenic detritus where colonies were overturned only during periods of rougher conditions.

In some cases, borings occur on all sides of the investigated colonies; generally, however, the lower and lateral surfaces were infested thus suggesting that most borers attacked overturned and already dead corals. Where a whole borehole, still containing its inhabitant, is entirely overgrown by the coral without any trace of disruption in the structure of the colony, it suggests that a bivalve (*Gastrochaena* (G.) cf. *deshayesea*) infested and lived within the growing portion of the coral.

The assemblage of boring organisms from this Upper Jurassic material is surprisingly similar to the associations known from Recent shallow water reefs (see MacGeachy and Stearn 1976, Bromley 1978, Carter 1978). The Jurassic corals under investigation, however, occurred as isolated colonies forming banks rather than in reef structures (Roniewicz 1984).

BORINGS OF THE UPPER JURASSIC GASTROCHAENIDS

All Recent gastrochaenid species secrete an aragonitic lining onto the inner wall of their borehole, which may extend outside of the boring (Savazzi 1982). This clearly was not the case among the investigated

Upper Jurassic gastrochaenids. Only two of them, *Spengleria recondita* (Phillips) and *Gastrochaena* (*G.*) cf. *moreana* (Buvignier) (pl. 40: 5), show a calcareous lining in the upper part of adult boreholes. None of the other investigated specimens, even larger than those of the above mentioned species, has even a trace of such encrustation. Dissolution of linings can be ruled out as the corals are also aragonitic and still preserved even in the finest details (see Roniewicz 1982, 1984); boreholes with and without lining are present in the same coral colony. Facultative secretion of borehole wall encrustation in the same species seems improbable because boreholes with and without lining differ in shape and their inhabitants clearly differed also in their anatomy (see descriptions). All this suggests that, at the Late Jurassic time, not all the gastrochaenid species acquired the ability to strengthen the borehole by secreting a calcareous lining around the borehole walls.

Recent gastrochaenid bivalves avoid empty spaces in the bored substrate, among boreholes of other bivalves (Carter 1978). This is achieved by the use of special probing tubules which serve a probing function in guiding the boring direction (Carter 1978). In case of the borehole damage, Recent gastrochaenids are able to repair it. None of these abilities seems to have existed among Upper Jurassic gastrochaenid bivalves, as different borehole generations very often cross each other without any traces of repair in my material. I have also not detected traces (small holes) of the activity of probing tubules, which are discernible in Recent material in the anterior part of the borehole wall.

SYSTEMATICS

Family Mytilidae Rafinesque, 1815

Genus *Lithophaga* Röding, 1798

Type species: Mytilus lithophagus Linnaeus, 1780.

Remarks. — Basing on even minor differences in the general outline and external morphology of the shell, numerous Upper Jurassic and Lower Cretaceous species of *Lithophaga* were described (see Deslongchamps 1838, Buvignier 1852, Pictet and Campiche 1867, Borissjak 1906, and others). From the Upper Jurassic of Europe alone, 47 species were described by the beginning of the century (Rollier 1914); though they usually are very poorly described and illustrated (or even not illustrated at all). That was an extremely typological approach; it did not take into consideration the intraspecific variability which is large in the Recent species and caused, for example, by the thickness of the substrate (Kleeman 1977). All this makes an attempt to synonymize Upper Jurassic lithophagids very difficult without a reexamination of the previously described material and also without a detailed study of the intraspecific variability among these bivalves. In the present paper, therefore, only some particularly well illustrated and described species and/or those for which the author investigated the holotype or syntypes, are included into the synonymy.

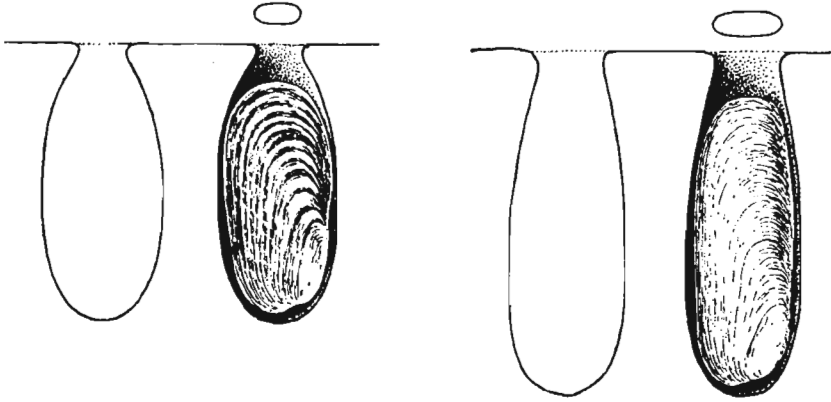


Fig. 1. Borehole of *Lithophaga lycetti* (Whiteaves) in longitudinal section and two morphologically different specimens inside their boreholes.

Lithophaga lycetti (Whiteaves, 1861)
(pl. 35: 1–5; pl. 36: 2–3; figs. 1–3)

1861. *Modiola Lycetti* Whiteaves: 146, pl. 9B: 5.

1929. *Lithophaga lycetti* (Whiteaves); Arkell: 60–61, pl. 2: 10.

Material. — 15 shells or valves.

Description. — Shell small and thin, smooth except for numerous growth lines which are very well pronounced (pl. 35: 1), often in a steplike fashion. Umbones strong and subterminal (pl. 36: 3c, f). General outline subrectangular, anterior rounded, posterior margin quadrangular and always thickened (pl. 35: 4; pl. 36: 3c). In the middle of the shell, starting from the umbones, well marked depression is running toward ventral margin and a little posteriorly. Thin calcareous encrustations, similar to those known from the Recent species of *Lithophaga* (see Wilson 1979, Kleeman 1977), were observed on some specimens.

