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A new occurrence of fossil acrothoracican cirripedes: *Trypetesa polonica* sp. n. in hermitted gastropod shells from the Korytnica Basin (Middle Miocene; Holy Cross Mountains, Central Poland), and its bearing on behavioral evolution of the genus *Trypetesa*

ABSTRACT: A new species of acrothoracican cirripedes, *Trypetesa polonica* sp. n., is established upon their borings emplaced in gastropod shells occurring in the Middle Miocene deposits (the Korytnica Clays) of the Holy Cross Mountains, Central Poland. The new species is recognized as an obligate commensal to the hermit crabs which inhabited some of the selected (thick-walled, high-spired, and/or spacious) gastropod shells. The morphology of borings is comparable to that of the present-day species, especially of the pan-Atlantic species *Trypetesa lampas* (HANCOCK, 1849) and the Californian species *Trypetesa lateralis* TOMLINSON, 1953, to the latter of which the new species was supposedly an ancestor. A peculiar feature of borings in some species of the genus *Trypetesa*, the newly established *T. polonica* sp. n. including, namely the presence of the accessory exit produced by the external mantle flap is interpreted as having been constructed to involve a passive flow of water (the so-called prairie-dog's effect). This was required by the *Trypetesa* specimens to ensure further food supplies and thus to survive in the case when the gastropod shell had been discarded by the hermit crab. The *Trypetesa* to hermit crabs relationship, recognized for the Miocene representatives, is postulated to have resulted from a refuge of one stock of acrothoracican cirripedes from their former endolithic mode of life. The behavior of the modern *Trypetesa* species, heritaged from their Miocene forerunners, is consequently dated back some over 15 m. y. ago (Langhian to Serravalian stage interval).

INTRODUCTION

The scope of the present paper is to report on a unique fossil material of borings produced by acrothoracican cirripedes in some gastropod shells, and occurring in the Korytnica Clays of Miocene age. The collected borings, which
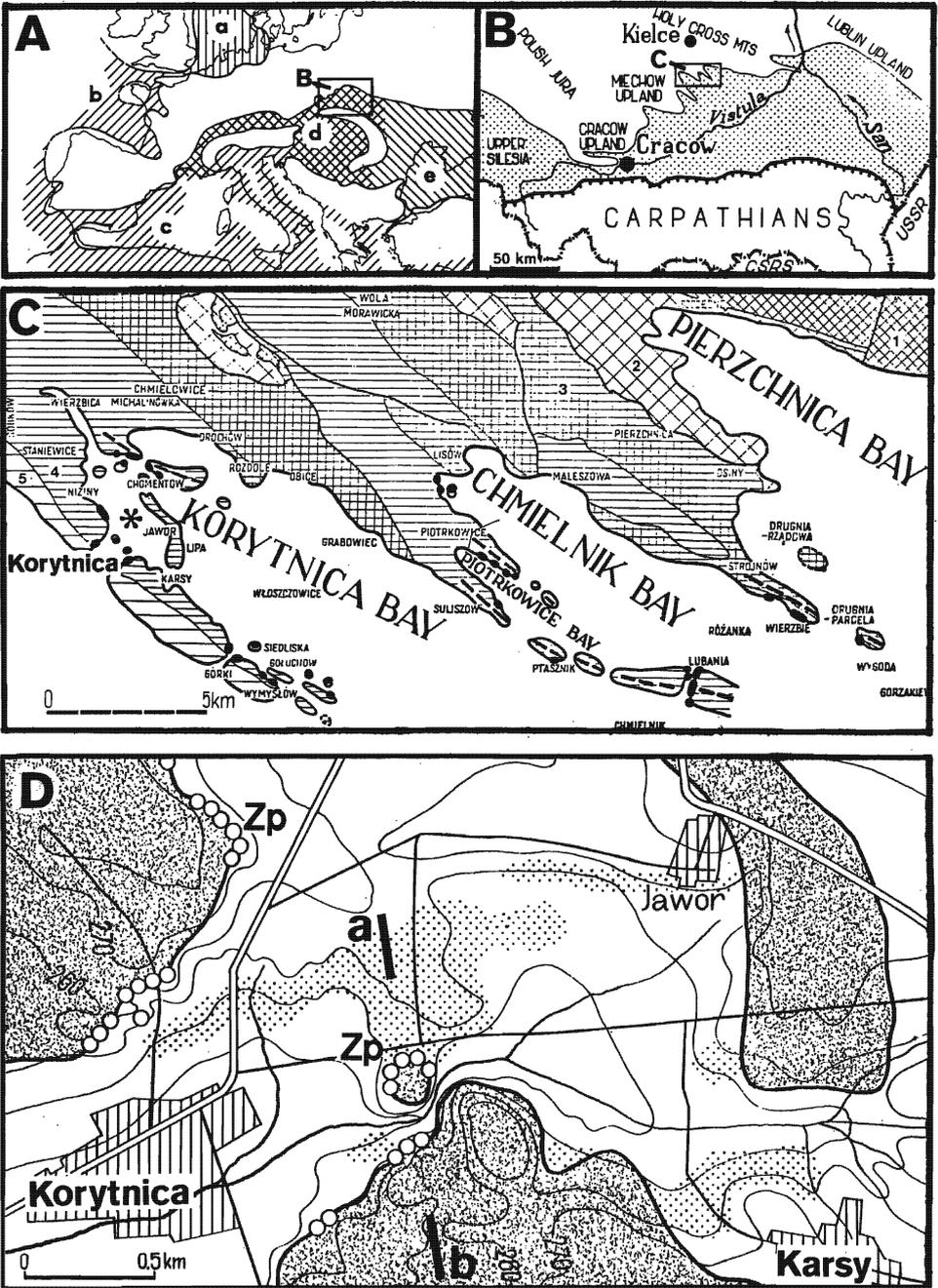
Fig. 1

Paleogeographic location of the Middle Miocene (Badenian) deposits yielding the investigated acrothoracican cirripedes, *Trypetesa polonica* sp. n., in the Korytnica Basin on the southern slopes of the Holy Cross Mountains, Central Poland (*adopted from*: BAŁUK & RADWAŃSKI 1977, Figs 1-2)

are reasonably distant to any of the hitherto known ancient borings attributed to acrothoracican cirripedes, are well compatible with those of the present-day genus *Trypetesa*. A morphological analysis of the borings classified as of a new species, *Trypetesa polonica* sp. n., and their paleobiological interpretation allow to demonstrate a new record of "the present-day taxa" in ancient times (*cf.* RADWAŃSKI 1977, p. 258; RINDSBERG 1990, p. 61; *see also* HÄNTZSCHEL 1975, pp. *W*136-*W*139), and to study the behavior of the genus *Trypetesa* back to the Miocene, some over 15 million years ago.

Within the ubiquitous organic communities which make the fame of the Korytnica Clays, the *Trypetesa* specimens belong to rather rare fossils. The total collected assemblage comprises about 260 specimens contained in less than 100 gastropod shells (*see* Table 1 and Plates 1-6).

GEOLOGIC SETTING OF THE LOCALITY

The Korytnica Clays which have yielded the *Trypetesa* material are making up an about 40-60 meters thick sequence of yellow clays deposited in the Korytnica Basin. This basin was a small (*c.* 5 sq kms) and shallow, terminal part of a larger bay, the Korytnica Bay, which developed during the Middle Miocene transgression onto the southern slopes of the Holy Cross Mountains in Central Poland (*see* Text-fig. 1 *and* RADWAŃSKI 1969, 1970; BAŁUK & RADWAŃSKI 1977).

A — Paleogeographic setting of the Korytnica Basin in the Middle Miocene of Europe: **a** — North Sea Basin, **b** — Atlanic gulfs (Brittany, Touraine and Anjou Basin, Aquitanian Basin, Lisbon Basin), **c** — Western Mediterranean Basin (= Tethys Basin), **d** — Paratethys basins (symbol *d* covers the area of the Vienna Basin, with the locality Grund, and the western part of the Pannonian Basin, with locality Várpalota, both mentioned in the text), **e** — Euxinian Basin; rectangled is the area enlarged in Text-fig. 1*B*

B — Extent of the Middle Miocene (Badenian) sea in the Fore-Carpathian Depression (*stippled*); rectangled is the area enlarged in Text-fig. 1C

C — Middle Miocene (Badenian) shoreline and extent of the bays on the southern slopes of the Holy Cross Mountains; preserved localities of littoral structures are marked with black spots along the shoreline; asterisked is the Korytnica Basin situated in the terminal part of the Korytnica Bay Within the inland areas distinguished are the occurrence zones of: *1* Cambrian (including locally Ordovician and Silurian), *2* Devonian, *3* Triassic, *4* Jurassic, *5* Cretaceous; marked with heavy dashes are the ridges in morphology that separate particular bays

D — Paleoenvironmental sketch of the southern part of the Korytnica Basin. Indicated are: marine area of the Korytnica Basin during the Middle Miocene (Badenian) transgression (*blank*) and present-day outcrops of the Korytnica Clays (*stippled*), preserved fragments of littoral structures (*circled*), land or island areas along the seashore (*hachured*)

Zp — Biotopes of the acrothoracican borings *Zapfella pattei* SAINT-SEINE, within the littoral rubble and fragmentary abrasion surface

a - **b** — Line of schematic cross-section presented in Text-fig. 2

The Korytnica Basin displayed a broad spectrum of biotic conditions favorable for development of ubiquitous communities of much diversified composition, structure, and density (*see* BAŁUK & RADWANSKI 1977, 1979a, 1984a). In result of these conditions the Korytnica Clays have become one of the most paramount, world-famous localities of the Upper Tertiary (Neogene) fauna, and their faunal content embraces representatives of the majority of all the animal phyla, both of invertebrates and vertebrates.

The environmental conditions during deposition of the Korytnica Clays were characterized by normal salinity and by depth ranging widely, from the shore to the shallow sublittoral, having been dependant upon the inundated morphology and progressing sedimentation (*see* Text-fig. 2). The maximum depth of the Korytnica Basin may roughly be estimated as corresponding to the thickness of the clays deposited throughout its area. The depth was gradually decreasing when the clay sedimentation was in progress and, finally, it reached almost sea level (*see* Text-fig. 2). The investigated *Trypetesa* material comes from the middle and upper to uppermost parts of the Korytnica Clays which were deposited when the basin had much reduced its depth (*see* Text-fig. 2).

The climatic and biogeographic conditions upon which the sequence of the Korytnica Clays was deposited, as apparently documented by a uniformitarianistic analysis of particular taxa and their communities, were tropical and/or subtropical with a dominating influence of the Indo-Pacific bioprovince (*see* BAŁUK & RADWAŃSKI 1977, 1979a).

CIRRIPEDE FAUNAS OF THE LOCALITY

The cirripede faunas in the Korytnica Basin were represented by various groups, the most common of which were the acorn barnacles (*Balanus*), associated with the scalpellids, the verrucids, and the chthamalids (*see* BAŁUK & RADWAŃSKI 1977, p. 98 and Fig. 5). Of the recognized genera, such as *Scalpellum, Conchoderma, Verruca, Chthamalus, Acasta, Creusia,* two have not as yet been reported from other Miocene occurrences (*Conchoderma* and *Chthamalus*), and only one, viz. *Creusia* (= *Ceratoconcha* auct.; *see* NEWMAN & ROSS 1976) has formerly subjected to monographic descriptions and ecological analysis (BAŁUK & RADWAŃSKI 1967, 1984b; *see also* BOUCOT 1990, pp. 17-18 and Figs 4-5). In the littoral zone of the Korytnica Basin, within the rocky substrate, was also recognized (*see* Text-fig. 1D) the presence of the borings *Zapfella pattei* SAINT-SEINE which are attributed to the acrothoracican cirripedes (RADWAŃSKI 1964, 1969, 1970; BAŁUK & RADWAŃSKI 1977).

STRATIGRAPHIC AGE OF THE LOCALITY

Stratigraphic age of the Korytnica Clays was precisely documented with the use of calcareous nannoplankton by MARTINI (1977) who indicated the presence of the biozones NN5 and the beginning of NN6. This places the age of the Korytnica sequence in the Middle Miocene, about 15 million years ago, precisely in the Badenian stage of the Central Paratethys basins in Central Europe (*cf.* Text-fig. 1A), or in the Upper Langhian — Lower Serravalian interval of the Mediterranean stage division.

OCCURRENCE OF *TRYPETESA* IN THE KORYTNICA BASIN

All the investigated *Trypetesa* specimens were found in gastropod shells of various genera and species, abundantly distributed in middle and upper to uppermost parts of the Korytnica Clays sequence (*see* Text-fig. 2). The other shelly or skeletal materials from the Korytnica Clays (other mollusks, corals, echinoderms) have not been infested by *Trypetesa*. No *Trypetesa* borings have also been found in rocky shores widely distributed along the shores of the Korytnica Basin which are well readable in the present-day topography. Within this littoral zone, all structural elements (abrasion surfaces, cliff rubbles) are profusely bored by diverse rock-borers (sponges, polychaetes, bivalves), among which *Zapfella pattei* SAINT-SEINE was noted rarely in very local occurrences (*see* Text-fig. 1D).

The frequency of the *Trypetesa*-infected gastropod shells in the Korytnica Clays was rather low. Of the scanned specimens, numbering over 30. 000, merely a hundred (99) was taken by *Trypetesa*. The majority of shells of the much diversified gastropod assemblage of the Korytnica Clays (total is about 800 species; *see* BAŁUK 1975; BAŁUK & RADWAŃSKI 1977, p. 98) were more or less rapidly buried, thus having been preserved almost fresh and even with their coloration. Only a part of the assemblage, estimated as about 10%, underwent to bioerosional damage, epibionthic overgrowth, and/or colonization by secondary inhabitants (= squatters). Of the squatters, the most spectacular is the slipper-limpet *Crepidula crepidula* (LINNAEUS) which preferably occupied the shells longer exposed on the bottom (*see* BAŁUK & RADWAŃSKI 1977, 1985).

The *Trypetesa* specimens appear within the gastropod shells of the Korytnica Clays (*see* Table 1) either singly or in groups composed of several (usually, up to 3 − 5) individuals. Greater numbers (17 − 18, and once 32) are quite sporadic (*see* Pl. 2, Fig. 1). The single borings, as a rule, are larger than those occurring in
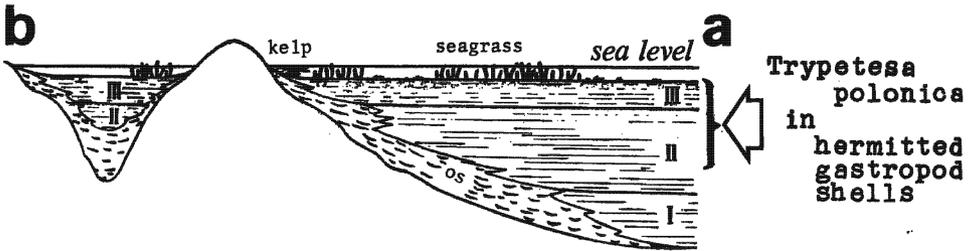

Fig. 2. Idealized section through the southern part the Korytnica Basin (*compare* Text-fig. 1D) during sedimentation of the topmost part of the Korytnica Clays, to show a part of the sequence yielding the investigated acrothoracican cirripedes, *Trypetesa polonica* sp. n., in hermitted gastropod shells (*adopted from*: BAŁUK & RADWAŃSKI 1977, Fig. 6C)

Within the sedimentary basin are indicated areas of deposition of the littoral oyster shellbed (*os*), successive numbers (*I, II*, and *III*) of the Korytnica Clays, as well as biotopes taken by littoral kelp and seagrass beds; for the distance to the shoreline see the scale in Text-fig. 1D

groups. In the latter case, when the specimens are more numerous, they become smaller due to restriction of the available space within the housing gastropod shell (*see* Pl. 1, Fig. 2*b*). Moreover, in such a case, position of the boring within the gastropod shell may also change (*see* Pl. 4, Fig. 4 *and* corresponding Text-fig. 6).

