

On fossil and recent borings produced by acrothoracic cirripeds

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Abstract

This study on recent and fossil acrothoracic cirripeds describes burrows of the recent species *Trypetesa lampas* in the same way as fossil burrows. Subsequently, fossil and recent burrows are compared. Recent burrows of *T. lampas* were found in whelk shells (*Buccinum undatum*) inhabited by pagurids; fossil burrows resembling *Brachyzapfes elliptica* in belemnites (*Oxyteuthis* sp.) from the Barremian of Alstätte, West-Germany. The burrows of *T. lampas* are smaller but relatively deeper and wider than the Alstätte material. This is probably due to the reduction of the abdomen and appendages in *T. lampas*. The brood pouch and ovaria of *T. lampas* are probably larger than those of the fossil borer. In the present material, burrows of *T. lampas* were mainly produced by young barnacles. This may be explained by a frequent change of shells by hermit crabs which causes an early death of the acrothoracics.

Introduction

Recent trypetesid acrothoracic cirripeds

Trypetesids are peculiar boring barnacles, living in gastropod shells inhabited by hermit crabs. Hancock (1849) was the first to describe a trypetesid, which he named *Alcippe lampas*. This still is the best known species. Darwin (1854) and Berndt (1903) studied its morphology and anatomy, Kuhnert (1935) its larval development and embryology.

The following trypetesids are now known:

Trypetesa lampas (Hancock, 1849)

Trypetesa lateralis Tomlinson, 1953

Trypetesa habei Utinomi, 1962

Trypetesa nassaroides Turquier, 1967

Trypetesa spinulosa Turquier, 1976

Alcippoides asymetrica Turquier & Carton, 1976

Generally, burrowing cirripeds of the order Acrothoracica have a soft mantle without calcareous plates. The cirri are reduced and concentrated towards the posterior end of the thorax. Adults have no abdomen. The animals are dioecious, i.e. with dwarf males. The females bore the holes; the males live attached to the female. The females adhere to the wall of the burrow by means of the mantle (horny disc).

Some characteristics of *Trypetesa lampas* are (after Turquier, 1967):

- a relatively large size, adults up to 10 mm (axis anterior/posterior);
- the ratio between the length of mantle opening and maximum length of the animal decreases during growth (0.5 to 1; never less than 0.3);
- the attachment site of the mantle is oblong.

The dwarf male lives attached to the horny disc of the female and consists mainly of one well developed eye and genital organs.

The burrow

The burrow protects the soft animals, which lack shelly plates and other skeletal elements. The barnacles start burrowing at the moment of metamorphosis from the cypris stage, in gastropods that are inhabited by pagurids (Hancock, 1849; Darwin, 1854; Berndt, 1903; Kühnert, 1935; Turquier, 1970). They usually settle on the columella, but burrows are seen on the inside of the bodywhorl as well. *T. lateralis* borings are exclusively found on the inside of the bodywhorl (Tomlinson, 1953). The boring process starts chemically (Berndt, 1903; Kühnert, 1935); Turquier (1968) discovered the importance of carbonanhydrase at the onset of burrowing. Ultrastructural study of fractures through the burrow revealed a chemical shell weakening process (Kamens, 1983; Carriker, 1983). Later on, burrowing is continued by rasping with chitinous teeth that are distributed over the surface of the mantle (Darwin, 1854; Tomlinson, 1955; Turquier, 1958; Tomlinson, 1969). Seilacher (1969) demonstrated the succession of chemical activity and mechanical processing in fossil burrows of Acrothoracica, by examining electron microscope photographs of replicas of burrows. The only body fossils of acrothoracic barnacles, in the Upper Cretaceous of New Jersey (Turner, 1973), reveal exceptionally large abrasive mantle teeth. This suggests a relatively large role for mechanical abrasion in this fossil species.

The burrow opening is a long slit, usually bent at one end and ending in a sharp point. This point is the original attachment site of the cypris larva. The shape of the burrow is, moreover, related to the thickness of the host shell. *T. lateralis*, for example, inhabits thin *Tegula* shells and is completely laterally orientated while *T. lampas* is orientated perpendicularly to the surface of the host gastropod in a much deeper burrow (Tomlinson, 1969).