Hinge margin curved, with delicate vertical striae, edentulous. Anterior adductor scar small and elongated, placed very close to the margin; posterior adductor scar

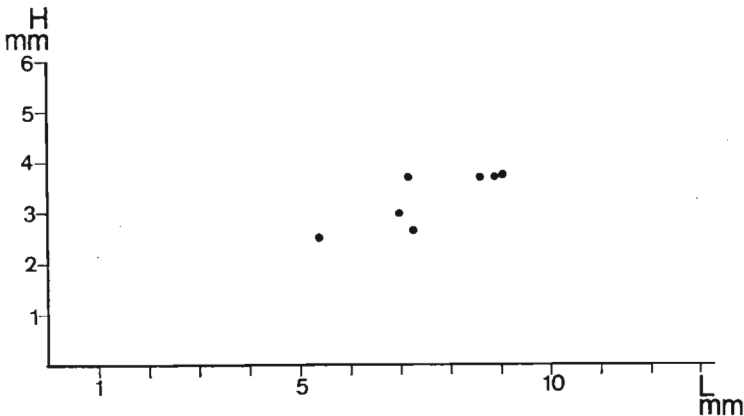


Fig. 2. Height/length ratio in *Lithophaga lycetti* (Whiteaves) shells.

much larger, oval in shape, with small pointed elongation in the upper part (fig. 3). Ligament nymph curved, extending from 1/3 to 1/2 of the length of the shell from umbo toward posterior.

Boring is simple with straight walls and rounded end, subcircular in cross section, narrowing near the opening. Opening is elongated and a little dumb-bell

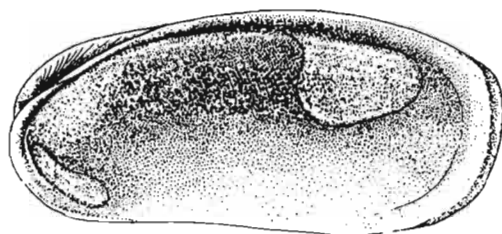


Fig. 3. Internal view of *Lithophaga lycetti* (Whiteaves) shell showing the shape and disposition of adductor scars and pallial line.

in shape. No lining was observed. Depth of the boring is only a little greater than the shell length.

Remarks.—My specimens differ a little from the specimen illustrated by Arkell (1929) but they closely resemble the one illustrated by Whiteaves (1861). Young specimens are similar to *L. fabella* (as illustrated by Eudes-Deslongchamps 1838), the latter, however, being more modioliform in shape.

Occurrence.—Upper Jurassic of Great Britain and Poland.

Lithophaga inclusa (Phillips, 1829)

(pl. 30: 1; fig. 4)

1829. *Modiola inclusa* Phillips: pl. 3: 19.

1838. *Modiola inclusa* Phillips; Eudes-Deslongchamps: 227—228, pl. 9: 39—40.

1852. *Modiola subcylindrica* Buvignier: 22, pl. 17: 20—21.

1852. *Modiola gradata* Buvignier: 22, pl. 17: 24—25.

1866. *Lithodomus amygdaloides* (Desh.), d'Orbigny; Pictet and Campiche: 518—519, pl. 139: 1—2.

1893. *Lithodomus gradatus* Buvignier; Loriol: 134, pl. 9: 9.

1893. *Lithodomus blauenesis* Loriol: 294—295, pl. 32: 1.

1906. *Lithodomus donetzianus* Borissjak: 16—17, pl. 2: 12—15.

1929. *Lithophaga inclusa* (Phillips); Arkell: 59, pl. 2: 13.

Material.—4 valves.

Description.—Shell oval-elliptic in outline, smooth except for growth lines. Umbones subterminal. Anterior rounded and narrower than posterior which is also very regularly rounded. The maximum height of the shell is at 1/3 of the length but its position may be subject to variation. Ventral margin straight. Hinge line edentulous, ligament nymph narrow and long, approximately 1/3 or a little more of the length of the shell. Anterior muscle scar elongated, somewhat triangular, posterior muscle scar in the form of an elongated triangle and relatively small (fig. 4). Boring is simple and straight, round in cross section, only a little deeper (no more than 1/3) than the length of the shell. Opening, when preserved uneroded, elongated and a little dumb-bell in shape.

Remarks.— Except for their smaller size, my specimens are identical with those illustrated and described by Arkell (1929). Comparative investigations of Borissjak's (1906) specimens leave no doubts about their conspecificity with the species *Lithophaga inclusa* (Phillips).

My specimens are more or less similar to different specimens illustrated by Buvignier (1852) under the generic name of *Modiola* and various specific names. The

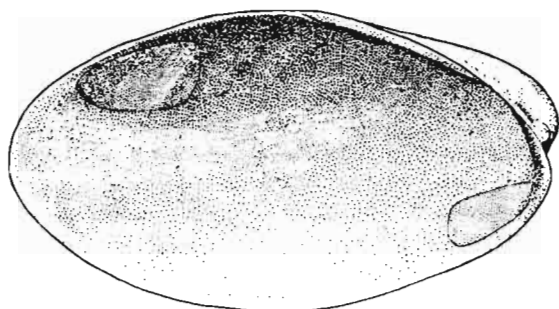


Fig. 4. Internal view of *Lithophaga inclusa* (Phillips) shell showing the shape and disposition of adductor scars and edentulous hinge margin.

range of variability in my specimens equal two of Buvignier's specimens that were considered different species; others not included in this synonymy need further study of their taxonomic position. Other species which are closely related to *Lithophaga inclusa* (Phillips) are: a species described from the Bathonian by Morris and Lycett (1853) as *L. inclusa*, *L. cf. inclusa* illustrated by Hölder (1972), and *L. bathonicus* (Rollier 1914).

Generally, this species shows a wide variability in elongation and umbone development. However, estimation of the real variability range needs further reexamination of the previously described material.

It is worth mentioning that my material comes from colonies of *Thamnasteria concinna*, the same ecological preferences as the one noted by Arkell (1929).

Occurrence.— Upper Jurassic of Great Britain, France, European part of USSR and Poland, Lower Cretaceous of Switzerland.

Family Hiatellidae Gray, 1824

Genus *Hiatella* Bosc, 1801

Type species: *Mya arctica* Linnaeus, 1767.

Hiatella (*Pseudosaxicava*) *phaseolus* (Deslongchamps, 1838)

(pl. 37: 1—4; figs. 5—6)

1838. *Saxicava phaseolus* Eudes-Deslongchamps: 227, pl. 9: 25—26, 33—34.

1838. *Saxicava dispar* Eudes-Deslongchamps: 227, pl. 9: 27—30.

1929. "*Arca*" *foetida* Cox: 140—141, pl. 1: 2—3.