The single borings dominate in the investigated material. Besides these emplaced at the inner surface of the outer wall in the last whorl of gastropod shells, and which constitute over a half of the studied specimens (59 of 99 total), always single are those within the columella of a gastropod shell. The number of the latter is, however, remarkably low in the investigated material since it attains one fifth of the total (19 specimens), and only 6 gastropod shells are infected solely within the columella.

The list of gastropod species, from the Korytnica Clays, whose shells have been infected by *Trypetesa* includes (*compare* Table 1):

Cerithium miospinosum SACCO — 1 specimen
Rostellaria dentata GRATELOUP — 2 specimens
Triton nodiferum LAMARCK — 2 specimens
T. tarbellianum GRATELOUP — 2 specimens
Ranella marginata (MARTINI) — 8 specimens
Murex spinicosta BRONN — 1 specimen
M. austriacus TOURNOUËR — 6 specimens
Ocenebra erinacea (LINNAEUS) — 1 specimen
Purpura exilis PARTSCH — 1 specimen
Fusus hoessi PARTSCH — 11 specimens
F. valenciennesi (GRATELOUP) — 2 specimens
Euthria puschi (ANDRZEJOWSKI) — 11 specimens
E. inflata BELLARDI — 1 specimen
Ancilla glandiformis (LAMARCK) — 16 specimens
Sveltia inermis (PUSCH) — 2 specimens
Clavatula granulatocincta (MÜNSTER) — 2 specimens
C. camillae (R. HOERNES & AUINGER) — 1 specimen
C. evae (R. HOERNES & AUINGER) — 1 specimen
C. styriaca (AUINGER) — 3 specimens
C. laevigata (EICHWALD) — 5 specimens
C. asperulata (LAMARCK) — 19 specimens
Terebra fuscata (BROCCHI) — 1 specimen.

All the investigated *Trypetesa* specimens were found in rather thick-walled gastropod shells. Their occurrence was recognized in shells of 13 gastropod genera (*see* Table 1), viz.: *Cerithium, Rostellaria, Triton, Ranella, Murex, Ocenebra, Purpura, Fusus, Euthria, Ancilla, Sveltia, Clavatula,* and *Terebra*. The infected shells were found either complete, with their apertures intact, or they were damaged, with a greater or lesser part of their whorls broken off. In both cases, the shells were usually looking unfresh, having been worn allover to a variable extent, and thus differing at the first sight from those making up the common findings of the Korytnica gastropods.

A sufficient thickness of the gastropod shell was one, but not the only space requirement for the studied *Trypetesa* specimens. Of many thick-shelled gastropods occurring in the Korytnica Clays, preferred by the *Trypetesa*

Table 1

Examples of distribution of *Trypetesa polonica* sp. n. in shells of some gastropod species from the Korytnica Clays

GASTROPOD SPECIES	Trypetesa polonica sp.n. in: outer wall	columella	Ctenostome bryozoans — Spathipora	Terebripora	Penetrantia	Helicotaphrichnus	Cliona	Polydora	Gastrochaena	Spirorbis	Serpulidae	Cheilostomata	Crepidula
Rostellaria dentata GRATELOUP:													
Specimen No. 1 — see Pl. 3, Fig. 3	2							+					
— " — 2 — see Pl. 3, Fig. 7	1												
Triton nodiferum LAMARCK:													
Specimen No. 3	1				+			+					
— " — 4 — see Pl. 3, Fig. 2	1							+					
Triton tarbellianum GRATELOUP:													
Specimen No. 5	2					+							
— " — 6	2							+					
Ranella marginata (MARTINI):													
Specimen No. 7 — see Pl. 2, Fig. 1	32												
— " — 8	5	1			+								
— " — 9	4					+							
— " — 10	3							+					
— " — 11	2				+	+		+	+	+			+
— " — 12	2				+								
— " — 13 — see Pl. 3, Fig. 4	1				+								
— " — 14	1				+		+						
Murex austriacus TOURNOUËR:													
Specimen No.15 — see Pl. 1, Figs 1a-1b	18							+	+	+			
— " — 16 — see Pl. 1, Fig. 4	17							+					
— " — 17	4												
— " — 18	2				+			+		+	+	+	
— " — 19	2					+		+					+
— " — 20	1							+		+			
Ancilla glandiformis (LAMARCK):													
Specimen No.21	8							+					
— " — 22	2	1	+					+		+			
— " — 23	2				+			+		+			
— " — 24	1	1				+		+					
— " — 25	1	1	+					+		+			
— " — 26	1	1	+					+		+			
— " — 27	—	1	+					+		+			
— " — 28 — see Pl. 6, Fig. 2	—	1	+					+					
— " — 29	—	1											
— " — 30	1		+	+		+		+					
— " — 31	1		+					+					
— " — 32 — see Pl. 3, Fig. 1	1							+					
Sveltia inermis (PUSCH):													
Specimen No.33 — see Pl. 5, Figs 2a-2b	5	1						+					
— " — 34	2							+					
Clavatula granulatocincta (MÜNSTER):													
Specimen No.35 — see Pl. 1, Figs 2a-2c	9							+		+	+	+	
— " — 36	1												
Clavatula asperulata (LAMARCK):													
Specimen No.37	4												+
— " — 38 — see Pl. 4, Fig. 2	3							+					
— " — 39	3							+					
— " — 40	3							+					
— " — 41	3							+					
— " — 42 — see Pl. 5, Figs3a-3b	2							+					
— " — 43	1	1						+	+				
— " — 44 — see Pl. 6, Figs 5a-5b	—	1											
— " — 45	1							+					
— " — 46	1							+					
Terebra fuscata (BROCCHI):													
Specimen No.47 — see Pl. 4, Fig. 1	2				+			+	+				

specimens (*see* Table 1) were the high-spired shells (such gastropod genera as *Cerithium, Rostellaria, Fusus, Clavatula, Terebra*), with an access of some less elongated shells (genera *Triton, Murex, Ocenebra, Euthria, Sveltia*), and a total absence of *Trypetesa* in isometric or flat-spired shells (*e.g.*, of moon snails so common in the Korytnica Clays). Preferred also were the slightly elongated shells with the last whorl rather spacious and their aperture distinctly wide (genera *Ranella, Purpura, Ancilla*). Noted is the absence of *Trypetesa* in any shells with narrow apertures (*e.g.*, in cone shells and cowries). To sum up, the infected shells may be characterized as thick-walled and either high-spired, or spacious with wide aperture, if the shell is less elongated.

The gastropod shells infected by *Trypetesa* in groups have apparently been damaged much more seriously than they were prior to the settlement of these acrothoracican cirripedes. The state of preservation of such shells when found in the Korytnica Clays, becomes consequently very poor (*see* Pl. 1, Fig. 1 and Pl. 2, Fig. 1).

To exemplify the distribution of *Trypetesa* in the shell specimens of particular gastropod species from the Korytnica Clays, a separate account is given (Table 1) which also contains a survey of various epi- and endobionts present in these shell specimens, and whose significance will be discussed hereafter.

GENERAL ACCOUNT ON MODERN AND ANCIENT TAXA
OF THE ACROTHORACICAN CIRRIPEDES

The modern acrothoracican cirripedes, which all bore in the organic, shell and/or other skeletal substrate, are classified by NEWMAN, ZULLO & WITHERS (1969) in the *Treatise on Invertebrate Paleontology*, part *R*, as a separate order, the Acrothoracica GRUVEL, 1905. A discussion of this treatment and new proposals have recently been claimed by NEWMAN (1987). In the *Treatise*, the order is subdivided (*see* NEWMAN, ZULLO & WITHERS 1969, pp. *R271-R272*), through the suborders, into the three families, as follows:

the **Lithoglyptidae**, with the type genus *Lithoglyptes* AURIVILLIUS, 1892, and five other genera;
the **Cryptophialidae**, with the only genus *Cryptophialus* DARWIN, 1854; [and subsequently added *Australophialus* TOMLINSON, 1969a];
the **Trypetesidae**, with the only genus *Trypetesa* NORMAN, 1903.

The first two families contain relatively smaller forms (up to several millimeters in diameter) boring in organic calcareous substrates which are accessible at various, usually greater depths in sea basins (*see* GRYGIER & NEWMAN 1985, NEWMAN 1987). Some reports, however, concern also a mass occurrence of one of the *Cryptophialus* species in New Zealand in the intertidal zone exclusively (BATHAM & TOMLINSON 1965), and of one lithoglyptid species, *Berndtia purpurea* UTINOMI, in the littoral zone of Japan (UTINOMI 1950).

The family Trypetesidae contains distinctly larger forms (even beyond

1 centimeter in diameter) boring in the interior of gastropod shells inhabited by hermit crabs in the shallowest waters (see TOMLINSON 1953, 1955, 1969a,b; NEWMAN 1979).

Of these three families, only the Trypetesidae were reported from ancient deposits. The two such records concern: (i) Unnamed forms occurring in an Upper Cretaceous echinoid test, presented and supposedly compared to *Alcippe* (= *Trypetesa*, see NORMAN 1903) by JOYSEY (1959), and subsequently attributed to the family Trypetesidae by TOMLINSON (1963, p. 165); (ii) Upper Paleozoic (Pennsylvanian to lowermost Permian) forms from the United States, named *Trypetesa caveata* by TOMLINSON (1963) who established this species upon the borings preserved in the exterior of bivalve shells; an attribution of these forms to the genus *Trypetesa* was objected by SEILACHER (1969, p. 709) and NEWMAN (1979, p. 410; see also HÄNTZSCHEL 1975, pp. W138–W139). Anyway, these two records speak clearly about a habitat of ancient *Trypetesa* species different than that of modern representatives of this genus, as already was noted by NEWMAN, ZULLO & WITHERS (1969, p. R272).

All other acrothoracican borings reported from ancient deposits dating back to the Middle Devonian (see SAINT-SEINE 1951, 1954; CODEZ & SAINT-SEINE 1957; VOIGT 1958, 1959, 1967b; SCHLAUDT & YOUNG 1960; RODDA & FISHER 1962; TOMLINSON 1963; TAYLOR 1965; RODRIGUEZ & GUTSCHICK 1970, 1977) have evidently got a status of trace fossils, and should therefore be classified as ichnotaxa, what was briefly argued by NEWMAN, ZULLO & WITHERS (1969, pp. R251–R252 and R272) who classified them into two (ichno)families of unknown systematic position, as follows:

the Rogerellidae, with the only genus *Rogerella* SAINT-SEINE, 1951;
the Zapfellidae, with the type genus *Zapfella* SAINT-SEINE, 1954, and two other genera.

Concerning the borings (incorrectly called the burrows, see BROMLEY 1970, p. 50), it was stated by NEWMAN, ZULLO & WITHERS (1969, p. R272) that in the fossil material only the genera *Trypetesa* and *Cryptophialus* can be recognized by the form of their borings alone.

A peculiar morphology of the *Trypetesa* borings, differing them from all other acrothoracican borings, will be described hereafter. In regard with the genus *Cryptophialus*, this statement appeared from the discovery of "migrating" or "motile" borings (BATHAM & TOMLINSON 1965), the features of which are also met in the ichnogenus *Rogerella*. Recent investigations by GRYGIER & NEWMAN (1985) showed, however, that such very features are shared by some representatives of the family Lithoglyptidae (genera *Lithoglyptes* and *Weltneria*). In the fossil material these features are also displayed by the classic material of the firstly discovered ancient acrothoracican borings by ZAPFE (1936) in gastropod shells from the Miocene deposits of Hungary (locality Várpalota) and Austria (locality Grund; see Text-fig. 1A). This material has still remained unnamed specifically, although it inspired SAINT-SEINE to establish a new genus *Zapfella* in 1954, and its original picture was twice used to illustrate that taxon (HÄNTZSCHEL

1962, Fig. 144/1a *and* 1975, Fig. 83/2c). Its close resemblance to the modern genus *Lithoglyptes* (the species *L. indicus* AURIVILLIUS) was emphasized already by ZAPFE (1936) himself, and noted by SAINT-SEINE (1954), as well as accepted recently by GRYGIER & NEWMAN (1985).

From ichnological point of view, presented in the *Treatise on Invertebrate Paleontology*, Part *W* (first edition 1962, second edition 1975) by HÄNTZSCHEL (1962, 1975), all ancient acrothoracican borings are classified as ichnogenera and any higher taxa (*e. g.*, ichnofamilies) are not taken into consideration.

Not discussed herein is the taxonomic system of the fossil acrothoracican borings established by TOMLINSON (1969a) which has neither been introduced by NEWMAN, ZULLO & WITHERS (1969) to the *Treatise on Invertebrate Paleontology*, Part *R*, nor by HÄNTZSCHEL (1975) to its Part *W* (second edition).

In this system, the ancient families Zapfellidae and Rogerellidae, the both based solely upon the borings, are treated as compatible with those establised upon present-day animals. They both are synonymized (TOMLINSON 1969a, pp. 31 and 151) with the family Lithoglyptidae AURIVILLIUS, 1892, the diagnosis of which is based on soft parts of the cirripede body.

Furthermore, the genus *Zapfella* SAINT-SEINE, 1954, is not accepted by TOMLINSON (1969a), and its type species, *Zapfella pattei* SAINT-SEINE, 1954, is distributed throughout the other genera and species (*see* TOMLINSON 1969a, pp. 134-138). The referenced specimens from the Korytnica Basin, reported by the co-author of the present paper (RADWAŃSKI 1964), are included by TOMLINSON (1969a, p. 138) to "*Nymites sacculus* MÄGDEFRAU, 1937". The latter ichnogenus [recte *Nygmites* (!)] is dubious, both in regard with its authorship, nature of taxa included, and paleobiological interpretation (*compare* HÄNTZSCHEL 1962, p. *W*230; *and* 1975, pp. *W*130-*W*131). In a comprehensive study of the Mesozoic belemnicolid borings, VOIGT (1972, p. 122) puts the ichnospecies *sacculus* of MÄGDEFRAU (1937) to the ichnogenus *Brachyzapfes* which should be correctly ascribed to CODEZ & SAINT-SEINE, 1957, and which is evidently separate to *Zapfella*, the latter having been regarded as a valid ichnotaxon (*see* HÄNTZSCHEL 1975, p. *W*136).

It should be noted, that some reports on ancient acrothoracican borings have not offered any taxonomy at all (SCHLAUDT & YOUNG 1960; RODDA & FISHER 1962; ROSS 1965; RODRIGUEZ & GUTSCHICK 1970, 1977).

Moreover, it is to note that still under discussion is the problem of the hosts being live or dead when bored by the ancient acrothoracicans (*see* review by RODRIGUEZ & GUTSCHICK 1970, 1977). In modern acrothoracicans, the nature of the substrate (dead or live) is not however fully recognized as yet (*see* UTINOMI 1950; TOMLINSON 1969a, b; SEILACHER 1969; BROMLEY 1970).

A reaction of the host to the acrothoracican borings in modern environments was once ascribed by BROMLEY (1970, p. 63, Fig. *4f*) to a lithoglyptid, *Kochlorine hamata* NOLL, living in the shell of the gastropod *Haliotis*. The original picture presented by NOLL (1875, Pl. 6, Fig. 16) does not, however, offer a basis for such thinking: it shows a broken piece of an abolone shell, in which a blister on the inner shellside has no connection to any *Kochlorine hamata* borings.

In ancient acrothoracicans, some forms of the ichnogenus *Rogerella*, when met in echinoid tests (*see* SAINT-SEINE 1951, 1955, 1956), were suggested by SEILACHER (1969, pp. 713-715 *and* Fig. 5) to had lived commensally with these echinoderms, but this interpretation was soonafter objected by BROMLEY (1970, pp. 69-70).