Ecology

All trypetesids burrow in gastropod shells, which are inhabited by hermit crabs. The relationship between hermit crab and barnacle is still not clear. It seems that the former provides a food and oxy-

gen current for the latter. The species of hermit crab is not important for the trypetesid. *T. lampas* burrows mostly in *Buccinum undatum*, but also in *Colus gracilis*, *Neptunea antiqua* and *Polinices alderi* (White, 1969). It seems that the bigger the shell, the more barnacles are found.

All species are littoral or sublittoral. Findings of *T. habei* in depths varying from 55 to 65 m. have been reported (Utinomi, 1964). *T. lampas* is found in depths from 5 to at least 46 m.

The Trypetesidae are a cosmopolitan family. *T. lampas* lives in the English Channel, the North Sea, the Mediterranean, the northern part of the Atlantic including the east coast of the U.S.A., and has been reported from the Philippines (Rosell, 1982) and the Gulf of Mexico (Spivey, 1979). *T. lateralis* is known from California, *T. habei* from Japan, *T. nassaroides* from the English Channel and *T. spinulosa* and *Alcippoides asymetrica* from Madagascar.

Fossil burrows of acrothoracic cirripeds

D'Eichwald (1868) mentioned already in his 'Le-thaea Rossica' the occurrence of oval boreholes in belemnite rostra. He thought these to be perforations through which belemnite embryos could leave the mother. In his point of view, perforated belemnites were female and the intact ones male.

Fossil tunnels of acrothoracic cirripeds were not recognized as such until the discovery in 1936 by Zapfe of burrows resembling those of the recent *Lithoglyptes indica* in shells of *Pyrula cornuta* and *Fasciolaria turbinella* from the Miocene of Hungary.

Tomlinson (1969) rearranged the classification of the fossil borings proposed by Codes & Saint-Seine (1957). He classified these into the family Lithoglyptidae Aurivillius instead of the families Rogerellidae De Saint-Seine and Zapfelliidae Co-dez. Trace fossils are, then, incorporated in recent soft body nomenclature; a practice not generally accepted.

Up to now, the following ichnogenera and ichnospecies have been described:

Ichnospecies	Geologic age
<i>Simonizapfes elongata</i> Codez & De Saint-Seine, 1957	Lias-Late Jurassic
<i>Simonizapfes davenporti</i> Tomlinson, 1969	Late Cretaceous
<i>Brachyzapfes elliptica</i> Codez & De Saint-Seine, 1957	Cretaceous
<i>Brachyzapfes elliptica elongata</i> Taylor, 1965	Early Cretaceous
* <i>Zapfella pattei</i> De Saint-Seine, 1954	Early Jurassic- Late Cretaceous Miocene-Pliocene
* <i>Nygmites sacculus</i> Mägdefrau, 1937	Late Jurassic
<i>Rogerella lecointrei</i> De Saint-Seine, 1951	Late Cretaceous
<i>Rogerella mathieui</i> De Saint-Seine, 1955	Middle Jurassic- Late Cretaceous Miocene-Pliocene
<i>Rogerella cragini</i> Schludt & Young, 1960	Early Cretaceous
<i>Rogerella caudata</i> Voigt, 1967	Late Cretaceous
** <i>Trypetesa caveata</i> Tomlinson, 1963	Late Carboniferous- Early Permian
** <i>Bascomella gigantea</i> Morningstar, 1922	Late Carboniferous- Early Permian
** <i>Bascomella fusiformis</i> Condra & Elias, 1944	Late Carboniferous

* *Nygmites sacculus* was first described as fungal borings. Tomlinson (1969) recognized this ichnospecies as acrothoracic tunnels. According to Tomlinson *Zapfella pattei* is synonymous with *Nygmites sacculus*.

** *Bascomella gigantea* was originally supposed to be a type of bryozoan borings (Morningstar, 1922; Condra & Elias, 1944). Later on, this proved to be a mistake (Elias, 1957). The ichnospecies *Bascomella fusiformis* was initially mistaken as bryozoan borings as well (Condra & Elias, 1944). *Trypetesa caveata* is questioned by Seilacher (1969), who identified it as *Bascomella gigantea*. Several unnamed acrothoracic tunnels have been described by the following authors:

	Geologic age
Zapfe, 1936	Miocene
Joysey, 1959	Cretaceous
Schludt & Young, 1960	Permian
Rodda & Fischer, 1962	Late Paleozoic
Ross, 1965	Miocene
Rodriguez & Gutschick, 1970, 1977	Late Devonian
Ettensohn, 1978	Late Carboniferous

The trace fossils

The burrows are mostly found in skeletal carbonate substrates, such as bryozoa, echinids and mollusc shells. Some burrows were observed in limestone pebbles and cobbles (Maubeuge, 1955; Radwanski, 1964; Merril, 1979), and in a Tertiary limestone cliff (Codez & De Saint-Seine, 1957) as well as in hard-grounds (Jahnke, 1966; Bromley, 1968).