1952. *Pseudosaxicava Bernardii* Chavan: 119—120, pl. 4: 69—71.

1972. cf. *Hiatella* (*Pseudosaxicava*) sp.; Hölder: 201—203, Abb. 2.

1980. *Hiatella* (*Pseudosaxicava*) *foetida* (Cox); Kelly: 773—774, pl. 96: 1—16, 19—20.

1985. *Hiatella* (*Pseudosaxicava*) *arcadiformis* (Keeping); Kelly: 172, fig. 1.

Material. — 13 shells or valves.

Emended diagnosis. — Shell subrectangular with one prominent ridge running posteroventrally from the beak and the second one weaker and shorter and running from the beak to the dorsal margin. Ligament nymph well pronounced but short. Hinge line straight, edentulous.

Description. — Shell subrectangular to trapezoidal in shape, often very irregular and inequivalve. In most cases, very prominent ridge runs from the beak toward the posteroventral edge; at younger stages it bears small spine-like projections. This ridge may be very weak or completely disappear at later stages. The other ridge is similar but smaller and quickly disappearing, runs from the beak very close and almost parallel to the dorsal margin of the shell. Shell surface is smooth except for very well pronounced and irregular growth lines. Wide and shallow depression runs from the beak toward the ventral margin and a little posteriorly. On the

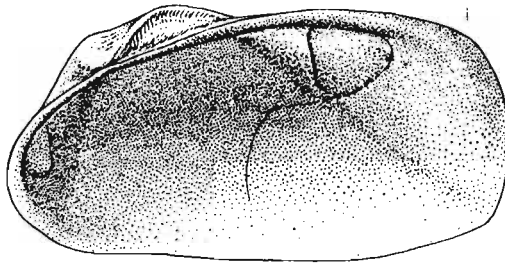


Fig. 5. Internal view of *Hiatella (Pseudosaxicava) phaseolus* (Deslongchamps) shell showing the shape and disposition of adductor scars and pallial line with sinus; hinge margin edentulous.

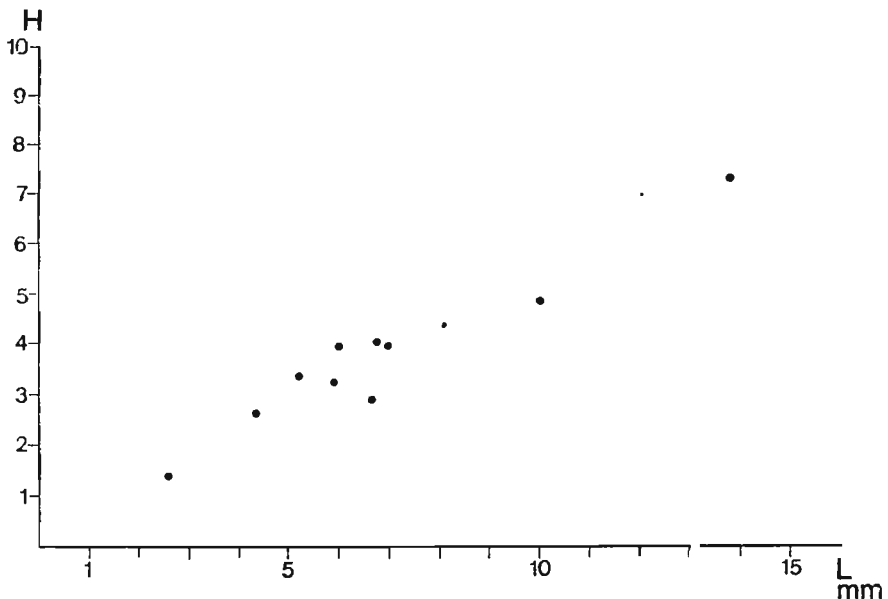


Fig. 6. Height/length ratio in *Hiatella (Pseudosaxicava) phaseolus* (Deslongchamps) shells.

younger portions of the shell surface, small granules (?periostracal spikes) are present; in some larger specimens they occur also in the above mentioned depression.

Hinge line is more or less parallel to the longer axis of the shell. No teeth have been observed. Ligament nymphs are short (about $1/5$ — $1/6$ of the length of the shell) but rather strong. Muscle scars are well developed, the posterior one being much larger than the anterior one, triangular to oval in shape (fig. 5). A part of the pallial line was observed, with some indication of a shallow sinus.

Burrow is simple, round in cross section, only a little deeper than the length of the shell, slightly narrowing posteriorly and widening a little at the opening. Quite often, however, this species was found also in gastrochaenid borings, sometimes even with the shell of *Gastrochaena* in place.

Remarks.—The investigated material shows great variability in shell outline and in development of the ridges running from the beak; the same range of variability is known in Recent species of the genus *Hiatella*, especially among boring and/or nestling forms (see Hunter 1949). In this light, the differences among the forms included into the synonymy reflect in my opinion only intraspecific variability. As the original description given by Deslongchamps (1838) is vague, the emendation of diagnosis is presented.

Occurrence.—Middle Jurassic of Germany, Upper Jurassic of France, Great Britain and Poland.

Family Gastrochaenidae Gray, 1840

Remarks.—Recent gastrochaenid bivalves are specialized boring forms with very few morphological features, except for the general outline, which could make up the basis for classification. The most recent approach to the problem is by Freneix and Roman (1979) who propose to divide Gastrochaenidae into genera and subgenera according to the hinge line development, the shape of pallial line, and the mode of life. Distinction between species within a single genus is largely based on differences in the general shape of the shell.

In the case of fossil gastrochaenids, especially Mesozoic ones, no information about internal characters of the shell is available. As a result, the current classification has been developed on the basis of the shell outline, and sometimes also the shape of the borehole which is correlated with the siphon development (see Carter 1978). If one tries to follow the traditional approach to species-level classification in the investigated Upper Jurassic gastrochaenids (*Spengleria* excluding), it is possible to discriminate between five different "species". They show differences in the height to length ratio, the degree of the anterior reduction (see fig. 8), the shape of the posterior, etc. Quite often, however, these features change at random and no consistent groupings could be formed (see fig. 12). It appears more reasonable to postulate a smaller number of species with greater intraspecific variability. Recent gastrochaenids show, in fact, a substantial variation in the shell height to length ratio (Carter 1978). My approach to species-level classification is to use a combination of such features as the pallial line development (characterizing siphon development), muscle scar shape and disposition, characters of the borehole (shape of the living chamber, siphonal part development, presence of a lining on the wall of the borehole). On the basis of these features, combined with the external morphology of the shell, I have been able to distinguish in the investigated material 3 species, each with considerable morphological variability. This approach, however, has one inconvenience. It is difficult to compare my material with those described and illustrated previously, which were subdivided in an extremely typological way and without any relation to the internal features of the shell and/or borehole characteristics.