An objection may also concern an interpretation of the acrothoracican cirripedes oriented on belemnite guards, and given by SEILACHER (1968, 1969) who assumed that they had bored in living belemnites whose guards were then covered with a very thin mantle and/or were bare at all. The event of boring of the guards by acrothoracican cirripedes and orientation of their borings may appear, however, also from current orientation of the borings when they rested on the bottom and were temporarily turned around so that all their sides were accessible for successive settlement of the cirripede larvae. In modern acrothoracican cirripedes, orientation was noted as almost typical in a *Lithoglyptes* species living on the deep-sea corals (GRYGIER & NEWMAN 1985, p. 6).

In modern thoracican cirripedes, orientation of various kind is known in many cases, not necessarily alongwith the current. To exemplify, in the genus *Coronula* noted was a tendency to keep orientation of the rostra directing ahead the whales or ships to which they had attached (CRISP & STUBBINGS 1957). Orientation, moreover, appears in vertically staying objects, on which acorn barnacles grow with their carinae upwards (BUCK 1937), and on ordinary gramophone records used by GREGG (1948) in natural-environment experiments, during which the barnacles grew oriented along the sound grooves (*see* GREGG 1948, Figs 1-2).

An evident case of the commensalism in ancient acrothoracicans is certainly that one recognized by SEILACHER (1969, p. 715 *and* Fig. 6a) for the above indicated forms first reported by ZAPFE (1936) whose original material from gastropod shells was interpreted by SEILACHER as evidencing a commensal relationship between acrothoracicans and hermit crabs inhabiting these shells, similarly as it takes place in the modern genus *Trypetesa*.

The above review displays apparently a disjunction in nomenclature and behavior of modern and ancient acrothoracican cirripedes, with the only exception kept by the genus *Trypetesa* which comprises both extinct and extant forms, though of different behavior. Moreover, a serious confusion is also apparent in recognition of the nature of many, if not most of the ancient acrothoracican borings, and in their attribution to any modern taxa. The following description of the Miocene specimens from the Korytnica Clays will serve to demonstrate the features typical of modern *Trypetesa* species present in the ancient material.

A COMPARATIVE NOTE ON THE ASCOTHORACICAN CIRRIPEDES

The ascothoracican cirripedes, whose borings may easily be confused with those of the acrothoracicans, are classified by NEWMAN, ZULLO & WITHERS (1969) as a separate order, the Ascothoracica LACAZE-DUTHIERS, 1880. Recently, their taxonomical status and their belonging to the Cirripedia have become a subject of thorough discussions (*see* GRYGIER 1981, 1983, 1985; NEWMAN 1987).

The group of the ascothoracican cirripedes comprises the genera of highly advanced host specifity, which live as ecto- or endoparasites on various coelenterates and echinoderms (*see* KRÜGER 1940; VOIGT 1959; NEWMAN, ZULLO & WITHERS 1969; GRYGIER 1981, 1983, 1985; ZIBROWIUS & GRYGIER 1985; NEWMAN 1987).

The fossil record of the ascothoracican cirripedes contains only the forms recognized by VOIGT (1958, 1959, 1967a), and which had formed cysts in Upper Cretaceous octocorals to whom they had become the commensals rather than the true parasites (*see* VOIGT 1959 *and* a remark by BROMLEY 1970, p. 67). A report on the ascothoracican occurrences in the Upper Cretaceous echinoid from Denmark (MADSEN & WOLFF 1965), commonly accepted (*see* HÄNTZSCHEL 1975, p. W139; BOUCOT 1990, p. 72) is

however not obvious since the original photos of poor quality (MADSEN & WOLFF 1965, Pl. 1, Figs 1 and 3-5) illustrate rather undeterminable borings of a gastropod-drilling appearance.

BORING BEHAVIOR OF MODERN *TRYPETESA*

General aspects of the biology and behavior of the modern species of *Trypetesa*, which have a bearing upon the development and the features of their borings, may be characterized following as taken from the reference data (HANCOCK 1849; DARWIN 1854; AURIVILLIUS 1894; BERNDT 1903; GENTHE 1905; NILSSON-CANTELL 1921; KÜHNERT 1934; TOMLINSON 1955, 1969a, b; GRYGIER & NEWMAN 1985).

The body of modern *Trypetesa* species is of a flattened sac shape. This is achieved by the females only which bore into the gastropod shells. The pygmy males are attached to the female, in her anterior part, and they supposedly acquire solely a reproductive role. Most of their organs are reduced, and any digestive tract is lacking, so that they do not eat at all. Not stated in *Trypetesa*, but recognized in one species of *Cryptophialus* is the fact that the males may bore their own, accessory hollows within the female boring (*see* BATHAM & TOMLINSON 1965, p. 150 and Figs 7-8).

The boring process in modern *Trypetesa* species starts with chemical dissolution when the cyprid larva settles upon the shell (*see* KÜHNERT 1934). It adheres to the inner surface of the gastropod shell, and thus the original part of the boring and the aperture of the adult forms are visible from that very side of the shell (*see* Text-fig. 3).

Further enlargement of the boring, after the metamorphosis, progresses mechanically through the action of chitinous teeth or thorns which are studding the mantle surface, and are renewed with each molt. The abrasive teech operate due to rhythmic strokes of the body. In result, fine striae radiating more or less regularly from the place of animal's attachment (*i. e.*, the horny knob; *see* Text-fig. 3), appear on both sides of the boring. The growing cirripede fills the boring tightly so that the boring itself reflects quite precisely the shape of the animal body (*see* GRYGIER & NEWMAN 1985, Fig. 8/III).

The boring is successively enlarged both on- and downwardly. An onward, that is posterior in accepted terminology (*see* Text-fig. 3), direction is responsible for the widening of the aperture, but this is associated with a slight twist, what gives the aperture a virguloid appearance. The older, thinner part of the aperture (that is anterior, *see* Text-fig. 3), called *the peduncular slit*, is plugged with the horny knob through which the cirripede attaches to the boring, and which is not shed off at time of ecdysis. The younger, more oval part of the aperture makes up an orificium (*see* Text-fig. 3).

Alongwith the aperture, especially at its middle part, *a bourrelet* composed of calcareous laminae (mechanically ground, or secreted material) may develop on one or both of its sides (*see* TOMLINSON 1955, 1969a, b; GRYGIER & NEWMAN 1985).

A downward enlargement of the boring realizes at various angles and directions. Originally, it progresses vertically, that is in the sagittal plane of the aperture. Further on, it acquires both on- and backward component in *Trypetesa lampas* (HANCOCK), as indicated by GRYGIER & NEWMAN (1985, Fig. 8/IIIa-b), but in *Trypetesa lateralis* TOMLINSON the boring slants to the right, to achieve horizontal position within the gastropod shell (*i. e.*, parallel to the inner surface of the shell). A sufficient thickness of the gastropod shell is believed to be the main selective requirement for the substrate, because the horizontal boring is placed just at the inner surface of the shell, to such an extent that its outline is easily seen through a thin, residual portion of the shell.

This part of the *Trypetesa* body which almost contacts the inner surface of the gastropod shell is called *right*, and the opposite one being *left* (TOMLINSON 1955). The left side is thus relatively distant to the outer surface of the gastropod shell, to which an external mantle flap of the body may bore an elongated, vent-like hole. This vent-hole drilling is shaped like a flattened pipe, slightly sinuous, and it pierces out the shell to produce an elongated perforation, called *the accessory exit*, to the outer surface (*see* photos of casted borings *in* SEILACHER 1969, Pl. 4: the vent-hole drilling molded as a projected lath). In *Trypetesa lateralis* TOMLINSON such a drilling realizes in some specimens only, whereas in *T. lampas* (HANCOCK) and other species of the genus it is unknown.

The function of the vent-hole drilling in *Trypetesa lateralis* TOMLINSON has long been a matter of discussion.

Formerly, TOMLINSON (1955, p. 113) noticed an outwardly directed movement of water through it, whereas SEILACHER (1969) ascertained the two, quite opposite thinkings, one about an inward motion from the perforation "*through which water can enter directly from the outside to the quarters of the dwarf males*" (SEILACHER 1969, p. 715), and another one, about "*an outside exit for the dwarf males*" (SEILACHER 1969, p. 717).

As recognized later by TOMLINSON (1969a), the accessory exit appears only in some adult specimens, that is the females, the majority of which were provided with the attached males. Nevertheless, the other females, much smaller in number, had the accessory drilling but no males. A few specimens, though provided with the males, did not produce the discussed drilling (*see* TOMLINSON 1969a, pp. 14-17 and Fig. 36c).

To sum up, the formation of the external mantle flap still remains unclear in respect to whether and how it serves to the males attached actually near the proximal end of this mantle flap. Anyway, as apparent from observations reported by TOMLINSON (1969a) the water, due to rhythmic strokes of the animal, is pumped through the exit in both directions, regardless of the male being. A new ecological interpretation of the nature of this accessory perforation will be given hereafter, when description of the investigated material is presented.

SYSTEMATIC ACCOUNT

As it is apparent from the foregoing description of the fossil acrothoracican borings from the Korytnica Basin, their overall structure, which is well defined in

everyone specimen, and their typical details allow to recognize that the cirripede body producing the boring differed from that of any present-day species. The studied Miocene material is therefore thought to represent a new species which is characterized in the category of the body fossils.

<div align="center">

Class **Cirripedia** BURMEISTER, 1834
Order **Acrothoracica** GRUVEL, 1905
Suborder **Apygophora** BERNDT, 1907
Family **Trypetesidae** STEBBING, 1910

Genus *Trypetesa* NORMAN, 1903
Type species: *Alcippe lampas* HANCOCK, 1849; *SD* STEBBING, 1910

Trypetesa polonica sp. n.
(Plates 1-6)

</div>

HOLOTYPE: The boring presented in Pl. 5, Figs 1a-1c.

TYPE LOCALITY: Korytnica, 24 km SSW of Kielce, southern slopes of the Holy Cross Mountains, Central Poland.

TYPE HORIZON: Middle Miocene (Badenian stage of the Central Paratethys, or the Upper Langhian — Lower Serravalian of the Mediterranean Realm).

DERIVATION OF THE NAME: Latin *polonicus* — after the country of the finding.

MATERIAL: Over 260 specimens in 99 gastropod shells from the middle and upper to uppermost parts of the Korytnica Clays.

DIAGNOSIS: Borings large (up to 13 mm in length), bipartite, with the smaller vestibule and the larger, fan-shaped chamber developed both anteriorly and laterally (in majority, right-sided) in regard to the aperture, tending to occur singly in thick-walled gastropod shells; some provided with an accessory exit.

DESCRIPTION OF THE BORING

The borings of *Trypetesa polonica* sp. n. are much variable in their overall shape, but some of their features are kept constant. This concerns location of the boring in regard to the aperture, subdivision of the boring into two parts, and the extent of the lobed part of the boring.

The aperture

The aperture is typically of a tapered slit appearance, the narrower part of which (*i. e.* the peduncular slit) is usually more or less twisted. In some specimens the apertures are almost straight (Pl. 1, Fig. 3; Pl. 2, Fig. 5; Pl. 5, Fig. 1a), but in others they become flexing (Pl. 1, Fig. 4; Pl. 2, Fig. 3) or even convolving to acquire an outline resembling a wriggling worm or a silverfish (Pl. 2, Fig. 4). The majority of apertures tend to be symmetrical in their sagittal (*i. e.* antero-posterior) section, but some attain a slightly bulbous appearance on one side (Pl. 5, Fig. 3a).

Along the aperture of some specimens, a lamellate construction forming the bourrelet is developed on one or both sides (*see* Text-fig. 3 and Pl. 2, Figs 2-5). The bourrelets are firmly attached to the apertural borders and they extend down the boring to a considerable depth (*see* Text-fig. 3A). Usually, the bourrelets are composed of a few sets of laminae, the boundaries of which are well pronounced (*see* Pl. 2, Figs 2-3 and 5).

The length of the aperture in adult specimens varies from 2.8 mm to 4.5 mm, with the maximum value of 5.5 mm; the width averages about 0.5 - 0.6 mm, and it reaches 0.8 mm in the most swollen specimens. In the holotype, the aperture is 3.0 mm long and 0.6 mm wide.

The boring

The boring is located anteriorly in regard to the aperture, and typically it is bipartite: an entrance part, called herein *the vestibule*, is situated adaperturally, whilst the other, called herein *the chamber*, extends anteriorly and slants usually to the right (*see* Text-figs 3-4).

In younger specimens the chamber slightly exceeds the vestibule in its size (Pl. 3, Fig. 1), and in the adult ones it is several times larger (Pl. 3, Figs 3-7).

The dimensions of the adult borings vary from 5 mm to 13 mm in length, and from 4 mm to 10 mm in width. The holotype is 7.5 mm long and 8 mm wide. The length/width ratio of the borings is so variable that an overall outline of the borings ranges from much elongated (*see* Text-fig. 5b and 5e), through isometric (*see* Text-fig. 5d), to that of the specimens wider than long, like the holotype (*see* Text-fig. 5a).

The vestibule in younger specimens is of an almost rectangular shape and it does not extend posteriorly beyond the aperture (Pl. 3, Fig. 1). In the adults, it becomes more oval (Pl. 3, Figs 3-5), or circular, with a pronounced constriction at the chamber boundary (Pl. 3, Figs 6-7). Posteriorly, it extends more (Pl. 3, Figs 3 and 6-7) or less (Pl. 3, Fig. 5) beyond the aperture. The whole surface of the vestibule is smooth (*see* Pl. 4, Figs 3a-3b, and thus it is demonstrated both on the "upper" (Pl. 3, Figs 1-7) and "lower" (Pl. 5, Figs 1b and 2a) side of the vestibule.