The burrows are described on the strength of their size, length/width/depth ratios, details of the aperture, such as size and shape, host shell, as well as geologic and geographic distribution. The burrow openings are oval, with one side ending into a slit (the openings are fan-shaped), the so-called peduncular slit. The slit's end represents the original attachment site of the cypris. In the genus *Rogerella* the apertures are sometimes bordered by a bourrelet (De Saint-Seine, 1951, 1955). When a bourrelet exists, it runs mostly along one side of the burrow. The presence of a peduncular slit is important for classification. *R. mathieui*, for instance, is a species with an extensive peduncular slit (De Saint-Seine, 1956).

The similarity in burrows of living barnacles of different families and the variation in the borings within one family make it difficult to create a natural system of classification for the fossil burrows, all what remains from what once was a tunneling barnacle.

Aim of this study

Trace fossils of the genera *Rogerella*, *Brachyzapfes*, *Simonizapfes*, *Zapfella*, *Nygmites*, *Trypetesa* and *Bascomella* reflect the history of the Acrothoracica from the Devonian onwards. Classification of the recent Acrothoracica is based on morphological and anatomical aspects of the barnacle; hardly any attention has been given to their recent burrows. This study aims to describe tunnels of the recent cirriped *T. lampas* in *Buccinum undatum* in the same manner as has been done with their fossil counterparts. A comparison is given between recent borings and fossil tunnels in Cretaceous belemnites.

Material

Whelk shells containing burrows of *T. lampas* were collected from a shell mound at Zoutkamp, where shell gatherers store material dredged from the bottom of the channels between the Dutch Wadden Isles.

Perforated belemnites (*Oxyteuthis* sp.) were collected in the mid-sixties by the second author from the Barremian in the clay pit Grosse-Hündfeld, south of Alstätte in West Germany, near the Dutch border. The belemnites were found in Pleistocene sediments of a meltwater gully, situated between outcropping Barremian and Aptian rocks. These Pleistocene beds contain many rostra derived from the Albian (*Neohibolitus minimus*) and the Barremian (*Oxyteuthis* sp.) (Kemper, 1976). Localities are rendered in Figure 1. The material has been deposited in the Rijksmuseum Geologie, Leiden, the Netherlands; it is numbered RGM 383217 – RGM 383220.



Fig. 1. Locality map showing the finding places of *T. lampas* (the Wadden Sea) and the fossil burrows (Alstätte, West Germany).

Methods

Whelk shells and belemnites with borings were selected from the material. Replicas of the burrows were made. For that purpose the material was first ultrasonically cleaned. Subsequently, the holes were filled with the acid resistant fluid, Palavit-G. This two-component synthetic substance is used by dentists to make models of teeth and molars. After hardening during at least half a day, the belemnites and the shells were dissolved in 34% HCl. The residue was filtered and the replicas were taken out.

By means of a Leitz/Orthoplan microscope with measuring equipment the burrow dimensions were determined (compare Fig. 2). For more detailed study of the burrows, SEM micrographs of the replicas were made.

Results

The distribution of the burrows on the host

The *Trypetesa* borings occur mainly in the columella of the whelk shells (Fig. 3a). Besides random distribution of the burrows on the columella or the bodywhorl, clustering was also observed. Perforations in clusters show a preferred orientation, probably along the stream line of the water current in the shell generated by the hermit crab. The borings in by far the largest number of belemnites are randomly distributed over the entire sur-

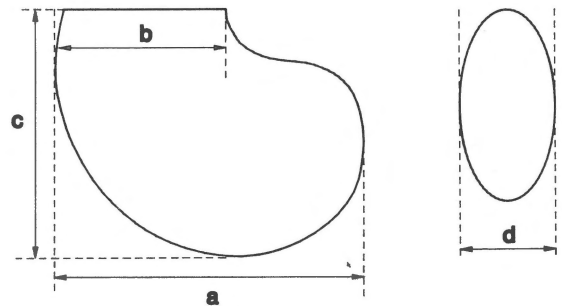


Fig. 2. Dimensions of the burrow: a = length of the burrow; b = length of the opening; c = depth of the burrow; d = width of the burrow (from below).

face (Fig. 3b). Only a few are perforated at one side, the side that happened to lay exposed. The borings do not have any preferred orientation, which indicates post-mortem infestation of the belemnites.