Genus *Spengleria* Tyron, 1862
(synonym *Gastrochaenopsis* Chavan, 1952)

Type species: Gastrochaena mytiloides Stoliczka, 1872.

Spengleria recondita (Phillips, 1829)
(pl. 38: 1—2; figs. 7—9)

1829. *Pholas recondita* Phillips: pl. 3. 19.
1838. *Fistulana unicostata* Eudes-Deslongchamps: 226, pl. 9: 23—24, 31—32.
1843. *Gastrochaena corallensis* Buvignier: 227, pl. 3: 4.
1852. *Gastrochaena corallensis* Buvignier: 7, pl. 6: 1—6.
1864. *Gastrochaena arcaeformis* Pictet and Campiche: 10—11, pl. 99: 3.
1933. *Gastrochaena recondita* (Phillips); Arkell: 313—314, figs. 1—4.
1952. *Gastrochaena* (*Gastrochaenopsis*) (nov. subg.) *unicostata* Deslongchamps; Chavan: 120—121, text-fig. 81.

Material. — 12 shells or valves.

Emended diagnosis. — Gastrochaenid with umbones situated at 1/4—1/5 of the length of the shell, and with distinct elevated posterior area bearing vertical lamellae.

Description. — Shell elongated with well pronounced prosogyrous umbones situated at 1/4 to 1/5 of the length of the shell from the posterior. Anterior end narrow, posterior end truncated. The elevated area, well separated from the rest of the shell, runs from the umbones toward the posterior end. It is delimited on both sides by a small furrow followed by a sharp bend of the surface of the shell. In the posterodorsal part, wing-like projections are developed. The surface of the shell is covered with very well pronounced growth ridges; they change direction at the shell bend and thus form also the sculpture on the elevated posterior area. On some well preserved specimens, in their younger parts, this sculpture has even the form of thin vertical lamellae. On younger shells (as well as at the younger stages of adult shells), tiny spikes are observed in the anterior and middle part. They are absent from the elevated posterior area. In adult shells, erosion of growth ridges is

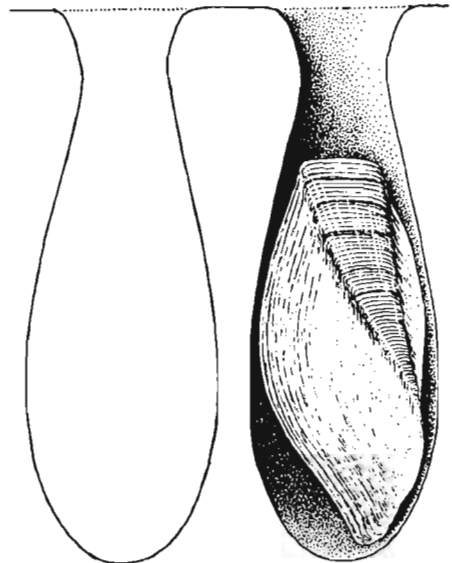


Fig. 7. Borehole of *Spengleria recondita* (Phillips) in longitudinal section and the shell inside of the borehole; calcareous lining not marked.

visible in the median area running from umbones toward ventral margin. Hinge margin edentulous, except for small irregular callosity or plate (occurring only in adult shells), extending downward and situated posteriorly from the umbones. Ligament nymph is short (1/5 of the shell length) but very strong and wide. Anterior adductor muscle scar triangular (fig. 8); small oval scar of the anterior pedal muscle occurs above it. Posterior adductor scar large, twice the size of anterior adductor, somewhat triangular in shape. Pallial musculature well developed, forming a continuous pallial line (fig. 8).

Boring of this species is circular in cross-section, flask-shaped and relatively shallow, about 1/3 deeper than the length of the shell itself (fig. 7). The opening of the boring is always somewhat eroded in my material, but it seems that it was dumb-bell in shape, with separate canals for each siphon. These canals were a little diverging but very short and interconnected. In the case of adult shells, the upper portion of the boring is lined with calcareous material, similar as in the borings of Recent gastrochaenid species.

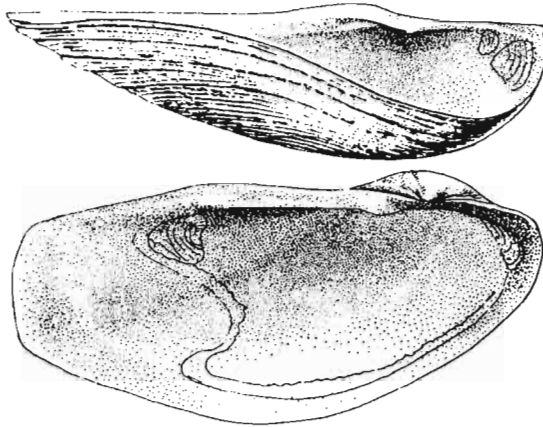


Fig. 8. Internal view of the *Spengleria recondita* (Phillips) shell (in two different views) to show muscle scar shape and disposition; pallial line with shallow sinus.

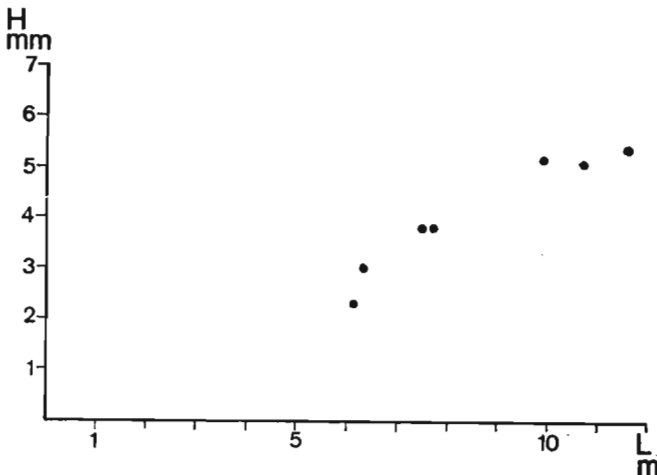


Fig. 9. Height/length ratio in *Spengleria recondita* (Phillips) shells.