To define, the "upper" and the "lower" side of the vestibule, the same as of the chamber (*see below*), is herein understood as that being closer either to the inner, or to the outer surface of the gastropod shell, respectively.
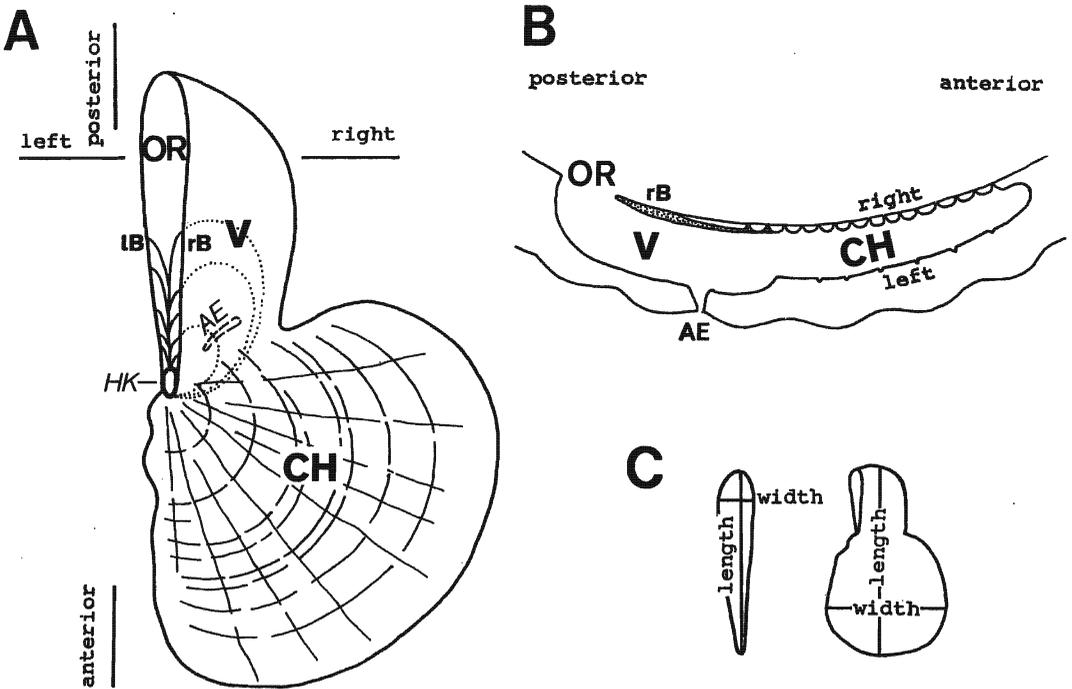
Fig. 3. Morphology of the right-sided, female borings of *Trypetesa polonica* sp. n.; their orientation and nomenclature

A — Apertural view of the boring, **B** — Section through the gastropod shell containing a boring, **C** — Measurements of the aperture (*left*), and of the boring (*right*)

Abbreviations: **OR** — orificium; **lB** — left bourrelet; **rB** — right bourrelet; **HK** — position of the horny knob; **V** — vestibule; **AE** — position of the accessory exit, situated on the "lower" side of the boring; **CH** — chamber
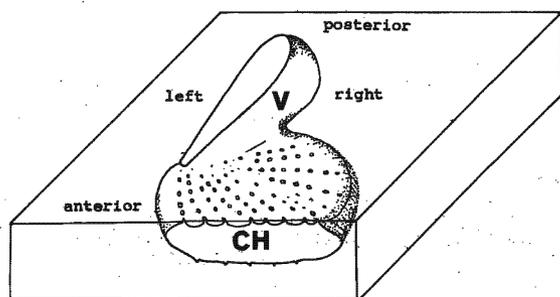
Fig. 4

Blockdiagram, to show space' orien-
tation of the right-sided, female boring
of *Trypetesa polonica* sp. n., viewed
from the inner surface of the gastropod
shell. (*compare* Text-fig. 3; abbrevia-
tions are the same: **V** — vestibule,
CH — chamber)

The chamber is generally fan-shaped, and typically extended to the right of the aperture [if we take
such orientation as used by TOMLINSON (1955) who describes it by viewing the specimens from their
apertures (*see* Text-figs 3-4); thus, all photos done from the outside of the gastropod shell (*e. g.*, Pl. 1,
Figs 1a-b and 2a-2b; Pl. 3, Figs 1-7; *etc.*) offer an opposite orientation, as having been taken
throughout the removed bottom of the boring], with a tendency to keep its adapertural margin
concordantly with the sagittal section of the aperture (Pl. 3, Figs 1 and 5-6). In some specimens, the
chamber more or less distinctly moves to the left (Pl. 3, Figs 2-3 and 7).

In few specimens, both the vestibule and the chamber are situated to the left of the aperture (Pl. 3,
Fig. 4 and specimen *1* in Pl. 4, Fig. 1), sometimes with a slight extent of the chamber to the right (Pl. 3,
Fig. 4); in the latter case, the chamber acquires a lobate outline, and it may be said that only one of the
lobes developed to the right.

The whole surface of the chamber is distinctly sculptured in two different patterns.

The "upper" side is provided with more or less continuous, slightly flexuose striae (*cf.* TOMLINSON
1955), some of which are additionally furnished with deep, denticle-like depressions (best visible in Pl.
3, Fig. 7). These denticle-like hollows may casually pierce throughout the "upper" wall of the boring,
producing thus the minute punctures in the inner surface of the gastropod shell (*see* Text-fig. 4; Pl. 5,
Fig. 3a; Pl. 6, Figs 1 and 5a). The striae are uniformly distributed on the chamber surface, but are
variously spaced in particular specimens: in some, they are rather loosely spaced (Pl. 3, Fig. 4), but in
others they are quite dense (Pl. 3, Fig. 5). All the striae radiate from the anterior region of the aperture
(*i.e.*, the peduncular slit), and indicate a boundary between the vestibule and the chamber in the
circumapertural part of the borings. Throughout the whole striated surface, indistinct growth lines
marked by the irregularities of this surface are detectable (best visible in Pl. 3, Figs 3 and 5). The above
mentioned denticle-like depressions appear at the intersection points of the growth lines and the striae
(Pl. 3, Fig. 7). The number of striae has been increasing during the animal growth, ranging from a few
in young specimens (Pl. 3, Fig.1) to over twenty in the adults (*see* Pl. 3, Fig. 5). The new striae are
always born as intercalatories (*see* Text-fig. 3 and Pl. 3, Figs 3-7), and thus they never bifurcate.

The "lower" side of the chamber is furnished solely by the sparsely distributed denticle-like
depressions, typically larger and deeper than those from the "upper" side of the chamber, and which
tend to be arranged radially and concentrically from the same region as in the case of the "upper" side
(Pl. 4, Figs 3a and 4; Pl. 5, Figs 1a-1b and 2a; Pl. 6, Fig. 3b).

In some specimens these denticle-like depressions are tailed with a slightly shallower furrow which
vanishes before the successive depression is met alongby the radius of the chamber (*see* boring *2* in Pl.
5, Fig. 2a).

The accessory exit

In some specimens, in the "lower" side of the borings (*left side* of TOMLINSON 1955) there appears an
accessory drilling, called herein *the vent-hole drilling*, which is opened to the outer surface of the
gastropod shell (*see* Pl. 5). This accessory exit is situated beneath the aperture, in the frames of the

vestibular region, and is oriented at an angle of about 50° — 60° to the aperture (*compare* Figs 1*a* and 1*b* in Pl. 5; *see also* Figs 2*a* and 3*a* in Pl. 5).

The vent-hole drilling is shaped like a flattened pipe, with rounded ends, and it is either almost straight (Pl. 5, Fig. 2*b*), slightly curved (Pl. 5, Fig. 3*b*), or more less flexuose (Pl. 5, Fig. 1*c*), when it reaches the outer surface of the gastropod shell. The shape of the drilling may change and, moreover, it may diminish when following from the "lower" side of the boring as far as the outer surface of the gastropod shell (*compare* Figs 1*b* and 1*c* in Pl. 5). Extremely, the accessory exit may be very tiny, almost circular or slightly oval while the beginning of the drilling is slit-like on the "lower" side of the boring (*compare* boring *1* in Figs 2*a* and 2*b* of Pl. 5).

Due to abrasion subsequent to the cirripede's life the whole vent-hole drilling is often much enlarged, and then large, ordinary holes appear on the outer surface of the gastropod shell (*compare* Figs 4*a* and 4*b* in Pl. 5).

In a few specimens, the vent-hole drilling remained unfinished: it is really small, but well advanced in the vestibule, and it does not reach the outer surface of the gastropod shell (*compare* boring *3* in Fig. 2*a* and its lack in Fig. 2*b* of Pl. 5).
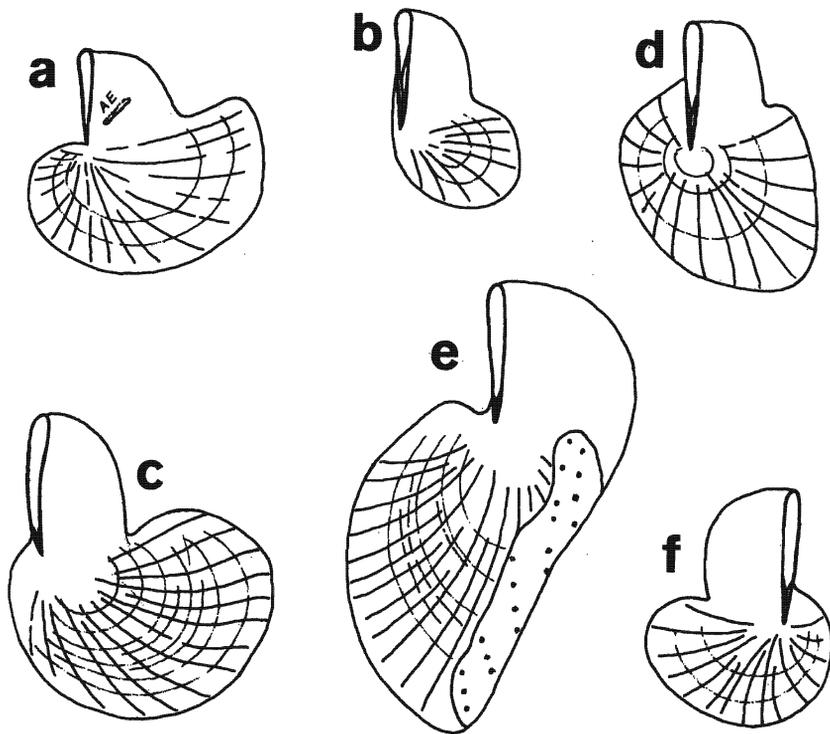
Fig. 5. Shape variability of the female borings of *Trypetesa polonica* sp. n. in apertural view: **a** — holotype, with location of the accessory exit (*AE*) indicated (*see* Pl. 5, Figs 1*a*-1*b*); **b** — juvenile specimen (*see* Pl. 3, Fig. 1); **c** — adult specimen with the strongly developed right-sided chamber (*see* Pl. 3, Fig. 5); **d** — adult specimen with almost equally developed sides of the chamber (*see* Pl. 3, Fig. 2); **e** — large, adult specimen with its right side distorted along the gastropod-shell suture, and thus displaying partly the sculpture of its "lower" side (*see* Pl. 3, Fif. 3); **f** — specimen with the left-sided vestibule and a major part of the chamber (*see* Pl. 3, Fig. 4); all taken about × 4

The columella borings

As stated above, the borings in the columella of gastropod shells occur always singly, regardless of the presence or absence of other borings of the species in the outer wall of the shell whorls. The majority of borings develop within a columella, near the margin of the gastropod shell, with their apertures oriented anteriorly up-whorl, *i.e.* with their peduncular slits directed to the apex, along the spire of the columella (Pl. 6, Figs 1 and 3-6). Exceptionally, the borings are oriented down-whorl, but in this case the aperture is oriented with its peduncular slit down the columella (Pl. 6, Fig. 2). In consequence, the borings are always oriented right to the aperture.

The extent of the chambers in particular borings produced in the columella is dependant on the structure of the latter which may reasonably differ in various gastropods (*see* Pl. 6, Figs 3b and 6). The wall of the "upper" side of the boring is so thin (*see* Pl. 6, Fig. 4) that a pattern of punctures (Pl. 6, Figs 1 and 5a) is met more often than in the whorl borings. The denticle-like depressions on the "lower" surface of the chamber are distributed (Pl. 6, Fig. 3b) less regularly than those in the whorl borings. Moreover, due to the space situation of the columella which in all infected gastropod shells is closed, none of the columella borings is furnished with an accessory exit.

Space control to the boring

The majority of the borings, especially those occurring singly, are well placed within the thickness of thick-walled gastropod shells, and they are usually located in the middle of the shell whorl height (Pl. 4, Figs 3a-3b). In such mid-whorl parts of the shells the borings acquire their typical shapes (*see* Pl. 3, Figs 1-7).

Some of the borings are located near the whorl suture, and then slant to follow the wall of that whorl in which they originated, and never to touch nor to cross an earlier whorl of the gastropod shell (Pl. 3, Fig. 3; Pl. 4, Figs 1-2).

If two borings appear not very near each other, they usually develop to their normal average extent, and a very narrow barrier is left between the chambers (Pl. 4, Figs 1 and 4; Pl. 5, Fig. 2a). If two or more larvae have settled very closely, it happens that the borings are produced in a tiering way: one

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PLATE 1

Trypetesa polonica sp. n.

1a-1b — Borings in the shell of *Murex austriacus* TOURNOUËR, exposed by chipping-off a part of the gastropod shell: **1a** — Overall view of the shell, nat. size; **1b** — Close-up, to show fragments of crowded borings (numbered *1 - 6*; the adjacent specimen, numbered *7*, is visible in Fig. 1a), × 5

2a-2c — Borings in the shell of *Clavatula granulatocincta* (MÜNSTER): **2a** — Overall view of the gastropod shell, with the borings exposed by chipping-off a part of the shell, nat. size; **2b** — Close-up, to show four closely neighboring borings of deviated shape and downgraded size (the so-called stenomorphic borings), associated with the boring (marked *Pc*) of *Polydora ciliata* (JOHNSTON) younger than the acrothoracican borings; **2c** — Apertural view of the borings presented in Fig. 2b; both *2b* and *2c* × 5

3 — Aperture of the boring in the shell of *Clavatula asperulata* (LAMARCK), and provided with two bourrelets (magnified in Pl. 2, Fig. 2), × 5

4 — Group of borings in another shell of *Murex austriacus* TOURNOUËR, and displaying a slight orientation, either wing-like (four borings, at upper left) or more or less linear (five borings, at mid-right), × 5