The apertures of the burrows

The openings of *T. lampas* burrows are oval slits, resembling apple pips (Fig. 3c). One end has a sharp point. Larger, fan shaped burrows, as described by Boekschoten (1966) and Tomlinson (1969) (Fig. 3a), were not found in the present material.

The apertures of the fossil burrows are oval slits, bent at one end and thus forming a short slit with a sharp point, the peduncular slit (Fig. 3d). In many cases, the peduncular slits are more or less eroded, and apertures acquire a more regular oval shape. The degree in which the openings have been eroded is an indication of the degree of abrasion of the substrate (Bromley, 1970). Juvenile openings are oval, and are incorporated in the peduncular slit in adult trace fossils.

The form of the burrows

The shape of the burrows of *T. lampas* and the fossil burrows is very similar (Fig. 3e and 3f). The length exceeds the depth in both cases. The form is sac-like. The posterior wall descends abruptly in parabolic shape, passing the pointed end of the opening. Here it gradually changes into the anterior wall, which goes up to 1/3 of the depth below the surface of the substratum. There the wall bends over towards the inside and continues in a faint curve to the anterior part of the aperture.

In relatively small burrows the anterior wall ascends in the shape of a 1/4 arc until the attachment site. Such small burrows have the form of half a water drop.

The dimensions of the burrows

The dimensions of the burrows of *T. lampas* (referred to as T) and the fossil burrows (referred to as F) were compared by means of a Mann/Whitney U

test with a level of significance α of 5%. The measurements and test results are listed in Table 1.

The size of the fossil burrows is significantly larger than that of the borings of *T. lampas*. Comparison of burrow length and length of the opening within the trace fossil group and the *T. lampas* burrows showed in both cases a significant larger length of the burrows (M-W. T.: $n_{1,2} = 73$, $Z = -2.99/F$: $n_{1,2} = 66$, $Z = -4.07$). The length of both burrows exceeds their depth (M-W. T.: $n_{1,2} = 73$, $Z = -6.29/F$: $n_{1,2} = 66$, $Z = -4.70$).

Indices were computed in order to form a notion of the ratios between the dimensions of the burrows. This method was introduced by Codez & De Saint-Seine (1957).

The following indices were calculated:

Codez & De Saint-Seine:

$$I = \frac{\text{width of the burrow}}{\text{length of the burrow}} \times 100 \quad \frac{l \times 100}{L}$$

$$I' = \frac{\text{depth of the burrow}}{\text{length of the burrow}} \times 100 \quad \frac{p \times 100}{L}$$

$$I'' = \frac{\text{length of the burrow}}{\text{length of the opening}} \times 100 \quad \frac{L \times 100}{\gamma}$$

The indices of *T. lampas* and the fossil borings were compared by means of a Kolmogorov-Smirnoff two-sample test. Level of significance α is again 5%. The ratios and the results of the Kolmogorov-Smirnoff tests are given in Table 2. The ratios I and I' of the burrows of *T. lampas* are significantly larger than those of the fossil burrows. I'' of the fossil borings is significantly larger than I'' of the *T. lampas* borings.

Remarkable are the differences between the values of the indices obtained in this study for the fossil burrows and the values calculated by Codez & de Saint-Seine (1957) for their trace fossils. The values of I, I', I'' are nearer to the calculations of *B. elliptica* than to those of *R. mathieui*, the other somewhat similar Cretaceous ichnospecies. Their indices are respectively 43–56–125 and 45–125–118. A complete comparison cannot be made, because basic data like sample size and standard deviation were not communicated by Codez & De Saint-Seine.