Remarks.—There are several fossil species described from the Upper Jurassic and Lower Cretaceous of Europe which are synonymized here, as they show no substantial differences. Judging from the illustration, the most distinct appears *Gastrochaena* (*Gastrochaenopsis*) *unicostata* (Deslongchamps) in Chavan (1952). Actually, the difference is in the structural separation of two carinae in the posterior from the rest of the shell. However, such a feature does not exist on the holotype as illustrated by Deslongchamps (1838); therefore, I regard it only as a convention of drawing which is rather schematic. In other respects, the specimen described by Chavan (1952) is identical with my material.

Recent *Spengleria* has completely separated siphons (Soliman 1973, Carter 1978). Also Buvignier (1852) indicates on his illustrations completely separated and diverging siphons in *Spengleria recondita*. In the investigated material, the degree of siphon separation is lesser. This may be merely an artifact, however, caused by erosion of the most posterior (siphonal) part of the borehole, as it is indicated by the very short siphonal part of the boring preserved. Since Phillips (1829) gave no description at all and Arkell (1933) described only poorly preserved specimens, the emendation of the diagnosis was necessary.

Occurrence.—Upper Jurassic of Great Britain, France and Poland, Lower Cretaceous of Switzerland.

Genus *Gastrochaena* Spengler, 1783

Type species: Gastrochaena cuneiformis Spengler, 1783.

Subgenus *Gastrochaena* s. s.

Remarks.—Carter (1978) included his Cretaceous gastrochaenid species to the subgenus *Rocellaria*. According to the more recent paper by Freneix and Roman (1979), all Mesozoic gastrochaenids should be included into *Gastrochaena* s. s., as they have no myophoral plates. This approach is adopted also in the present paper.

Gastrochaena (*G.*) cf. *deshayesea* Buvignier, 1852 (pl. 39: 1–3; pl. 40: 1, 3; figs. 10–12)

cf. 1852. *Gastrochaena deshayesea* Buvignier: 7, pl. 6: 7–12.

Material.—25 shells or valves.

Description.—Shell relatively large, up to 21 mm in size. Posterior rounded or subsquare; pedal gape limited to the very anterior part of the shell and extending about 1/3 of the whole length. Umbones prosogyrous, placed very close to the anterior margin. Shell usually more or less constant in height over the whole length. Exterior ornamented only with comarginal growth ridges, in the posterior irregularly developed. In the posterodorsal area, numerous calcareous granules on the surface of the shell occur in the younger portion. Ligament nymph well developed and extending about 1/2 to 1/3 of the whole shell length. In smaller specimens, hinge margin edentulous; in older ones, irregularly developed callosity in the right valve and the corresponding concavity in the left valve are present. Pallial line with round and relatively shallow sinus. Anterior adductor scar much larger than the posterior one, somewhat triangular, placed close to the dorsal margin (fig. 11).

The borehole is elongated, with no distinct division between the shell chamber and siphonal part which is relatively long (fig. 10). No wall lining was observed

even in the largest specimen. Siphonal part shows two distinct ridges (in adult individuals only) indicating a certain degree of siphon separation. Borehole aperture is rounded eightlike.

Remarks.—My specimens very closely resemble *Gastrochaena deshayesea* Buvignier in their general shape and the borehole. However, some diagnostic features as used in this paper are not visible on the illustrations by Buvignier; hence one can not be sure of their conspecificity. *Gastrochaena zitteli* (Boehm, 1883) and *G. valfinensis* (Loriol, 1888) also are close in morphology, but they are more elongated and intraspecific variability can not be excluded. The species under discussion differs from *G. (G.) cf. moreana* Buvignier chiefly in adductor scar shape and in the shape of the borehole which has no wall lining.

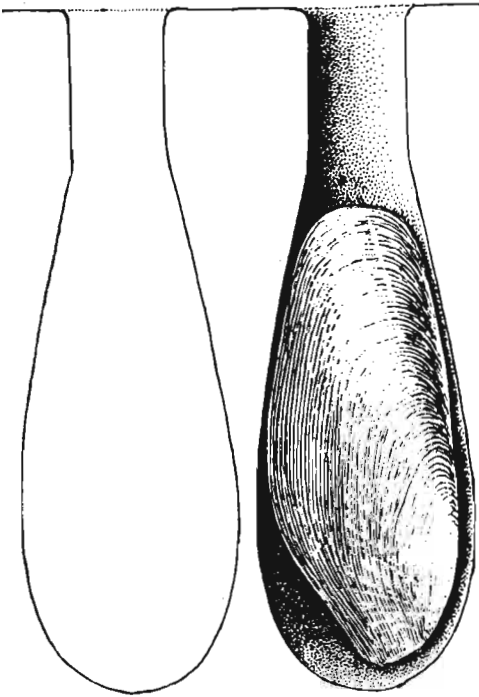


Fig. 10. Borehole of *Gastrochaena (G.) cf. deshayesea* Buvignier in a longitudinal section and shell inside the borehole.

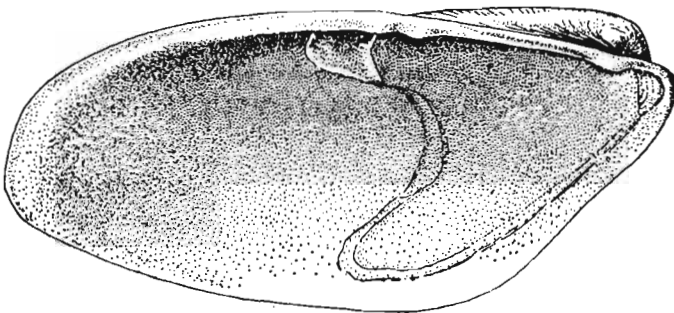


Fig. 11. Internal view of the *Gastrochaena (G.) cf. deshayesea* Buvignier shell showing the shape and disposition of adductor scars and pallial line with sinus; note small and high placed posterior adductor scar; on the hinge margin small irregularities visible (teeth?).