All photos taken by B. DROZD, M. Sc.
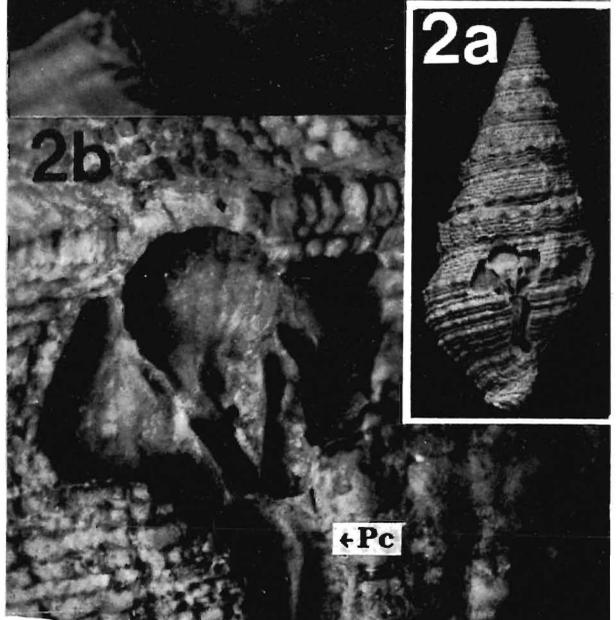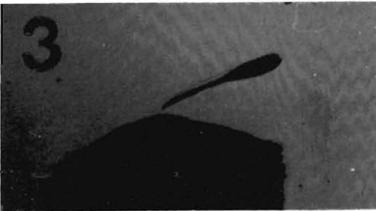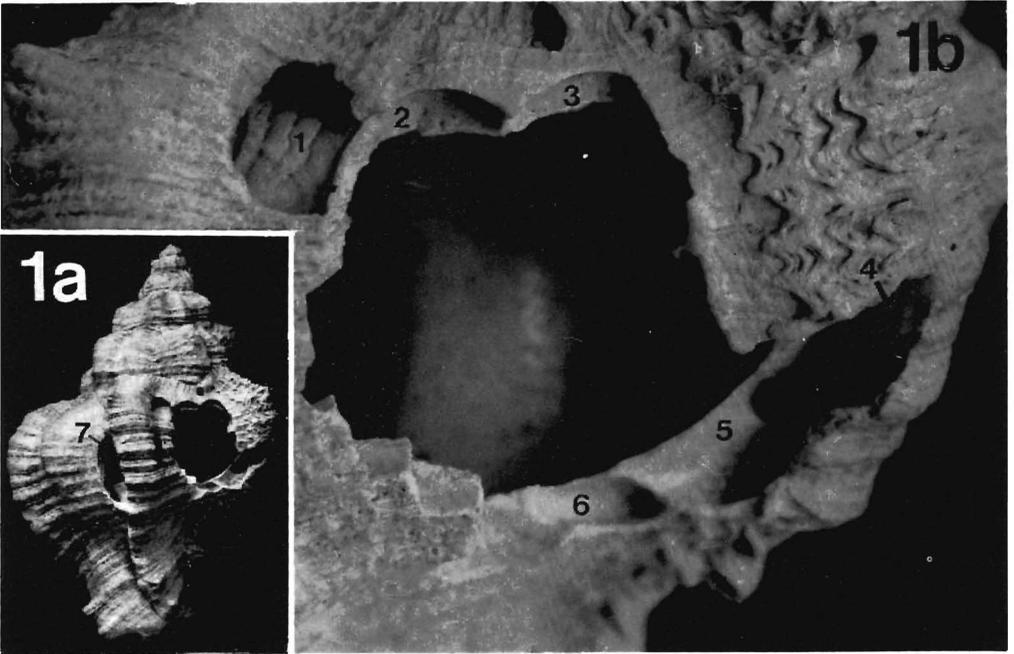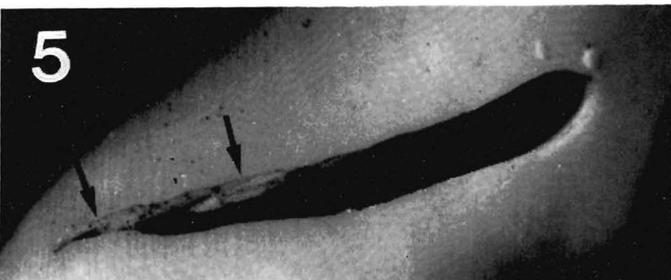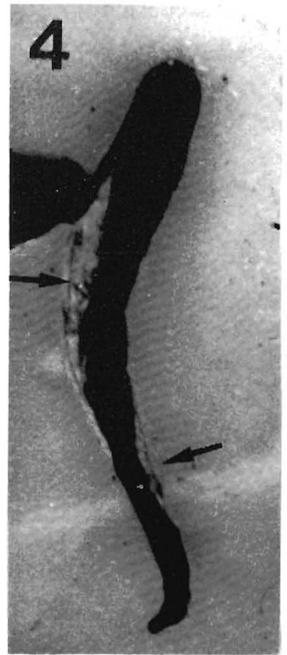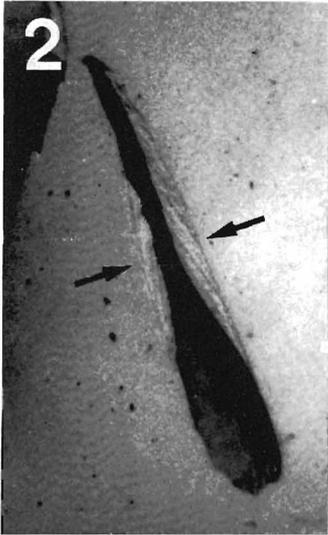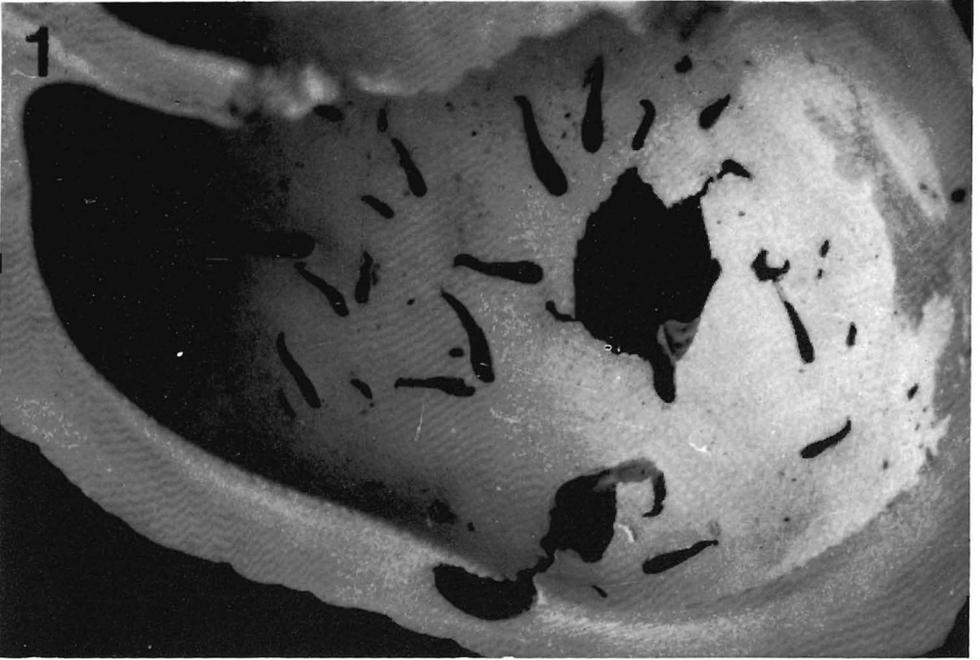
beneath the other, with a partial overlap near the contact, and a free development in other directions (Text-fig. 6 and Pl. 4, Fig. 4)

In the case of more numerous borings, assumed to be coeval, their shape tends to adjust to the space having been left by the neighboring borings. In this case the borings behave the same as benthic shelly animals, for instance acorn barnacles, growing in dense aggregations. The acquired shape may then much deviate from that typical of isolated borings; moreover, the size of the swarmed borings is much downgraded (Pl. 1, Fig. 2b), what justifies calling them *the stenomorphic borings*. Commonly, only one boring in a group of few is stenomorphic (*see* boring *2* in Pl. 4, Fig. 1; boring *3* in Pl. 4, Fig. 4; boring *3* in Pl. 5, Fig. 2a).

Biological interpretation of some features

Some features recognized in the borings of *Trypetesa polonica* sp. n. may be commented in regard to the biology of their producers as follows.

The lamellate construction of the bourrelets, and the extension of their lobes deeply into the vestibule of the boring (*see* Text-fig. 3A) to make a closure of the peduncular slit (*see* Pl. 2, Figs 2-5) indicate their functional significance rather than accidental accumulation of the material ground during the boring processes. The nature of the bourrelets in the modern *Trypetesa* species has long been discussed (HANCOCK 1849; DARWIN 1854, p. 553; TOMLINSON 1969a, pp. 12-23; GRYGIER & NEWMAN 1985). The structure of the bourrelets in *Trypetesa polonica* sp. n. invokes their chemical secretion by the animal which was producing calcareous laminae when needed for its better location and protection inside the boring.

The radial striae on the "upper" side, *i.e.* the right one in the majority of borings of *Trypetesa polonica* sp. n., have originated from action of chitinous teeth (or thorns) when the animal body was making the rhythmic strokes. Because the body is attached to the wall of the boring by its horny knob which is not shed off at time of ecdysis, the striae must radiate from this very knob. The center of radiating striae therefore indicates always the position of the horny knob (*see* Text-fig. 3A).

The growth lines in the borings of *Trypetesa polonica* sp. n. are distributed repeatedly, with more

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PLATE 2

Trypetesa polonica sp. n.

1 — Swarm of borings, displaying apertures slightly oriented radially, in the shell of *Ranella marginata* (MARTINI), to show the adult forms associated with their spat; taken × 5, by B. DROZD, M. Sc.

2-5 — Apertures provided with bourrelets (*arrowed*); taken × 15, by B. MALINOWSKA

2 — Close-up of the aperture presented in Pl. 1, Fig. 3, of the boring in the shell of *Clavatula asperulata* (LAMARCK), to show symmetric bourrelets, composed of several sets of laminae, and developed along both sides of the aperture

3-4 — Close-up of the apertures presented in Pl. 4, Fig. 4 (numbered *1* and *2*), of the borings in the shell of *Clavatula laevigata* (EICHWALD), to show: 3 — Left bourrelet, with two sets of laminae visible, and developing deeply into the vestibule of the boring; 4 — Two bourrelets (left one, and right one) developed asymmetrically along various parts of the aperture

5 — Close-up of the aperture presented in Pl. 6, Fig. 5a, of the boring in another shell of *Clavatula asperulata* (LAMARCK), to show the left bourrelet, composed of two distinctly bound sets of laminae, the older of which (*at left*) has sealed the peduncular slit almost completely

or less equal distances between them (*see* Text-fig. 5 and Pl. 3). They were thus formed during the periodical stoppage of the animal's growth which may be ascribed to the molting cycle. These growth lines correspond to the major ridges in the shell of the thoracic cirripedes which are usually formed one per ecdysis (*see* DARWIN 1854; these are the prominent ridges of BOURGET 1980). The sparsely distributed, finer lines in some borings of *Trypetesa polonica* sp. n. (*see* Text-fig. 5c and 5e; Pl. 3, Figs 3 and 5) may consequently be interpreted as formed during minor changes in the growth ratio, relatable primarily to the environmental stress (*compare* BOURGET 1980).

On the other hand, it is likely to ascribe to the molting cycle the development of successive sets of calcareous laminae within the bourrelets (*see* Pl. 2, Figs 2-5).

Some borings of smaller size that occur singly and are devoid of the accessory exit are interpreted as produced by the juveniles (*see* Pl. 2, Fig. 1; Pl. 3, Fig. 1; borings 4 and 5 in Pl. 5, Fig. 2a; boring 5 in Pl. 5, Fig. 4a).

A peculiar feature displayed by the borings of *Trypetesa polonica* sp. n., and not as yet reported from the modern *Trypetesa* species, is that to bend the chamber at the sutural part of the gastropod shell. The chamber in the borings of *Trypetesa polonica* sp. n. is thus confined to the last whorl of the gastropod shell (or, its fragmented part), and it never encroaches upon the former whorl (*see* Pl. 3, Fig. 3; Pl. 4, Figs 1-2). This peculiar feature should be interpreted as a reaction of the cirripede against the presence of the periostracum, composed of conchiolin, and which was not pierceable by the cirripede. Another, certainly more vulnerable interpretation is that it was a matter of thermophilic sensibility of the cirripede in regard to the hermit's body which was contained (*see below*) in the whorl of a complete or broken shell.


PLATE 3

Trypetesa polonica sp. n.

Shape variability of borings exposed by chipping-off a part of the gastropod shell (thus, oriented reversely to the apertural views in Text-fig. 5): *1-3* and *5-7* are right-sided specimens, whereas *4* is a left-sided one; detailed explanations in the text

Arrowed are the anterior ends of the peduncular slits in particular borings, and closed by bourrelets developed along each side of the aperture

1 — Juvenile specimen (outlined in Text-fig. 5b) in the shell of *Ancilla glandiformis* (LAMARCK).

2 — Adult specimen (outlined in Text-fig. 5d) in the shell of *Triton nodiferum* LAMARCK, and displaying the chamber developed almost equally on both sides of the aperture

3 — Large, adult specimen (outlined in Text-fig. 5e) in the deeply broken shell of *Rostellaria dentata* GRATELOUP, with its right part of the chamber deeply curved into the sutural part of the gastropod shell; fine growth lines are well marked

4 — Adult, left-sided specimen (outlined in Text-fig. 5f) in the shell of *Ranella marginata* (MARTINI); the outline of the boring is partly indicated by a broken line

5 — Adult specimen (outlined in Text-fig. 5c) in the shell of *Fusus hoessi* PARTSCH, and displaying its chamber strongly developed: both dense striae and fine growth lines are well marked

6 — Adult specimen in the shell of *Fusus valenciennesi* (GRATELOUP)

7 — Adult specimen in another deeply broken shell of *Rostellaria dentata* GRATELOUP
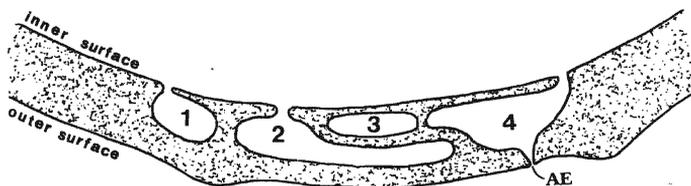
All photos × 5; taken by B. DROZD, M. Sc.
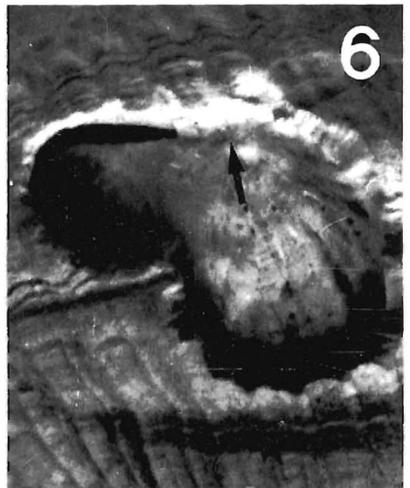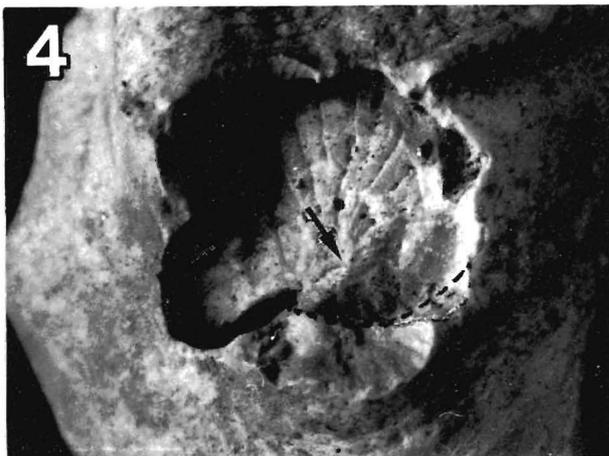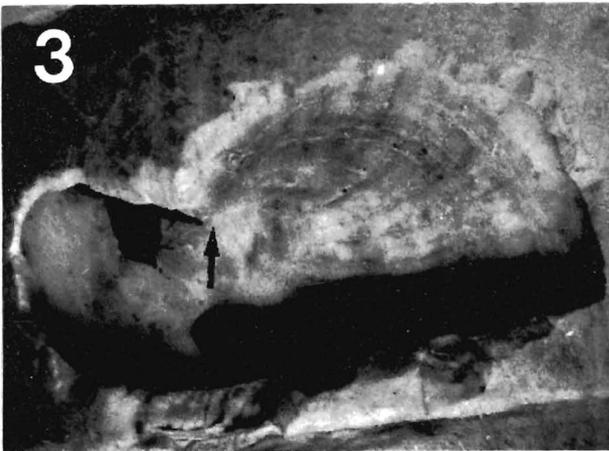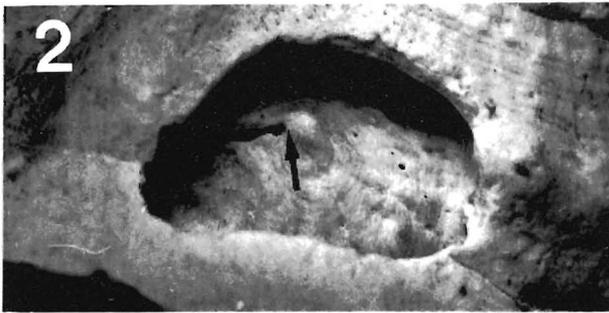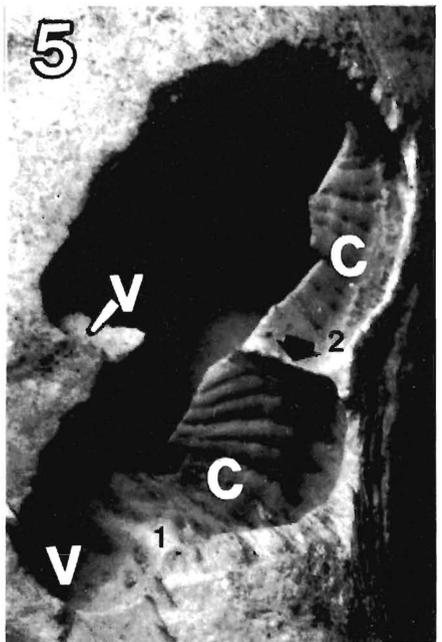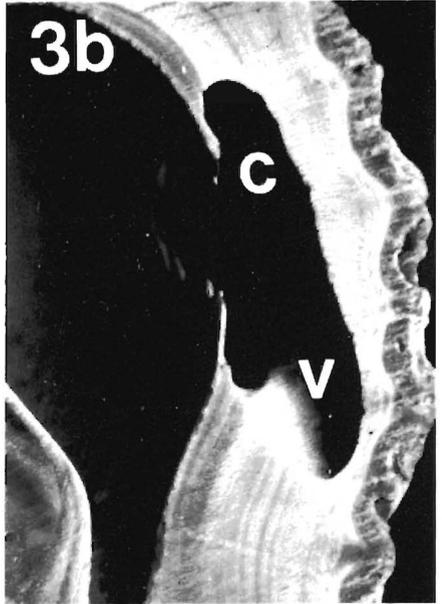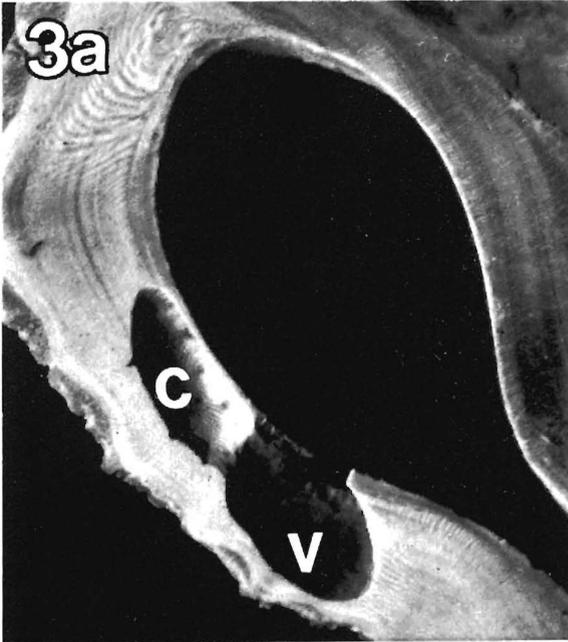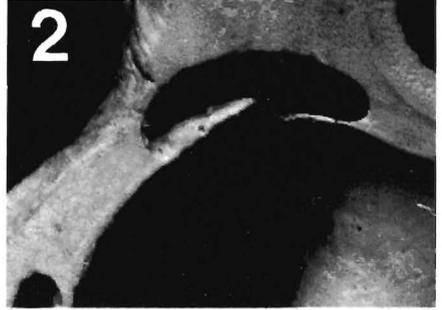
Fig. 6. Tiering of borings of *Trypetesa polonica* sp. n. in a gastropod shell presented in Pl. 4, Fig. 4 (numbering of borings the same); the feature the best pronounced in the boring numbered *2* whose chamber is developed below that of *3*, and influences the extent of the vestibule of *4* (the chamber of the latter is framed to that of *3*); position of the accessory exit (*AE*) in the boring numbered *4* is indicated