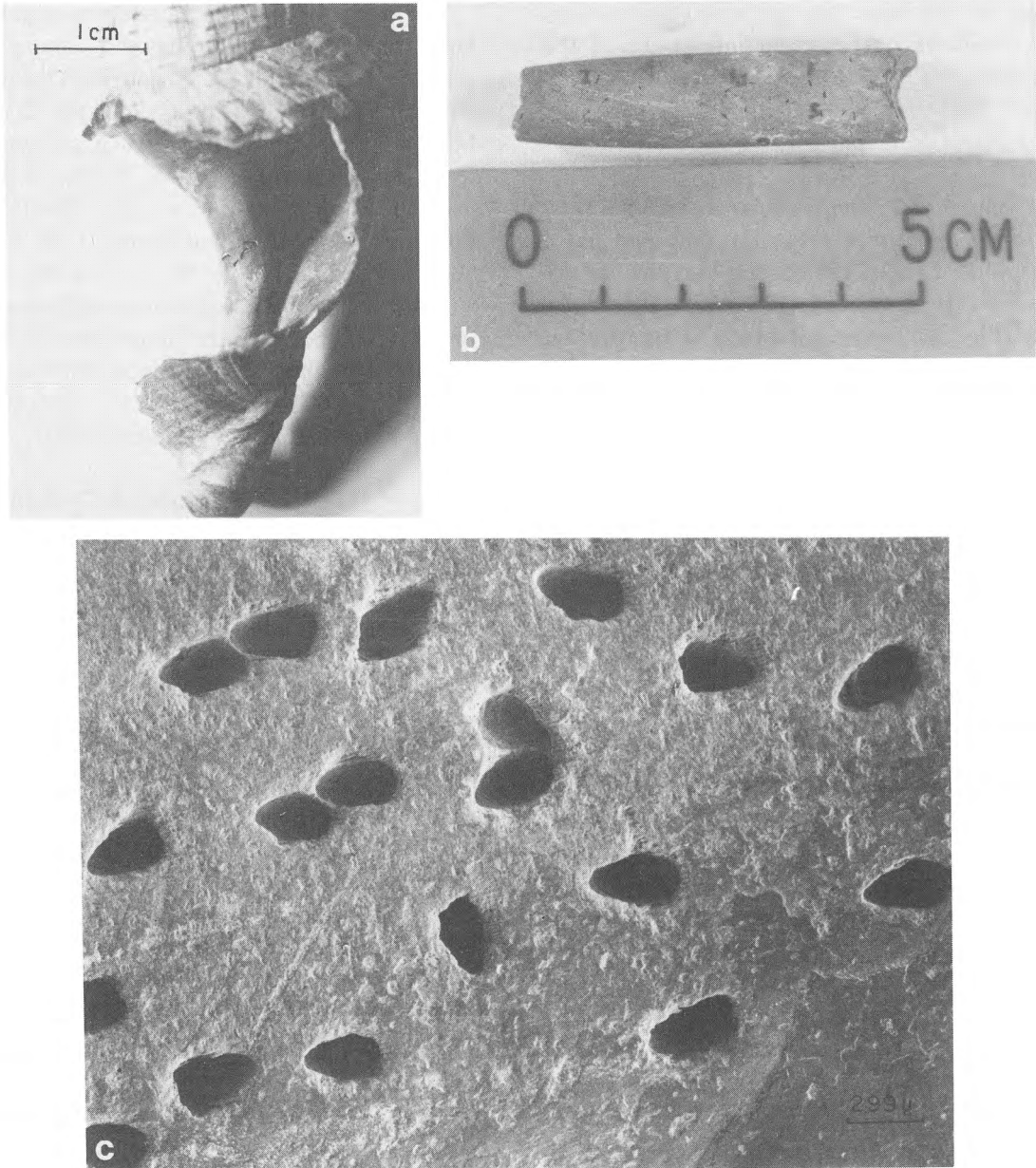


Fig. 3. (a) Large *Trypetesa* borings in columella of *Buccinum*. Recent Wadden Sea. This type of borings has not been found in the sample studied. (b) *Oxyteuthis* rostrum with borings of acrothoracic cirripeds. Barremian, Alstätte, West Germany. (c) Small *Trypetesa* borings in *Buccinum*, enlarged.

In order to investigate the correlation between the dimensions of the burrows, the following regression lines were computed:

length burrow-length opening;

depth burrow-length burrow;

width burrow-length burrow.