Gastrochaena (G.) cf. *moreana* Buvignier, 1852
(pl. 40: 4—5; figs. 12—14)

cf. 1852. *Gastrochaena moreana* Buvignier: 7, pl. 6: 13—18.

non 1934. *Gastrochaena moreana* Buvignier; Arkell: 314, pl. 43: 5—6.

cf. 1978. *Gastrochaena moreana* Buvignier; Carter: 60, figs. 54—56.

Material. — 10 shells or valves.

Description. — Shell relatively small (up to 12.2 mm in length and 6.5 mm in height) and short, narrowing posteriorly from the end of the pedal gape. Posterior end rounded. Exterior ornament limited to comarginal growth ridges. In the younger portion of the shell, very subdued furrow occurs, running from the umbo in the posteroventral direction. Shell prosogyrous, with the umbo placed close to the anterior margin. Ligament nymphs well developed and extending about 1/4 of the shell length from the umbo toward the posterior. Hinge margin edentulous. Pallial line with deep and probably acute sinus (fig. 14). Anterior adductor scar small and ovals triangular in shape, placed very near the margin. Posterior adductor scar relatively large, oval in shape, placed low (i.e. far from the dorsal margin) and relatively near the posterior part of the shell. Above this large scar, a very small muscle scar, triangular in shape and placed very near the margin occurs; this is probably the pedal retractor scar.

The borehole is short, with distinct shell and siphonal parts (fig. 13). The upper part of the shell chamber and the whole siphonal portion are covered with calcareous material (in adult specimens), as in the Recent gastrochaenid boreholes. Siphonal part short, with two ridges which partly separated the inhalant and exhalant siphonal tubes. Borehole aperture is eightlike.

Remarks. — My specimens are close in shape to *Gastrochaena moreana* as illustrated by Buvignier (1852); also the shape of the boring is similar. Since no information about the internal structures of the shell, the borehole aperture, and the lining is available, it cannot be proved that my material is conspecific with that of Buvignier. The specimens described and illustrated under the name *G. moreana* by Arkell (1934: pl. 43: 5—6) are more similar to *G. (G.) cf. deshayesea* Buvignier, and, according to the criteria applied in the present paper (the shape of the borehole with a long siphonal part), can not be included into the synonymy. Very similar morphologically is the shell described as *G. moreana* Buvignier by Carter (1978). The borehole of this specimen is similar in shape, with a short siphonal part and a lining of the borehole wall in the upper part.

Gastrochaena (G.) sp.
(pl. 40: 2; figs. 12, 15—16)

Material. — One right valve.

Description. — Shell relatively large, 12,2 mm long and 7.5 mm high; pedal gape limited to the anterior part of the shell, height to length ratio much larger than in the other investigated gastrochaenid specimens. Umbones prosogyrous, lying at about 1/5 of the length of the shell toward the posterior. Posterior somewhat quadrangular. Sculpture represented only by comarginal growth ridges and calcareous granules (present on the earlier portion of the shell). Hinge line edentulous, ligament nymph well developed, extending about 1/4 of the shell length from the umbo toward the posterior. Pallial line with deep but rounded sinus (fig. 15); anterior adductor scar small, triangular in shape, placed very close to the margin. Posterior adductor