COMPARISONS

As far as the borings of modern species of the genus *Trypetesa* are concerned, the newly established species displays a set of features different to that of any hitherto known species, although some features are common with those of one or more modern species (*see* Text-figs 7-8).

The species *Trypetesa lampas* (HANCOCK, 1849), the type of the genus, produces the borings of comparable size, and attaining the diameter of 11 mm or more (BERNDT 1907 reports on some specimens even 2.5 times larger, distinguis-

PLATE 4

Trypetesa polonica sp. n.

1 — Two borings (numbered *1* and *2*: their apertures are indicated by empty arrows) in the deeply broken shell of *Terebra fuscata* (BROCCHI), exposed by chipping-off a part of the gastropod shell; the boring numbered *1* is left-sided and it turns into the sutural part of the gastropod shell; the boring numbered *2* is stenomorphic, and is separated from the former by a narrow barrier (*solid arrow*)

2 — Section, to show a part of the boring (chamber) in the sutural part of the shell of *Clavatula asperulata* (LAMARCK)

3a-3b — Section, to show two borings in the shell of *Ocenebra erinacea* (LINNEAUS): 3a — Longitudinal section, to show the vestibule (*v*), and the chamber (*c*) sculptured by denticle-like depressions; 3b — Slightly oblique section, to show a thin, residual portion of the gastropod shell on the right side of the chamber (*c*), and the position of the vestibule (*v*)

4 — Group of four borings (in apertural view), whose "upper" walls of the chambers are partly removed, to show a tiering arrangement of the borings (*see* Text-fig. 6) in the shell of *Clavatula laevigata* (EICHWALD); apertures of borings numbered *1* and *2* are magnified in Pl. 2, Figs 3 and 4, respectively; the boring numbered *3* is stenomorphic; the boring numbered *4* (empty arrow points to the left margin of its aperture) is provided with the accessory exit (*solid arrow*)

5 — Two neighboring borings (numbered *1* and *2*), separated by a narrow barrier (*solid arrow*), in the shell of *Euthria puschi* (ANDRZEJOWSKI); the borings exposed by chipping-off a part of the gastropod shell; both vestibules (*v*) and chambers (*c*) are partly preserved

All photos × 5: taken by B: DROZD, M. Sc.

hed as *Alcippe lampas gigantea;* see TOMLINSON 1963, 1969a, pp. 127-128; TURQUIER 1985, 1987). The borings are always developed much more anteriorly in regard to the aperture (*see* HANCOCK 1849, Pl. 8, Figs 1-2; DARWIN 1854, Pl. 22, Fig. 3). As may be ascertained from the shape and structure of the cirripede body (*see* HANCOCK 1849, Pl. 8, Figs 3-5; DARWIN 1854, Pl. 22, Fig. 1) the borings should typically be symmetrical (*see also* TOMLINSON 1969a; TURQUIER 1976, 1987), although some highly distorted forms may also appear (*see* DARWIN 1854, Pl. 22, Fig. 2; TURQUIER 1967, Fig. 1). The borings provided with an accessory exit remain as yet unknown.

The species *Trypetesa lateralis* TOMLINSON, 1953, produces borings of a much smaller size, attaining not more than 5 mm of the greatest diameter. The borings are uniform in their outline, not bipartite, extending exlusively to the right from the aperture, and not stretching either anteriorly or posteriorly beyond it (*see* TOMLINSON 1953, Fig. 1; *and* 1955, Fig. 20). The borings provided with an accessory exit are common.

The species *Trypetesa habei* UTINOMI, 1962, from Japanese offshores, produces borings of a moderate size (the holotype is 7 mm long), but the largest specimens attain even 20 mm; the borings are located almost exclusively within the columella, but some specimens were also noted in the sutures of the gastropod shells (*see* UTINOMI 1962, 1964) and in the floor of the last whorl

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PLATE 5

Trypetesa polonica sp. n.

1a-1c — **Holotype**: the boring in the shell of *Fusus hoessi* PARTSCH; **1a** — Apertural view: "upper" wall of the boring is partly removed; **1b** — The same, with the chamber almost completely exposed (empty arrow points to the apertural margin, the same as in Fig. 1a), to show the accessory exit (*solid arrow*); **1c** — Accessory exit (*arrowed*) on the outer surface of the gastropod shell

2a-2b — Group of five borings in the deeply broken shell of *Sveltia inermis* (PUSCH); **2a** — Apertural view: "upper" wall of the chambers is partly removed (apertural margins in borings *1, 2* and *3* are indicated by empty arrows; a thin barrier between borings *2* and *3* is indicated by the smaller, solid arrow), to show the accessory exits (*solid arrows*): in the stenomorphic boring numbered *3* the accessory exit remains unfinished (*solid arrow, rimmed white*); the borings numbered *4* and *5* are juvenile; **2b** — Outer surface of the gastropod shell, to show accessory exit of the borings numbered *1* and *2*; unfinished vent-hole drilling of the boring numbered *3* does not pierce out the gastropod shell; the juvenile borings (*4* and *5*) not detectable

3a-3b — Boring in the shell of *Clavatula asperulata* (LAMARCK); **3a** — Apertural view, to show fine punctures on the inner surface of the gastropod shell ("upper" wall of the chamber is partly damaged), and the position of the accessory exit (*double asterisked*); **3b** — Accessory exit on the outer surface of the gastropod shell (*arrowed*)

4a-4b — Group of five borings in the shell of *Fusus hoessi* PARTSCH; **4a** — Apertural view, in partly sectioned gastropod shell: the borings numbered *1, 2* (associated with a juvenile, numbered *5*), and *3* are oriented in a wing-like series; **4b** — Outer surface of the gastropod shell, to show heavily damaged accessory exits of four borings

All photos × 5; taken by B. DROZD, M. Sc.
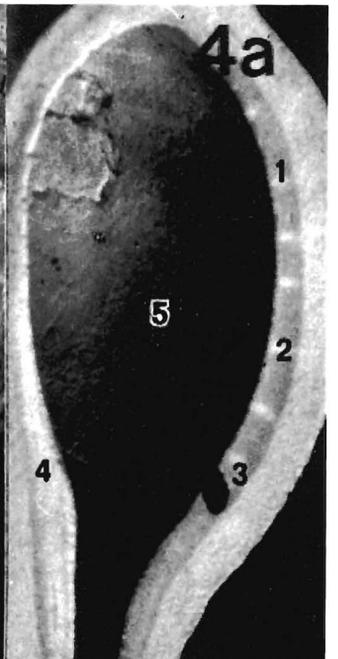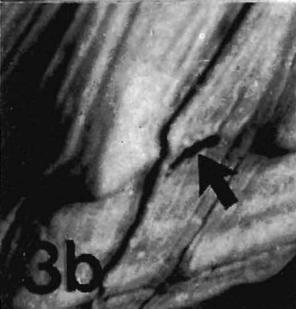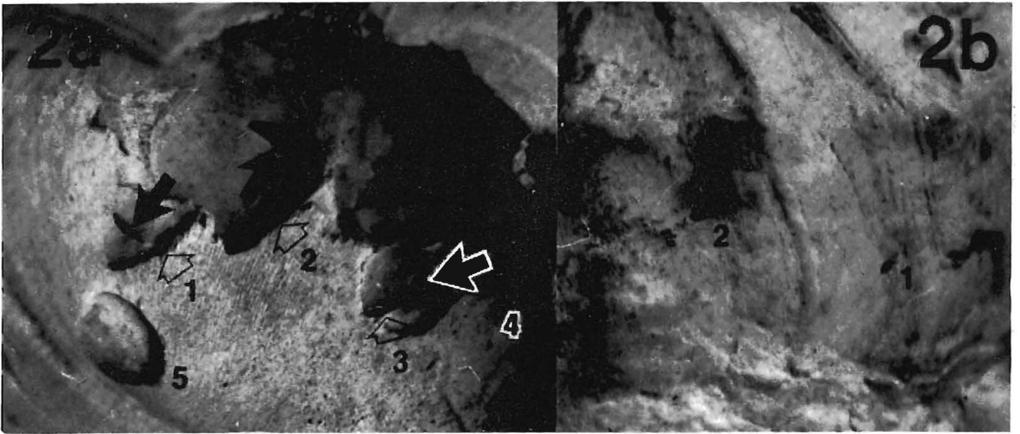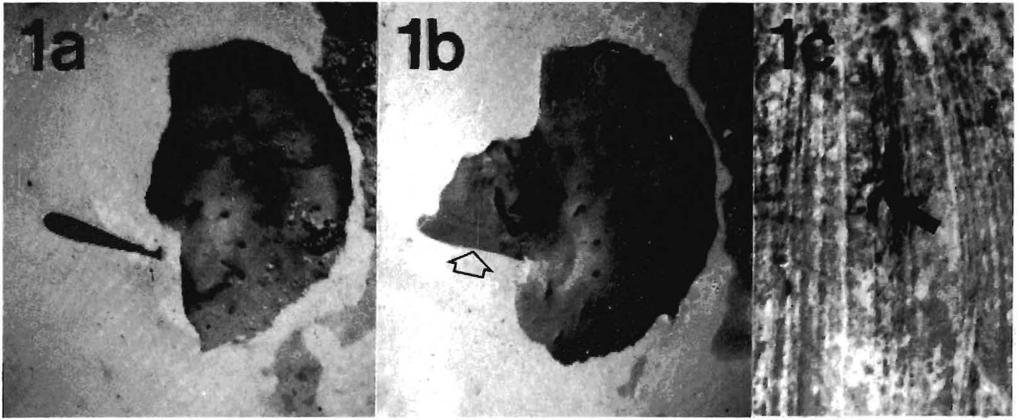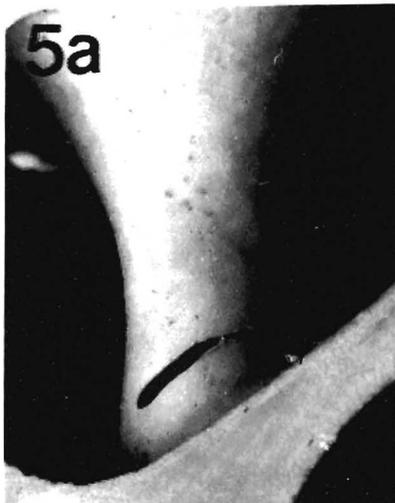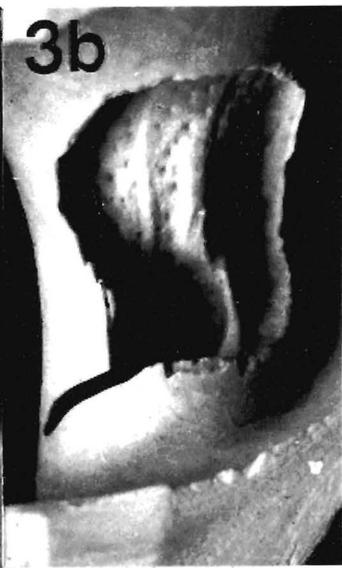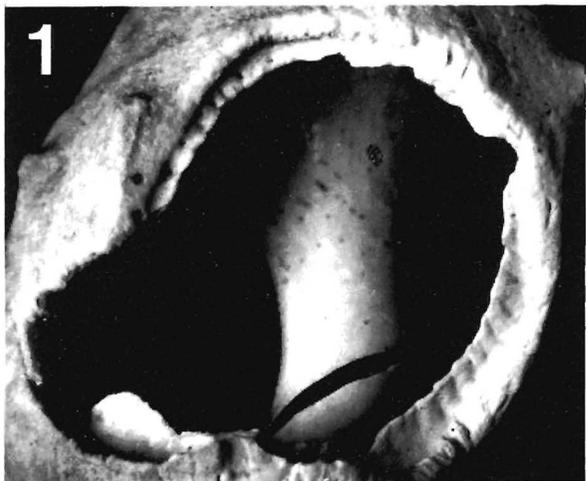
(TOMLINSON 1969, p. 130). The shape of the borings is very variable (*see* UTINOMI 1964, Fig. 2). The apertures are typically much elengated, rather narrow, and not so gently curved like in *T. lampas* (HANCOCK, 1849) but rather straightened, sinuous or wriggling, like in *T. polonica* sp. n.; some of them are provided with well developed bourrelets (*see* UTINOMI 1964, Fig. 1).

The specimens of *Trypetesa habei* UTINOMI, 1962, are typically also provided with an extension of the body which was referred by UTINOMI (1964, pp. 123-124 and Pls 3-4) to as a "*mantle flap*" and characterized as projecting dorsoanteriorly somewhat parallelly to the shell surface and filled with egg masses. This extension, peculiar to the species, has nothing in common with the mantle flap in *T. lateralis* TOMLINSON (as already noted by TOMLINSON 1969a, p. 131, who did not find this structure in the personally investigated population of this Japanese species) and in *T. polonica* sp. n.

The species *Trypetesa nassarioides* TURQUIER, 1967, described originally from the French coast of the English Channel, produces borings exclusively within the columella and thus acquires a helical shape, much deviated from that of any other congeners (*see* TURQUIER 1967; *and* TOMLINSON 1969a, Fig. 37).