The differences between the corresponding lines of *Trypetesa* and the fossil burrows were tested by

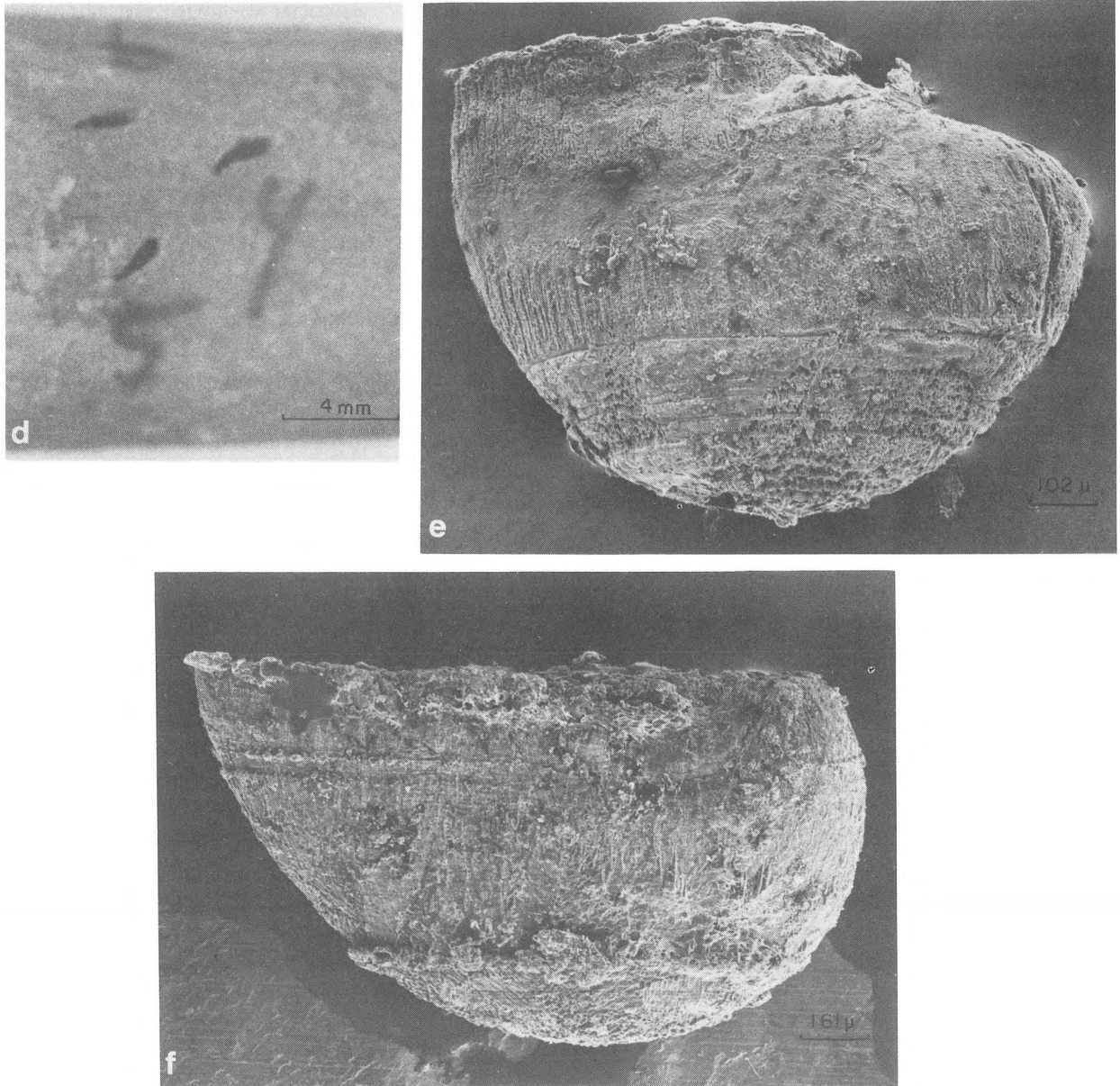


Fig. 3 cont. (d) Borings in *Oxyteuthis*, enlarged. (e) Palavit-G infilling of *Trypetesa* boring. (f) Palavit-G infilling of acrothoracic boring in *Oxyteuthis*.

comparing the regression coefficients of the curves and transforming the obtained value to a Student-t distribution. The level of significance α is 5%. Calculations of the regression lines and the Student-t distribution values are listed in Table 3.

Both groups of burrows show a significant correlation between the dimensions. There is an in-

dication of difference in the regression lines of depth/width for both groups of burrows. Comparison of the curves depth/length and width/length within the groups of burrows show in both cases a significant difference. (Stud.-t: T.: $\nu = 142$, $t = 6.22$; T.: $\nu = 128$, $t = 10.25$).

Table 1. Mean values of the dimensions of the burrows, their standard deviation and Z-values of the Mann-Whitney U tests.