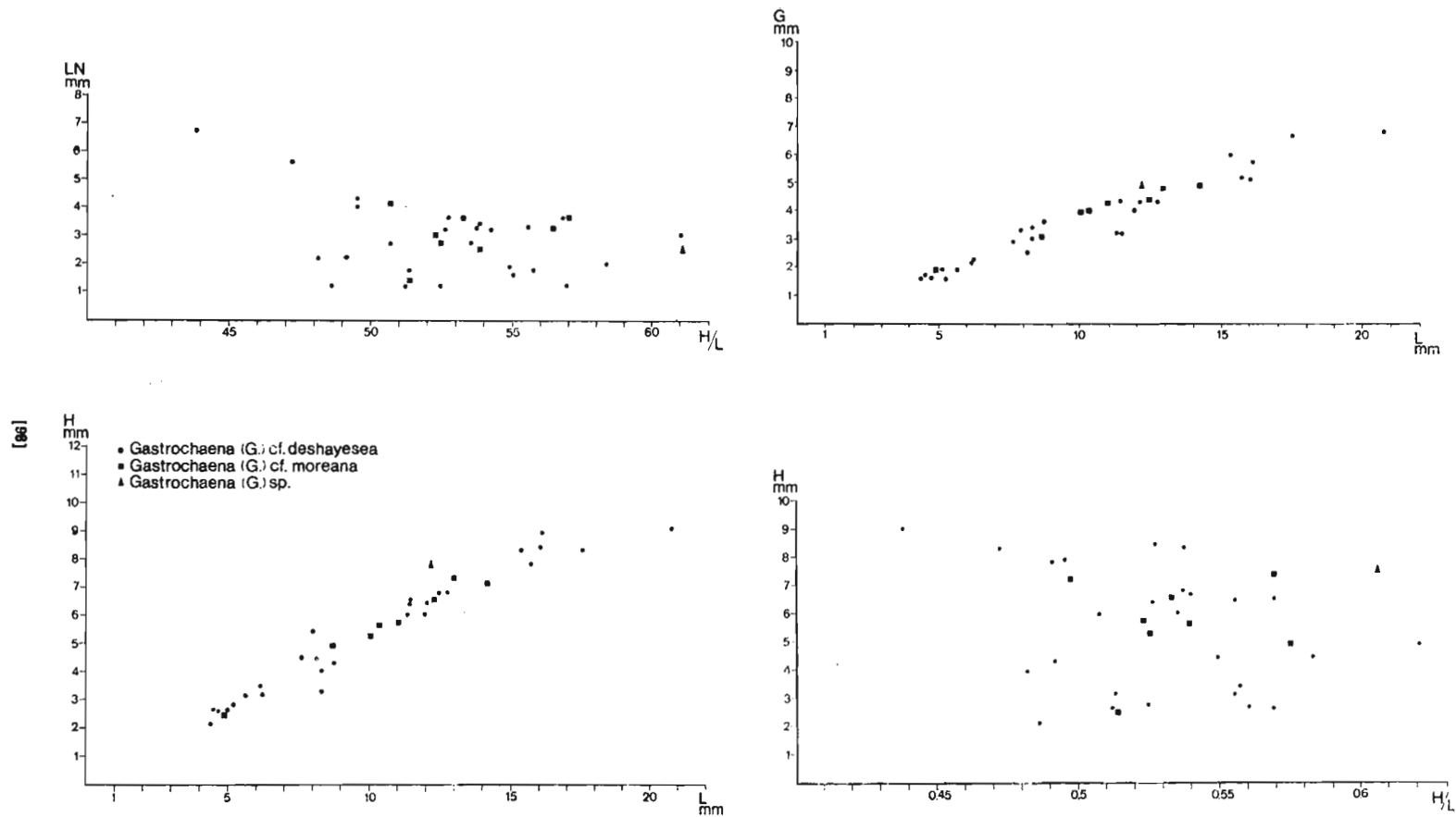


Fig. 12. Morphological ratios in *Gastrochaena* (G.) cf. *deshayesea*, *Gastrochaena* (G.) cf. *moreana* and *Gastrochaena* (G.) sp. H — height, L — length, G — pedal gape length, LN — ligament nymph length.

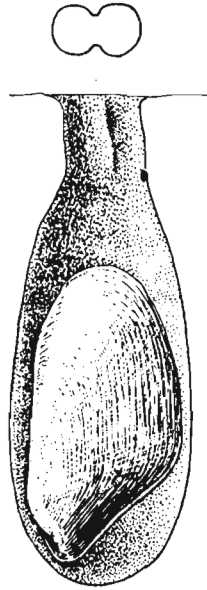


Fig. 13. Borehole of *Gastrochaena* (G.) cf. *moreana* Buvignier with the shell inside; shape of an aperture shown at the top.

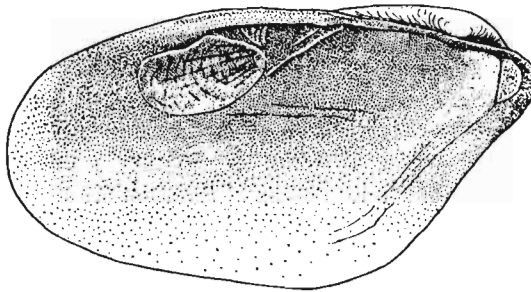


Fig. 14. Internal view of the *Gastrochaena* (G.) cf. *moreana* Buvignier shell showing the shape and disposition of adductor scars and pallial line with deep sinus; note a large and oval posterior adductor scar with small separate (probably pedal retractor) muscle scar above.

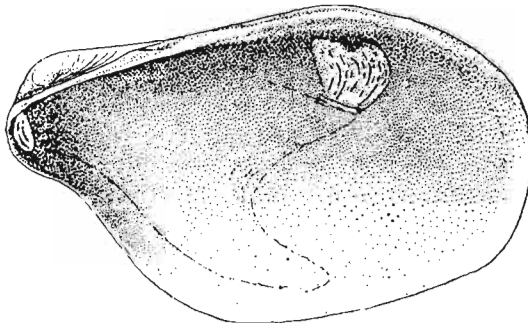


Fig. 15. Internal view of the *Gastrochaena* (G.) sp. shell showing the shape and disposition of adductor scars and pallial line with sinus.

scar also somewhat triangular in shape, much larger than the anterior one, and placed very close to the dorsal margin.

The borehole is flask-shaped, with its siphonal part directed at 90° in relation to the shell chamber (fig. 16). The siphonal part is rather short and it shows ridges delineating siphons on the whole length of the shell. No lining of the chamber wall was observed.

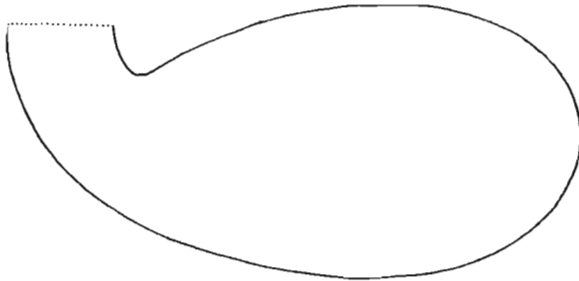


Fig. 16. Borehole of *Gastrochaena* (G.) sp. in longitudinal section.

Remarks.—There is only one valve in the collection, which does not allow for any species determination. Its external morphology is similar to the Lower Cretaceous species, *G. valanginensis* Pictet and Campiche (1864), but no data on the borehole shape of this species are available. Muscle scars are similar as in *G. (G.)* cf. *deshayesea* Buvignier, but the investigated species has a different pallial line and the shape of a borehole.

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WIERCĄCE I GNIAZDUJĄCE ORGANIZMY Z GÓRNOJURAJSKICH KOLONII
KORALOWYCH Z POLSKI PÓŁNOCNEJ

Streszczenie

Kolonie górnojurajskich koralii z glacialnych osadów Polski północnej wykazują obecność licznych organizmów wiercących i gniazdujących. Najliczniejsze są małże wiercące reprezentowane przez 4 gatunki gastrochen (*Gastrochaena s. s.* i *Spengleria*) oraz 2 gatunki litofag. Za pozostałe wiercenia odpowiedzialne są sipunculidy oraz najprawdopodobniej gąbki. Wśród form zasiedlających wiercenia i inne naturalne zagłębienia występują małże *Hiatella* (prawdopodobnie posiadające również zdolność drażenia), *Plicatula* i ostrygi oraz serpulidy. Zespół organizmów wiercących jest zaskakująco podobny do analogicznych zespołów ze współczesnych raf koralowych.

Wyjątkowy stan zachowania (zachowany pierwotny aragonit) pozwolił po raz pierwszy na dokładne zbadanie i opisanie wewnętrznej struktury muszli i wierceń. W oparciu o nie zaproponowano nowe cechy diagnostyczne dla klasyfikacji oraz przeprowadzono rewizję niektórych opisanych wcześniej gatunków.