By its strange shape, *Trypetesa nassarioides* TURQUIER, 1967, is convergent with the still more peculiarly shaped forms, originally assigned as "*Alcippoides asymetrica* nov. gen., nov. sp." by TURQUIER & CARTON (1976), from Madagascar, and regarded by them, within the family Trypetesidae, as representing a separate genus that has soonafter been renamed as *Tomlinsonia* by TURQUIER (1985).

The last of the hitherto known *Trypetesa* species, namely *Trypetesa spinulosa* TURQUIER, 1976, from Madagascar, resembles the Japanese species *T. habei* UTINOMI, 1962, but it is smaller (the holotype is 4.3 mm long).

PLATE 6

Trypetesa polonica sp. n. within the columella of various gastropod shells

1 — Apertural view of the boring situated deeply in the shell of *Euthria puschi* (ANDRZEJOWSKI), and displaying fine punctures in the "upper" wall of the boring; the boring is visible through the other one, completely chipped-off, and situated a half-whorl from the gastropod-shell's aperture

2 — Boring oriented with its peduncular slit down the spire of the partly sectioned shell of *Ancilla glandiformis* (LAMARCK)

3a-3b — Boring in the partly sectioned shell of *Clavatula laevigata* (EICHWALD); **3a** — Apertural view, with the boring intact; **3b** — The same, but with "upper" wall of the boring removed, to show the sculpture of the "lower" side

4 — Partly damaged boring in the shell of *Euthria puschi* (ANDRZEJOWSKI), to show a thin, residual portion of the gastropod shell on the right side of the chamber (indicated by a leader)

5a-5b — Boring in the partly sectioned shell of *Clavatula asperulata* (LAMARCK); **5a** — Apertural view, to show the left bourrelet along the aperture (magnified in Pl. 2, Fig. 5), and the fine punctures on the surface of the columalla; **5b** — Exposed "upper" side of the boring, seen from the opposite side of the same columella

6 — Boring in the partly sectioned shell of *Clavatula laevigata* (EICHWALD), with partly exposed chamber, to show the structure of the gastropod shell reflected

All photos × 5; taken by B. DROZD, M. Sc.

From the above review it is apparent that such set of features as the lateral development of the body, its extension anteriorly, a larger size, and the presence of the external mantle flap, distinguishes *Trypetesa polonica* sp. n. from other species of the genus. Of the five modern species of that genus, comparable are (*see* Text-figs 7-8) only two, *Trypetesa lampas* (HANCOCK, 1849) and *T. lateralis* TOMLINSON, 1953, the three others being confined exclusively to the columella, and thus much deviating in their shape. Of the two comparable species, *Trypetesa polonica* sp. n. shares its features more pronouncedly with *T. lateralis* TOMLINSON (lateral development of the body, the presence of the external mantle flap) than it does with *T. lampas* (HANCOCK), to which it closes by less important features (comparable size, anterior extension of the body).

Consequently, the newly established species *Trypetesa polonica* sp. n. is thought to have belonged to the same stock of species as does *T. lateralis* TOMLINSON, 1953, to which it is most likely an ancestor.

When discussing the taxonomy of the modern *Trypetesa* species, TURQUIER (1976, pp. 572-573; *see also* TURQUIER 1987) postulates a distinction of the three groups of species, possibly of the subgeneric rank, as follows:

— the group of rather larger species, with weak or no torsion: *T. lampas* (HANCOCK, 1849), *T. habei* UTINOMI, 1962, and *T. spinulosa* TURQUIER, 1976;

— the species living within the columella, much distorted: *T. nassarioides* TURQUIER, 1976;

— the species of rather smaller size, lateral development of the body, with the external mantle flap: *T. lateralis* TOMLINSON, 1953.

If this suggested taxonomy were accepted, the newly established species, *Trypetesa polonica* sp. n., would evidently belong to the third of the indicated "subgeneric" groups.

As compared to the mode of occurrence in modern species of the genus *Trypetesa*, the studied material displays some differences which are apparently of no taxonomic importance. Firstly, the maximum frequency of *Trypetesa*
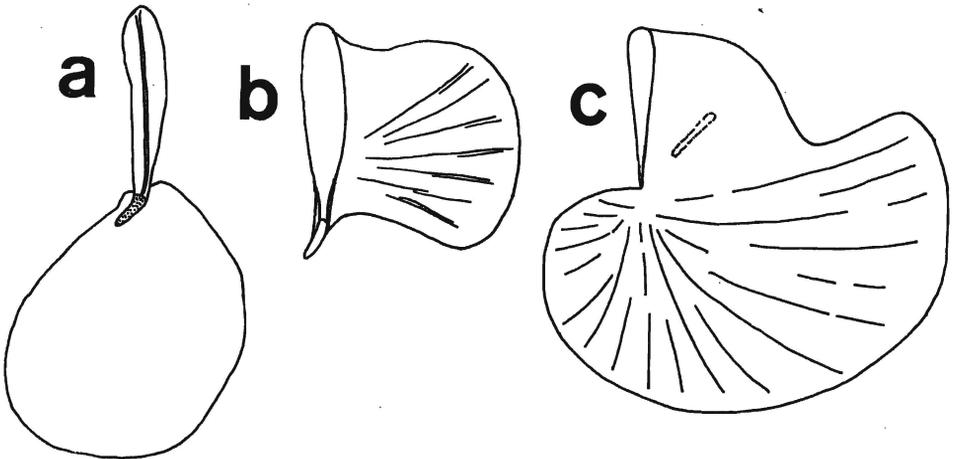

Fig. 7. General organization of the female borings in comparable species, apertural view: **a** — *Trypetesa lampas* (HANCOCK, 1849) [*taken from*: TOMLINSON (1976a, Fig. 34c)], **b** — *Trypetesa lateralis* TOMLINSON, 1953 [*taken from*: TOMLINSON (1955, Pl. 4, Fig. 20)], **c** — *Trypetesa polonica* sp. n. (position of the accessory exit is indicated)

polonica sp. n. in one gastropod shell is distinctly smaller than reported in *Trypetesa lampas* (HANCOCK), *e.g.* by BOEKSCHOTEN (1966) who counted over ninety specimens in a shell of the whelk from the Dutch coast. Secondly, a frequent association of the spat located nearby adult specimens, of the latter species and occurrence as also stated by BOEKSCHOTEN (1966), has been recovered in *Trypetesa polonica* sp. n. only once (*see* Pl. 2, Fig. 1).
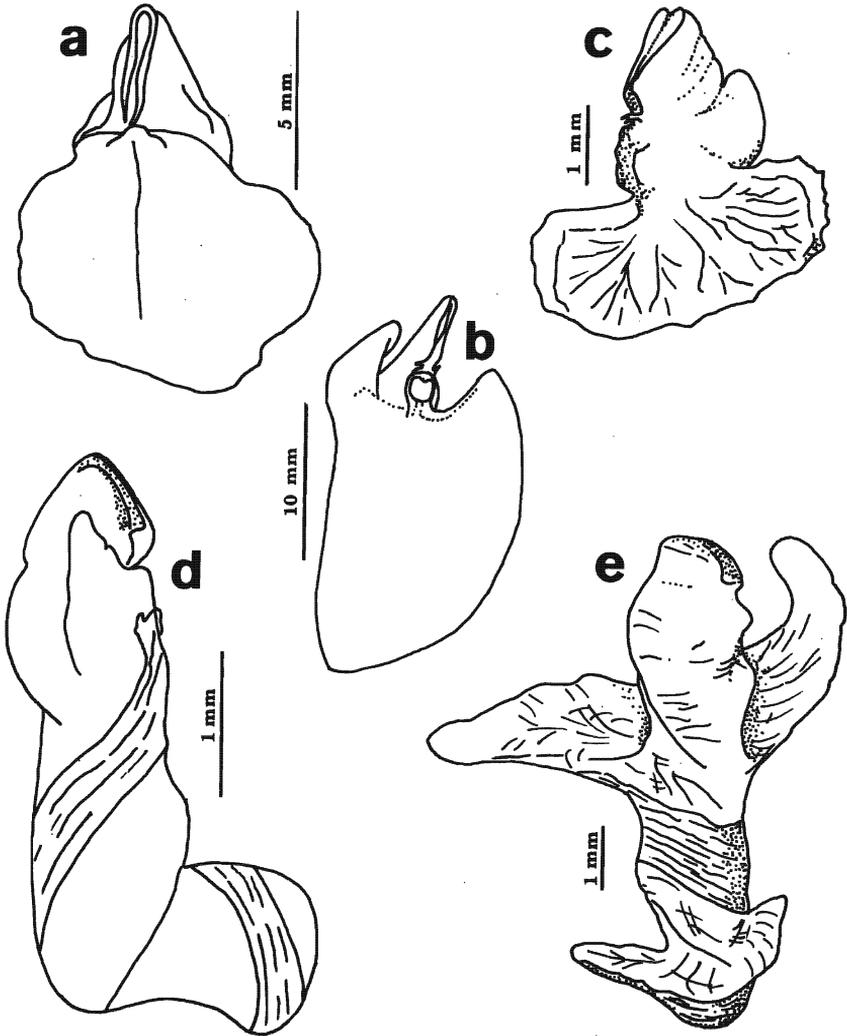

Fig. 8. Comparative modern species of the family Trypetesidae

a — *Trypetesa lampas* (HANCOCK, 1849); *taken from* GENTHE (1905, Pl. 11, Fig. 5),
b — *Trypetesa habei* UTINOMI, 1962; *taken from* UTINOMI (1964, Fig. 2),
c — *Trypetesa spinulosa* TURQUIER, 1976; *taken from* TURQUIER (1976, Fig. 1*B*),
d — *Trypetesa nassarioides* TURQUIER, 1967; *taken from* TOMLINSON (1969a, Fig. 37*a*),
e — Convergent trypetesid *Tomlinsonia asymetrica* (TURQUIER & CARTON, 1976); *taken from* TURQUIER & CARTON (1976, Fig. 1*A*)

THE HABITAT OF *TRYPETESA POLONICA* sp. n.

As stated above, the occurrences of *Trypetesa polonica* sp. n. concern rather thick-walled gastropod shells which remained superficially damaged to various extent. A relatively greater thickness of the gastropod shells was certainly required by the *Trypetesa* individuals which selected such very shells to get sufficient space for location of their borings inside. The more or less advanced damage of the shells was acquired by their long-timed resting empty on the sea bottom, when they underwent to both mechanical abrasion and/or bioerosion. The reasonably major part of the gastropod shells domiciled by *Trypetesa polonica* sp. n. were bioeroded by diverse rock-borers of the same kind as those inhabiting the rocky shores of the Korytnica Basin (*see* RADWAŃSKI 1969, BAŁUK & RADWAŃSKI 1977). Of these rock-borers the most abundant are (*see* Table 1):

— sponges *Cliona celata* GRANT and *C. vastifica* HANCOCK;
— polychaetes *Polydora ciliata* (JOHNSTON) and *P. hoplura* (CLAPARÈDE);
— bivalves *Gastrochaena dubia* (PENNANT).

Moreover, associated are (*see* Table 1) minute borings, usually located along circumapertural parts of the gastropod shell and produced by the boring ctenostomate bryozoans *Spathipora* sp., *Terebripora* sp., and *Penetrantia* sp., the presence of which is attributable to the occurrence of hermit crabs inhabiting the bored shells (*see* BAŁUK & RADWAŃSKI 1979b). Along the columella of some shells domiciled by *Trypetesa polonica* sp. n. developed is (*see* Table 1) the boring classified as the ichnofossil *Helicotaphrichnus commensalis* KERN, GRIMMER & LISTER which is attributed to some spionid polychaetes commensal to the hermit crabs (*see* KERN 1979, BAŁUK & RADWAŃSKI 1984a). All borings of this type make up an approach to suggest a stable relation between *Trypetesa polonica* sp. n. and the hermit crabs.

Another approach to the *Trypetesa* — hermit relation appears from the recognized location of *Trypetesa polonica* sp. n. within the gastropod shells. The majority of the studied specimens inhabited shells having their apertures almost intact. The other specimens are contained in shells with their adapertural, or even deeper parts broken off. In both cases the settlement of *Trypetesa polonica* sp. n. is the same: about half a whorl either from the aperture or from the margin of the broken shell. Such stable settlement is interpreted as resulting from location of *Trypetesa polonica* sp. n. in a definite place in relation to the hermit's body, regardless of nature of the shell margin.

The latter situation, the settlement of hermit crabs in fragmented gastropod shells, as it may be inferred from location of *Trypetesa polonica* sp. n. (*see* Pl. 3, Figs 3 and 7; Pl. 4, Fig. 1; Pl. 5, Fig. 2), was very similar to that reported by HYDEN & FOREST (1980) who illustrate from the Early Miocene of New Zealand a unique specimen of an *in situ* hermit crab preserved in a deeply broken gastropod shell (*see* HYDEN & FOREST 1980, Fig. 1; reproduced recently by BOUCOT 1990, p. 357: Fig. 292).

When location of *Trypetesa polonica* sp. n. in gastropod shells occupied by hermit crabs is apparent, a selection of the high-spired shells also becomes obvious. These were the shells in which the hermit crabs could emplace their bodies the best.

A superficial wear of many gastropod shells bored by *Trypetesa polonica* sp. n. has resulted both from their mechanical abrasion and/or bioerosion prior to the hermits' settlement, as well as from their further damage by the hermits' commensals (*see* Table 1) and by their dragging by the hermits themselves over the sea bottom (*see* BAŁUK & RADWAŃSKI 1979b, p. 249 and Pl. 8, Fig. 2).

Concerning the time of action of the organisms to which the gastropod shells were the substrate, it is most likely that the rock-borers (*see* Table 1) have settled prior to the usage of these shells by the hermit crabs, though the otherwise aged specimens are also present (*see* Pl. 1, Fig. 2b: boring of *Polydora ciliata* younger than *Trypetesa*). A time of the settlement of various epizoans (*see* Table 1) cannot be precisely indicated, and the same may be said about the squatter, *Crepidula crepidula* (LINNAEUS), which is the rarest guest of the *Trypetesa*-infected shells (*see* Table 1).

The latter inhabitant of the gastropod shells, *Crepidula crepidula* (LINNAEUS), has always been noted in the Korytnica Basin as having been confined to empty shells, long resting free on the sea bottom and/or partly anchored in it (*see* BAŁUK & RADWAŃSKI 1977, 1985). In modern environments, *Crepidula* was however observed as often present in shells taken by the hermit crabs and infected by *Trypetesa lampas* (HANCOCK) along the Atlantic shores of the United States (GENTHE 1905, p. 182). Another *Crepidula* species, *C. grandis* (MIDDENDORF), that occasionally lives inside the shells inhabited by the hermit crabs has recently been recorded also from Japan (VERMEIJ 1989). Some more examples of similar behavior are briefly discussed by the latter author (VERMEIJ 1989, p. 89).

The bathymetric conditions under which *Trypetesa polonica* sp. n. lived in the Korytnica Basin are recognized as shallow sublittoral up to almost subtidal (*see* Text-fig. 2 *and* BAŁUK & RADWAŃSKI 1977).

To sum up, the data on the life habitat of *Trypetesa polonica* sp. n. indicate that the occurrence of these acrothoracican cirripedes was confined to the gastropod shells occupied by the hermit crabs, and distributed throughout the shallowest parts of the Korytnica Basin. Such a habitat was thus identical to that displayed by all modern species of the genus *Trypetesa*.

All the hitherto presented reports on the modern *Trypetesa* species clearly speak about their occurrence within the columella and the inner side of the last whorl of gastropod shells occupied by hermit crabs. Such very gastropod shells are called either *pagurized* (SEILACHER 1969), or **hermitted** as suggested by Professor W. A. NEWMAN and used in the subsequent chapters of this paper.

