acta geologica polonica

Vol. 46, No. 3-4, pp. 279-304 Warszawa 1996

WACŁAW BAŁUK & ANDRZEJ RADWAŃSKI

Stomatopod predation upon gastropods from the Korytnica Basin, and from other classical Miocene localities in Europe

ABSTRACT: The predation of the stomatopod crustaceans (order Stomatopoda, subclass Eumalacostraca, superclass Crustacea) upon diverse gastropods is recognized within the much diversified, shallow-marine communities of the Korytnica Basin (Middle Miocene; southern slopes of the Holy Cross Mountains, Central Poland). The results of both the spearing and smashing activity of stomatopods are evident, to document diverse methods of their attacks upon the gastropods, and to be well comparable to those recently presented either from the Plio-Pleistocene of Florida, or from the Holocene of Benguela region, off south-western Africa. The reparated ("regenerated") injuries in shells, indicative of the stomatopod attacks upon live gastropods, are first recorded from the Geologic Past. The larger damages, that destroy the gastropod shells almost totally, are compared to those produced by predatory crabs. A high percentage (up to 54.4%) of the shells subjected to stomatopod attacks suggests the stomatopod predation to have been of considerable importance in the ecological history of the tropical/subtropical, Indo-Pacific influenced, Korytnica Basin. An overview of the gastropod monographs from other Miocene basins in Europe (the Tethyan Mediterranean, the Atlantic Gulfs, the North Sea Basin, and the so-called Paratethys basins) delivers many examples of shell damages by stomatopods, compatible with those from the Korytnica Basin. All these recognitions extend importantly the range of the predatory behavior of stomatopods down to the Tertiary, precisely to the Miocene epoch, the Korytnica Basin of which is dated as about 15 m.y. ago, close to the Langhian/Serravallian stage boundary in the standard geochronologic scale.

INTRODUCTION

The stomatopods, that is the crustaceans of the order Stomatopoda LATREILLE, 1817, commonly known as the mantis shrimps, are important components of many Recent circumtropical, shallow-marine communities in which they are serious predators of gastropods, bivalves, other crustaceans, polychaetes, and some fish (*see* HOLTHUIS & MANNING 1969; CALDWELL & DINGLE 1975, 1976). Due to relatively very weak mineralization of the exoskeleton, their preservation potential is, however, extremely low, and their body remains are thus of very scanty record in the Geologic Past. Despite of the long history of the order, ranging credibly since the Upper Jurassic, Tithonian of Solnhofen (*see* MÜNSTER 1839; H. WOODWARD 1879; HOLTHUIS & MANNING 1969, p. *R*541; BARTHEL 1978, pp. 150 and 326), or Lower Oxfordian of Normandy (*see* CORNELISSE 1996, p. 18), little is known about their behavior and life requirements in ancient environments.

Under these circumstances, there recently appeared two reports on the shell damages of fossil mollusks caused by stomatopods, what remarkably extend the knowledge on the behavior of mantis shrimps into the past conditions. The first of these reports, by GEARY, ALLMON & REAKA-KUDLA (1991), offers an insight into the stomatopod predation upon the Plio-Pleistocene gastropods of Florida, whereas the second one, by PETHER (1995), upon the Holocene bivalves and some gastropods of the Benguela region, off southwestern Africa.

In the first of the indicated reports, the gonodactylid stomatopods, *Gonodactylus* sp. div., are recognized as preying upon gastropods (GEARY & *al.* 1991), and in the second one the squillid stomatopod, *Pterygosquilla armata capensis* MANNING, preying chiefly upon the bivalves (PETHER 1995). These two groups of stomatopods, classified recently as separate families (*see* HOLTHUIS & MANNING 1969, *and* SCHRAM 1968), the Squillidae LATREILLE, 1803, and the Gonodactylidae GIESBRECHT, 1910, respectively, embrace the forms of diverse morphology of their second thoracopods transformed into raptorial claws serving preferentially either to the smashing, as in *Gonodactylus*, or to the spearing, as in *Pterygosquilla*, mode of an attack and damage upon a prey.

The recommended newly reports, by GEARY & *al.* (1991) and PETHER (1995), give a very thorough and critical review of the present-day state of knowledge on the predatory activity of Recent stomatopods, to document expressively an interpretation of damages recognized in the fossil mollusks (Holocene bivalves and Plio-Pleistocene gastropods). From these two novelty accounts, either by own observations of the authors or through the older references (CALDWELL & DINGLE 1975, 1976; CALDWELL 1977; BERTNESS 1982), some general statements are apparent, as follows.

(*i*) Some Recent stomatopods, except of the spearing and smashing, use also other methods of the predatory techniques, especially as concerns the gastropods, namely: (*a*) extracting the prey directly through the shell aperture; (*b*) peeling the shell along the aperture, and (*c*) crushing the shell into bits. The results of such predatory techniques become either unreportable in the fossil record (as in *a*), poorly distinguishable from those produced by crabs (as in *b*), or unidentifiable as concerns their producers (as in *c*).

(*ii*) Some Recent stomatopods may use all the discussed predatory techniques. Thus, the spearing and smashing altogether take only a part, presumable low, within the whole spectrum of damages caused by a definite group of stomatopods.

(*iii*) The damages caused by stomatopods are always performed from one side of the shell. This allows to distinguish them from those produced by crabs, the attack of which is always performed upon two opposite parts of the shell (*cf. also* SHOUP 1968, BERTNESS & CUNNINGHAM 1981, VERMEIJ 1987). The latter case has recently been demonstrated by the co-Author for shell damages of the latest Cretaceous ammonites *Hoploscaphites constrictus* (J. SOWERBY) from the Middle Vistula Valley in Central Poland (RADWAŃSKI 1996).