	<i>T. lampas</i> burrows			Fossil burrows			Mann-Whitney U	
	n	mean	SD	n	mean	SD	Z	
length burrow	73	0.44	0.27	66	1.54	0.78	-9.44	significant
length opening	73	0.38	0.22	66	1.14	0.60	-9.04	significant
depth burrow	73	0.32	0.27	66	1.04	0.62	-8.76	significant
width burrow	73	0.24	0.11	66	0.57	0.32	-8.42	significant

Discussion

Characteristics of the burrows

It is remarkable that the observed burrows of *Trypetesa* in this study are quite small, the largest length being 1.51 mm., the mean 0.44 mm. Berndt (1903) mentioned very large specimens, up to 12 mm. Boekschoten (1966) described a sample of burrows with a mean length of about 0.5 mm. Because his material also originated from the Dutch Wadden Sea it seems that environmental factors have a big influence on the growth and development of these barnacles. Boekschoten frequently observed a large number of small holes around some large ones, probably the offspring that settled around the mother and died off in an early stage.

In the present material, such a concentration of small burrows around large ones was not found. It seems that environmental factors influence the larvae and mature barnacles in the Wadden Sea to such an extent that only a few reach their maximum length and longest lifespan. One of the factors determining the lifespan of the barnacles may be that the pagurids, which are essential for the cirriped, changes shells frequently (Bromley, 1970).

Deprived from the company of the pagurid, the barnacles die.

The following data characterize the investigated *Trypetesa lampas* burrows. The mean length of the opening is 0.38 ± 0.22 mm. The mean length of the burrow is 0.44 ± 0.27 mm., its mean depth 0.32 ± 0.27 mm. and its mean width 0.57 ± 0.32 mm.

The length of the burrow exceeds the length of its aperture and its depth. During growth the burrows deepen gradually. The calculated indices are:

$$I = 59.15 \pm 10.70 \quad I' = 80.83 \pm 21.73 \quad I'' = 115.74 \pm 20.01$$

The following characteristics of the Alstätte burrows were observed. The mean length of the opening is 1.14 ± 0.60 mm. The mean length of the burrow is 1.54 ± 0.78 mm., its mean depth is 1.04 ± 0.62 mm. and its mean width is 0.57 ± 0.32 mm. The burrow length exceeds the length of the aperture and the depth. During growth the burrows deepen gradually. The calculated indices are:

$$I = 37.34 \pm 7.63 \quad I' = 66.00 \pm 10.93 \quad I'' = 138.54 \pm 31.68$$

Table 2. Mean values of the ratios of the burrows, their standard deviation and χ^2 -values of the Kolmogorov-Smirnoff tests.

	<i>T. lampas</i> burrows			Fossil burrows			Kolmogorov-Smirnoff	
	n	mean	SD	n	mean	SD	χ^2	
I	73	59.15	10.70	64	37.34	7.63	96.25	significant
I'	73	80.83	21.73	66	66.00	10.93	23.30	significant
I''	73	115.74	20.01	66	138.54	31.68	16.98	significant

Table 3. Regression lines $y = ax + b$. Regression coefficient = r . Values of the Student-t distributions are shown. n.s. = not significant; n.s.* = almost significant: $t_{135; 0.05} = 1.65$.

	<i>T. lampas</i> burrows				Fossil burrows				Student-t	
	n	a	b	r	n	a	b	r	ω	t
length burrow/ length opening	73	0.91	0.08	0.71	66	1.22	0.16	0.85	135	0.05 n.s.
depth burrow/ length burrow	73	0.89	-0.07	0.80	66	0.76	-0.15	0.91	135	1.63 n.s.*
width burrow/ length burrow	73	0.33	0.10	0.64	66	0.35	0.03	0.71	135	-0.33 n.s.

According to the data provided by Codez & De Saint-Seine (1957), the fossil burrows could be *Brachyzapfes elliptica*. The indices computed in this research ($I = 37$, $I' = 66$, $I'' = 138$) are closer to the given values of *B. elliptica* ($I = 43$, $I' = 56$, $I'' = 125$) than to those of *R. mathieui* ($I = 45$, $I' = 125$, $I'' = 118$). The index I' of *Rogerella* indicates a relatively large depth, and this is the way in which Codez & de Saint-Seine describe the *Rogerella* burrows. However, the Alstätte specimens are not really very deep, the depth does not exceed the length, like *R. mathieui*. This is reflected in the moderate value of I' . The absence of a clear, narrow peduncular slit, the description of the burrow and the values of the indices respond more to *B. elliptica* than to *R. mathieui*. The differences between the indices may be caused by environmental factors such as the structure of the substratum, which influences the growth of the animal.