EXPLANATIONS OF PLATES 33—40

All specimens are from erratic boulders, Ostromice
Oxfordian

Plate 33

- 1—4. Associations of different borings as visible on the lower surface of various *Thamnasteria* specimens (surfaces slightly eroded), $\times 2$; G — gastrochaenid borings, S — sipunculid boring, C — ?sponge borings; 1. ZPAL VXI/1, 2. ZPAL VXI/2, 3. ZPAL VXI/3, 4. ZPAL VXI/4.
5. Gastrochaenid and sipunculid borings as visible on the broken surface of coral colony, $\times 2$; ZPAJ. VXI/5; G — gastrochaenid boring, S — sipunculid boring.
6. Gastrochaenid (probably *Gastrochaena* (G.) cf. *deshayesea*) borehole in longitudinal section, $\times 2$; ZPAL VXI/6.

Scale bars 1 cm

Plate 34

Various squatting organisms associated with borings and other natural cavities in *Thamnasteria* colonies.

1. *Plicatula* sp.: ZPAL LI/77, a upper valve exterior; b lower valve exterior; c upper valve interior; lower valve interior. All figures $\times 5$.
2. *Plicatula* sp. sitting on the wall of the bivalve borehole: ZPAL LI/78, $\times 2$.

3. Oyster growing in natural cavity formed by growth of coral: ZPAL LI/79, $\times 2$.
4. Plicatulid bivalves growing in the bivalve boreholes (lower surface of the colony): ZPAL LI/80, $\times 2$.
- 5—6. Serpulids growing in the bivalve boreholes, $\times 2$; 5. ZPAL VXI/7. 6. ZPAL VXI/8.

Plate 35

Lithophaga lycetti (Whiteaves)

1. ZPAL LI/53, *a* left valve exterior; *b* right valve exterior; *c* right valve interior; *d* left valve interior; *e* dorsal view of the whole shell. All figures $\times 5$.
2. ZPAL LI/33, $\times 5$; *a* left valve exterior; *b* left valve interior.
3. ZPAL LI/45, $\times 5$; *a* right valve exterior; *b* right valve interior, note the presence of large posterior adductor scar (white).
- 4—5. *Lithophaga lycetti* in its boreholes, openings of boreholes somewhat eroded, $\times 5$; 4. ZPAL LI/39, 5. ZPAL LI/82.

Plate 36

1. *Lithophaga inclusa* (Phillips): ZPAL LI/54, scale bar 5 mm; *a* left valve exterior; *b* right valve exterior; *c* left valve interior; *d* right valve interior; *e* dorsal view of the shell; *f* ventral view of the shell.
- 2—3. *Lithophaga lycetti* (Whiteaves), scale bars 2 mm; 2. ZPAL LI/61, *a* right valve exterior; *b* left valve exterior; 3. ZPAL LI/36, *a* right valve exterior; *b* left valve exterior; *c* dorsal view of the shell; *d* ventral view of the shell; *e* posterior view of the shell; *f* anterior view of the shell.

Plate 37

Five differently shaped specimens of various size of *Hiatella* (*Pseudosaxicava*) *phaseolus* (Deslongchamps).

1. ZPAL LI/40, $\times 7$, *a* right valve exterior; *b* left valve exterior; *c* dorsal view of the shell; *d* ventral view of the shell.
2. ZPAL LI/52, $\times 5$, *a* left valve exterior; *b* right valve exterior; *c* left valve interior; *d* right valve interior.
3. ZPAL LI/47, right valve exterior in another specimen, $\times 5$.
4. ZPAL LI/48, right valve exterior in another specimen, $\times 5$.
5. ZPAL LI/66, shell of *H. (Pseudosaxicava) phaseolus* (Deslongchamps) in a borehole, $\times 5$.

Plate 38

Spengleria recondita (Phillips)

1. ZPAL LI/32, *a* left valve exterior; *b* left valve interior.
2. ZPAL LI/35, *a* right valve exterior; *b* left valve exterior; *c* right valve interior; *d* left valve interior; *e* dorsal view of the shell; *f* ventral view of the shell.

All figures $\times 5$

Plate 39

- 1—2. *Gastrochaena* (G.) cf. *deshayesea* Buvignier, $\times 3$; 1. ZPAL LI/3, *a* right valve exterior; *b* left valve exterior; *c* dorsal view of the shell; *d* ventral view of the shell; 2. ZPAL LI/4, *a* right valve exterior; *b* left valve exterior; *c* dorsal view of the shell; *d* ventral view of the shell; *e* right valve interior; note the presence of a small callosity on the hinge margin in the posterior part of the valve.
3. Boreholes of *Gastrochaena* (G.) cf. *deshayesea* Buvignier with single valves inside, ZPAL VXI/9, $\times 2$. Note that boreholes containing their inhabitants were completely overgrown by coral.
4. Borehole of *Gastrochaena* (G.) cf. *moreana* Buvignier (ZPAL LI/18) with the shell inside and containing also secondary inhabitant—shell of *Hiatella* (*Pseudosaxicava*) *phaseolus* (Deslongchamps) (ZPAL LI/40), $\times 2$. Boring made on the upper surface of the colony.

Plate 40

1. Right valve of *Gastrochaena* (G.) cf. *deshayesea* Buvignier showing borehole of predatory gastropod, ZPAL LI/10, $\times 5$.
2. *Gastrochaena* (G.) sp.: ZPAL LI/31, $\times 5$, *a* right valve exterior; *b* right valve interior.
3. *Gastrochaena* (G.) cf. *deshayesea* Buvignier: ZPAL LI/2, $\times 3$, *a* right valve exterior; *b* left valve exterior; *c* dorsal view of the shell; *d* ventral view of the shell.
4. *Gastrochaena* (G.) cf. *moreana* Buvignier: ZPAL LI/7, $\times 3$, *a* right valve exterior; *b* left valve exterior; *c* dorsal view of the shell; *d* ventral view of the shell.
5. Borehole of *Gastrochaena* (G.) cf. *moreana* Buvignier (the same specimen as on fig. 4): ZPAL VXI/11, $\times 3$, *a* with the shell inside, and *b* without shell, showing calcareous lining of the upper part. Boring made on the upper surface of the colony.