Of these modern species, *Trypetesa lampas* (HANCOCK, 1849) is known from common occurrences in the Atlantic province. In Europe it ranges from the British Isles, English Channel and Dutch coast, through the North Sea to the west coast of Sweden (HANCOCK 1849; DARWIN 1854; AURIVILLIUS 1894; BOEKSCHOTEN 1966; TURQUIER 1967, 1987). In a disjunct region, it also appears in the Mediterranean

Sea (BERNDT 1907, TURQUIER 1987). From the western Atlantic, it is known from the United States shores (GENTHE 1905, NEWMAN 1979), the Mexico Gulf including (SPIVEY 1979).

The other modern species are much restricted in their geographic distribution, as *Trypetesa lateralis* TOMLINSON, 1953, is known from limited occurrences in California (TOMLINSON 1953, 1955, 1969a; NEWMAN 1979), *T. nassarioides* TURQUIER, 1967, from the French coast of the English Channel (TURQUIER 1967), whereas *T. habei* UTINOMI, 1962, and *T. spinulosa* TURQUIER, 1976, from Japan and Madagascar, respectively (UTINOMI 1962, 1964; TURQUIER 1976).

A biological relationship between the acrothoracican cirripedes *Trypetesa* and the hermit crabs in modern occurrences has originally (HANCOCK 1849, DARWIN 1854) been overlooked. It was first exposed by AURIVILLIUS (1892, 1894), and soon commented by GENTHE (1905).

The nature of this relationship becomes clear when a reaction of the acrothoracican cirripedes to the removal of the crab is studied.

As noted by AURIVILLIUS (1894) and GENTHE (1905), the specimens of *Trypetesa lampas* (HANCOCK) cannot be kept alive very long after the hermit crab has been removed from the shell. This statement is contradicted, to some extent at least, by TOMLINSON (1969a) who reared specimens of *Trypetesa lateralis* in a cold box for over a year; under these laboratory conditions the studied specimens did not grow, however (*see* TOMLINSON 1969a, pp. 7 and 11).

Under natural conditions, the biological relationship between *Trypetesa* and hermit crabs is always obligate, and it is now commonly accepted to fall into the category of commensalism (*sensu* AGER 1963), as first advocated precisely by GENTHE (1905, p. 183).

When the above uniformitarianistic premises are taken into account, a commensal relationship between *Trypetesa polonica* sp. n. and the hermit crab must consequently be postulated.

THE BEHAVIOR OF *TRYPETESA POLONICA* sp. n.

As recognized above, the specimens of *Trypetesa polonica* sp. n. emplaced themselves in a part of the gastropod shell identically situated in relation to the hermit's body. It is therefore thought that *Trypetesa polonica* benefited from the presence of a hermit crab to whom it was the commensal, to the same extent how it realizes in all modern *Trypetesa* species. The cirripedes certainly gained from the water motion, induced by the hermit crab, oriented backwardly to the latter, and which was supplying food for the suspension feeding cirripedes. The water motion was reinforced by a pumping effect of the expanding and contracting cirripede body, which resulted in an active flow, along the external mantle flap, to the vent-hole drilling in the gastropod shell.

It is to suggest that some specimens of *Trypetesa polonica* sp. n. could certainly survive in the case of hermit's escape for molting, or its death. This is

justified by the fact that the construction of a discarded gastropod shell, lying on the bottom and having been provided with a vent-hole drilling in its projected part, makes up a system in which, as a consequence of BERNOULLI'S principle, a passive flow of water must be induced from the shell interior towards the outside. This is the case of fluid motion in any perforated construction situated within an active flow (projected tube, burrow in the bottom), of either liquid or gas, and it is well exemplified in a spectacular way by the ventilation of continental burrows of the prairie dogs in open air (see VOGEL & BRETZ 1972, VOGEL & al. 1973, VOGEL 1978).

The recognition of the passive flow mechanism allow to suggest that the above discussed function of the external mantle flap (see TOMLINSON 1955, 1969a; SEILACHER 1969) is just to produce a vent-hole drilling which would be able to involve a "prairie-dog's effect" ensuring the cirripede survival when the commensal partner (i. e., the hermit crab) becomes absent from the habitat (i. e., from the gastropod shell). As concerns the studied specimens of Trypetesa polonica sp. n., it is consequently interpreted that the specimens provided with the vent-hole drilling are those which survived after the loss of their commensal. Such specimens, not very common in the environment, had to drill a vent-hole to involve a passive flow of water ensuring a supply of food for their further life. The presented interpretation allows to understand why any vent-hole drilling is missing in specimens which bored within the columella of the gastropod shell. As all these specimens were located near the aperture, they always met sufficient motion of water, and thus, they did not need to produce an additional opening even if the partner had been lost.

The orientation of the studied borings of Trypetesa polonica sp. n. is low. The specimens occurring within the columella are preferentially oriented with their peduncular slits up the gastropod whorls (see Pl. 6). In specimens located in the outer part of the whorl such an orientation is not distinct. The specimens occurring in groups, and which may thus be interpreted as growing more or less coevally (e. g. those with the spat; see Pl. 2, Fig. 1) slightly tend to radiate rather than to parallel each other. In smaller groups, several specimens may tend to locate parallelly or in a wing-like series (see Pl. 1, Figs 2c and 4). Generally, it cannot be indicated whether such a poor orientation might have resulted from competition with the conspecificans in the water flow induced by the hermit crab. Anyway, this water flow was likely microturbulent rather than laminar in which a rheotaxy of the borings should be expected.

BEHAVIORAL EVOLUTION OF THE GENUS TRYPETESA

The newly established species Trypetesa polonica sp. n. is very close to the modern species T. lateralis TOMLINSON, to which it is claimed to be an ancestor. It

is therefore said that the phyletic lineage of this modern species is dated as back as the Miocene. An earlier provenience of the whole stock remains unclear.

The reports on older occurrences of *Trypetesa*, as indicated above, are very poorly documented. The Upper Cretaceous forms from England, recognized by JOYSEY (1959) can hardly be identified as possibly belonging to this genus. Not much more may be decided about *Trypetesa caveata* TOMLINSON established by TOMLINSON (1963) on Upper Paleozoic materials from the United States. These two reports, if they really concern the genus *Trypetesa* indicate, however, that the borings were produced from the outer side of the shell (of echinoid, and bivalves, respectively), and thus their nature was the same as that of any borings produced in any rocky substrate (thus, they are called herein *the endolithic borings*).

Even if we accept a congenerity of all the above species, it is apparent that the commensal relationship between *Trypetesa* and hermit crabs has well been manifested since the Miocene. This is obviously due to the appearance of the hermit crabs in shallow marine environments, and which evolved somewhen at the Mesozoic decline to achieve their bloom already in the Miocene (*see* KRÜGER 1940; PAPP, ZAPFE, BACHMAYER & TAUBER 1947; GLAESSNER 1969). A formation of the new habitats in gastropod shells in which a water motion was involved by the inhabiting hermit crabs, enabled a settlement of *Trypetesa* in the interior of such shells. These acrothoracicans have found here highly favorable life conditions, and therefore have left their former, endolithic mode of life. In such a sense this new habitat is regarded as a refuge for *Trypetesa* which has become, since the Miocene, unknown in any endolithic occurrences. This refugial habitat has focused a host specifity of *Trypetesa* which acquired an obligate commensal relationship to the hermit crabs, and thus triggered an evolutionary change to introduce a new link in the taphonomic feedback of the shallow marine benthic communities (*compare* KIDWELL & JABLONSKI 1983, KIDWELL 1986).

The highly advanced host specifity of *Trypetesa* to the hermit crabs living in gastropod shells has presumably resulted from trophic selection. These acrothoracicans have gained effectively from the life activity of hermit crabs competing with them for food particles and thus being their messmates, or have utilized their garbage or feces.

An ability to produce the vent-hole drilling in some specimens of *Trypetesa polonica* sp. n., the same as in *T. lateralis* TOMLINSON, is interpreted as a further step of evolution in some stocks of the genus, which could thus prevent their life conditions when the commensal partner had become lost. This step of evolution has been established as early as the Miocene and continued till now, and thus it is not a top event typical of modern habitats as it was assumed by SEILACHER (1969, pp. 709 and 715 and Fig. 1).

Finally, it is somewhat surprising that the borings of the newly established species, *Trypetesa polonica* sp. n., exhibit a paradigm which seems to be advanced evolutionary much more than that of almost all the modern species. It is unlikely to decide whether this results from ecological reasons, precisely from higher environmental stress in the Miocene littoral habitats of the Korytnica Basin, or it is simply involved by an inadequate recognition of the modern *Trypetesa* species.

SIGNIFICANCE OF *TRYPETESA POLONICA* sp. n.
IN THE KORYTNICA BASIN

The newly recognized acrothoracican species, *Trypetesa polonica* sp. n., has tended to occur rather singly or in patches of several specimens within some of the gastropod shells distributed throughout the Korytnica Basin. This contrasts with a mass infestation of the hermitted shells by the present-day *Trypetesa* species, *T. lampas* (HANCOCK) particularly (*see* HANCOCK 1849, DARWIN 1854, GENTHE 1905, BOEKSCHOTEN 1966), and with ancient examples of hermitted shells colonized by the acrothoracicans other than *Trypetesa* (see ZAPFE 1936; *and* SEILACHER 1969, Fig. 6a). A low frequency of *Trypetesa polonica* sp. n. in the Korytnica Basin and in its particular shells has however been balanced by the remarkable size of particular specimens, the largest of which have lived rather singly (*see* Table 1 *and* Pls 3 and 6).

An inferred occurrence of the hermit crabs to which *Trypetesa polonica* sp. n. was commensal, enriches the spectrum of structures attributable to life activity of diverse crabs in the Korytnica Basin (*see* FÖRSTER 1979). Their activity is well manifested in the middle and upper to uppermost parts of the Korytnica Clays sequence, that is, the same in which *Trypetesa polonica* sp. n. does occur (*see* Text-fig. 2). The predatory attacks of the hermit crabs upon the gastropods and scaphopods are here recorded in many shells, the owners of which have either fallen or, quite often, survived and could then regenerate their damaged shells (*see* RADWAŃSKI 1969, 1977; BAŁUK & RADWAŃSKI 1977).

On the other hand, the acrothoracican cirripedes follow the hydroids related to *Hydractinia,* the spionid polychaetes, and the boring ctenostomate bryozoans in the list of the commensals to the hermit crabs formerly reported from the Korytnica Basin (*see* Table 1; *and* KERN 1979; BAŁUK & RADWAŃSKI 1979b, 1984a).

FINAL REMARKS

The presented study gives the first account on the virtually defined ancient species of the genus *Trypetesa* NORMAN, 1903. This genus since the time when the first species attributed recently to it, *Alcippe lampas* HANCOCK, 1849, was established has been known over a century solely from this very species. A burst of new records on the modern *Trypetesa* species has begun in the fifties of this century, and resulted in the description of four species from various parts of the world: *T. lateralis* TOMLINSON, 1953, from California, *T. habei* UTINOMI, 1962, from Japan, *T. nassarioides* TURQUIER, 1967, from the French coast of the English Channel, and *T. spinulosa* TURQUIER, 1976, from Madagascar.

The two reports on the ancient species of the genus, namely those given by JOYSEY (1959) and TOMLINSON (1963, 1969a) remain open to discussion upon their possible assessment to the genus.

Of the features recognized in the above listed four recently established modern species of the genus *Trypetesa*, all of which were investigated by a limited number of specimens and/or occurrences, some remain controversial. To exemplify this, the following data on one species, *Trypetesa habei* UTINOMI, 1962, are to be indicated.

In the type collection of *Trypetesa habei* UTINOMI, 1962, from the Japanese offshore (depth ranging from about 30 to 50 fathoms), as studied by UTINOMI (1962, 1963), the boring activity was displayed in the columellas and occasionally in the sutural parts of gastropod shells, all the specimens were provided with an extension of the body (as discussed above), and the presence of the males had not been stated. On the other hand, in a eulittoral population studied by TOMLINSON (1969a, pp. 129-132) bored were also floors of the last whorl, there were no extensions of the body detected, and the males were present.

The above data clearly speak about necessity of keeping a caution when any comparisons between modern and ancient taxa of the genus *Trypetesa* are taken into consideration.

All the modern species of the genus *Trypetesa* display the shape of their body, and thus the corresponding shape of their borings, so distant to each other that the investigated ancient material from the Korytnica Clays, of Middle Miocene age, is claimed to represent a separate species. It is evidently understood that this new species, *Trypetesa polonica* sp. n., is established solely upon their borings, which make, however, an almost ideal replica, or a cast of the external morphology of the animal's body. These borings bear so significant wealth of information about the morphology of their producers that their meaning in taxonomy is not lesser than that of the external cast of the shelled fossils. The newly established species is thus regarded as belonging to the body fossils, and it is well comparable to the modern "soft-part" species. Its taxonomic status is thus of the same nature as that of almost all the boring ctenostomate bryozoans (*see* POHOWSKY 1974, 1978; *cf. also* BAŁUK & RADWAŃSKI 1979b, p. 244).

Of the modern *Trypetesa* species, only one is well comparable with the newly established species, *Trypetesa polonica* sp. n. This is *Trypetesa lateralis* TOMLINSON, 1953, to which the new species is regarded to be an ancestor. If we accept a belonging of these two species to one phyletic stock, some differences are indicated to be a scope for further investigation.

The first difference concerns the ability to lodge the body within either thick- or thin-walled gastropod shells, as it happens in *Trypetesa polonica* sp. n. and in *T. lateralis* TOMLINSON, 1953, respectively. This difference is herein postulated to have resulted from host specifity of the hermit crabs rather than the varied space requirements of these species. Another, certainly less important difference is in life habitat which is recognized by TOMLINSON (1953, 1955, 1969a) as an open shore with low intertidal pools (NEWMAN 1979) for *Trypetesa lateralis* TOMLINSON, 1953, and which is shallow subtidal for *T. polonica* sp. n. as given in this paper (*see also* BAŁUK & RADWAŃSKI 1977).

Not fully understood as yet are in *Trypetesa polonica* sp. n. two features which concern the location of the borings within the different parts of the gastropod shells, and the presence of the variously oriented specimens.

The nature of the ability of *Trypetesa polonica* sp. n. to colonize both the floor of whorls and the

columella of gastropod shells might have been quite accidental, but one should remember that some of the modern *Trypetesa* species are located within the columella exclusively. The latter specialization is thus thought as not having been yet displayed by the philogenetically older (Miocene) representatives of the genus.

The occurrence of some left-sided specimens of *Trypetesa polonica* sp. n., instead of those typically right-sided ones, may indicate a tendency to unilateral, asymmetrical growth in ancient (Miocene) *Trypetesa* stocks, and which has been deleted in the modern *Trypetesa* species. This peculiar feature, anyway, is comparable to that displayed by the verrucimorph cirripedes in which both the right- and left-sided specimens are developing in equal numbers (*see* DARWIN 1854, RUNNSTRÖM 1926).

The modern species *Trypetesa lateralis* TOMLINSON, 1953, well comparable to the newly established ancient species, is geographically confined to the Eastern Pacific, to which it is postulated by NEWMAN (1979) to be a short-range endemic of the ancient Tethys origin. The latter origin is quite evidently displayed by *T. polonica* sp. n. from the Korytnica Basin in Poland. Of other acrothoracican borings known from the Neogene deposits of Europe, those first reported by ZAPFE (1936) are comparable to the modern species *Lithoglyptes indicus* AURIVILLIUS, whose Indo-Pacific provenience is obvious. Consequently, the recognized acrothoracican cirripedes in the Korytnica Basin in Poland, and most likely also the others from the Paratethys basins in Europe, those reported by ZAPFE (1936) including, are indicative of the Indo-Pacific influences in Europe at the Miocene time. In regard to the Korytnica Basin, this statement is compatible with conclusions drawn from the occurrence and bioprovince distribution of many components of its organic communities (*see* RADWAŃSKI 1975; BAŁUK & RADWAŃSKI 1977, 1984a).

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