Comparisons of the recent and fossil burrows

The statistical tests that were applied to the measurements of the dimensions demonstrate the difference in size between the fossil and recent borings. The fossil borings are three to four times as large as the recent ones. This is possibly due to the juvenile aspect of the recent burrows. The fossil burrows were made by acrothoracics like the Lithoglyptidae which do not require the presence of hermit crabs, less prone to die off when still young. Furthermore, the length/width/depth ratios differ significantly. The ratios of the depth and the length and those of the width and the length of

Trypetesa are bigger than those of the Alstätte material. This may be explained by supposing relatively bigger ovaries and brood pouch. Furthermore, burrows more broad than deep can be accommodated in thin host shells and still reach an adequate size (Seilacher, 1969).

Considering the ratio between the length of the burrow and length of the opening, it is clear that the *Trypetesa* burrows are smaller than the Alstätte material. This seems to be due to the regression of the abdomen (Codez & de Saint-Seine, 1957). This regression is connected with an endolithic way of life, which limits size and, consequently, determines the evolution of tunneling organisms.

According to Turquier & Carton (1976) and Petriconi (1977), morphological evolution in acrothoracics is confined to the appendicular structure and the feeding mechanism. The loss of thoracic and caudal appendages in the Trypetesidae (Tomlinson, 1969) underlines this evolutionary trend. One can see from the regression lines of both *Trypetesa* and the Alstätte material that, the longer the burrows, the relatively deeper they become. This is probably caused by a marked growth of the reproductive part of the animal. In the related species *T. lateralis*, Tomlinson (1953) has found a rapid growth of the reproductive system during adulthood, reflected in deepening of the burrow. There is a strong indication that this deepening of the burrow is bigger in *Trypetesa* than in the Alstätte material. Besides the relatively bigger ovaries and brood pouch, *Trypetesa* also shows a more rapid growth of its reproductive system. The cirriped that bored the Alstätte belemnites certainly was, at least generically, different from *Trypetesa*.

Palaeoecology

Only a few belemnites show borings on one side. The random distribution of the burrow on the rostra, without a preferred orientation, indicates post-mortem infestation (Seilacher, 1968). This is common in fossil and recent species of non-trypetesid acrothoracic cirripeds (de Saint-Seine, 1954, 1955; Codex & De Saint-Seine, 1957; Schlaudt & Young, 1960; Hallam, 1963; Pugaczewska, 1965; Boyd & Newell, 1972; Rodriguez & Gutschick, 1970, 1977; Etensohn, 1978).

In vivo infestation, characterized by a uniform orientation of the burrows, has been described or supposed as well (Schlaudt & Young, 1960; Rodda & Fisher, 1962; Voigt, 1967; Seilacher, 1968, 1969; Petriconi, 1971; Rodriguez & Gutschick, 1977; Gargouri, 1982; Ghare, 1982). Shells are generally probed at the exposed side by boring organisms. To obtain borings at all sides, the belemnites must have changed position very often. It is probable that bioturbation may result in various exposure of *Oxyteuthis* rostra to settling acrothoracic cypris larvae. This applies to the Barremian clays of Alstätte, which were certainly not laid down in turbulent waters.

Boyd & Newell (1972) found *Rogerella*- and *Zapfella*-like burrows in broken shells from a Permian fossil layer. The shell remains were laid down in sediments in which predating fishes had caused considerable bioturbation. Maubeuge (1955) and Codez & De Saint-Seine (1957) came to the conclusion that their Acrothoracica used to live in shallow, turbulent water. The descriptions of their characteristic burrows in a hardground by Jahnke (1966) and Bromley (1968) support this, because hardgrounds develop under shallow and turbulent water conditions.

According to Radwanski (1964, 1970) *Zapfella pattei* preferred a littoral environment. Shell remains from the Upper Cretaceous of South India containing the ichnospecies *Z. pattei*, *Brachyzapfes elliptica* and *Rogerella mathieui*, were according to Chiplonkar & Ghare (1977) deposited in shallow, littoral waters as well. The discovery of algal borings and the ichnospecies *B. elliptica* in belemnite rostra from the same South Indian Late

Cretaceous (Ghare, 1982) indicated shallow, slightly turbulent waters.

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