The two announced reports, by GEARY & *al.* (1991) and PETHER (1995), offer also the references to the other, then available, data on the behavior (nesting, burrowing, the preying procedures, the strength and speed of attacks including), habitat, and life requirements of Recent stomatopods.

Of newer reports on fossil stomatopods, a few concern European forms (FÖRSTER 1982, LIENAU 1985, QUAYLE 1987, CORNELISSE 1996). In one of them, FÖRSTER (1982, Fig. 15) illustrates small burrows produced presumable by stomatopods, from the Upper Eocene of Germany, and with a reference to the present-day burrows from the Seychelles (*see* BRAITHWAITE & TALBOT 1972, p. 281 and Pl. 2, Fig. 4), and from the Atlantic coast of the United States (*see* HERTWECK 1972, p. 136). Some present-day forms, that live in their own-made burrows, are known to carry a booty into, to consume (CALDWELL & DINGLE 1976).

As concerns the stomatopod exoskeletons, it is to note that the most strongly mineralized parts are certainly the raptorial claws, armed with a multispined dactyl, and thus they sometimes are found as the only remains of some specimens preserved in a fossil state (*see* LOVISATO 1894; VIA 1949; FÖRSTER 1982, Fig. 4; QUAYLE 1987, Pl. 67, Fig. 8; KARASAWA & NAKAGAWA 1992, Pl. 1, Fig. 1).

Finally, it worths also noting that an increasing interest in the stomatopod crustaceans, both Recent and fossil, employed allover the world in last years (*see* CORNELISSE 1996, KARASAWA 1996, DE ANGELI & MESSINA 1996) has realized in researches of much variable kind. One of the topics has brilliantly been shown in a *National Geographic EXPLORER* program, aired this year (February 4, 9 p.m. ET; *see* NATIONAL GEOGRAPHIC, Vol. 189, No. 2, p. 135, February 1996) and titled “Animal Minds” in which the *Deceitful Mantis Shrimp* was a case to illustrate animal intelligence of higher order, comparable to that of creative dolphins and self-aware chimpanzeens (!).

THE SCOPE OF THE PRESENT STUDY

The scope of the present study is to describe the damages of gastropod shells identical to those caused by stomatopods, as documented by GEARY & *al.* (1991) or inferred by PETHER (1995), but coming from much older geologic succession of the Tertiary Period in Europe, precisely from the Miocene epoch, thus ageing about 15 m.y. ago.

The basic material for this study (*see* Pls 1 – 9) comes from the world-famous Korytnica Clays, a peculiar facies of the terminal part of a shallow bay developed along the dismembered, rocky shore of the southern slopes of the Holy Cross Mountains, Central Poland (*see* RADWAŃSKI 1969, 1970, 1977; BAŁUK & RADWAŃSKI 1977, 1991; JOHNSON 1988a,b; RADWAŃSKA 1992). The occurrence area of this facies, known from its ubiquity of gastropod shells, is one of the classical localities of the Miocene fauna in Europe. Its Middle Miocene age is close to the Langhian/Serravallian stage boundary, corresponding to the Badenian stage in the so-called Paratethys basins (*see* MARTINI 1977, BAŁUK & RADWAŃSKI 1977, BAŁUK 1995). The fame of this locality reaches back to the 18th century, and the number of the gastropod species accounts to about 800 (*see* BAŁUK 1975, 1995, 1997; BAŁUK & RADWAŃSKI 1977, 1979a).

The Authors' own studies through the last tree decades allowed to recognize a wide spectrum of biogenic damages in the gastropod shells collectable within the Korytnica Clays sequence. These are the damages caused by ordinary rock-borers (sponges, polychaetes, some bivalves; *see* RADWAŃSKI 1969, 1970; BAŁUK & RADWAŃSKI 1977), carnivorous gastropods (*see* HOFFMAN & *al.* 1974, KOWALEWSKI 1990), various crabs, the hermits including (*see* RADWAŃSKI 1969, 1970, 1977; BAŁUK & RADWAŃSKI 1977), and by the commensals to the hermits, such as polychaetes (*see* KERN 1979, BAŁUK & RADWAŃSKI 1984a), hydrozoans (*see* BAŁUK & RADWAŃSKI 1984a), ctenostomate bryozoans (*see* BAŁUK & RADWAŃSKI 1979b), and acrothoracican cirripedes (*see* BAŁUK & RADWAŃSKI 1991).

Until the report by GEARY & *al.* (1991) appeared, still another, quite great number of damages in the Korytnica gastropods had remained mysterious to the Authors. This group, typically of rather ordinary shapes (*see* Pls 1 – 4) was interpreted as of enigmatic biogenic origin, and the Authors were aware of their being no artifacts as anyone could easily classify. An argument of their being the original biogenic damages was fourfold: (*i*) their similarity to the damages caused by diverse predators (*see* reviews by VERMEIJ 1987, KABAT 1990, KOWALEWSKI 1993), the crabs including (*see* Pl. 8); (*ii*) their nature of usually very sharp punctures penetrating the shells, thus being not referrable to any physical tools accessible during the gastropod life, burial of the shells and/or their exhumation in the exposures over the cropland; (*iii*) the reparation ("regeneration") of the shells by the live gastropods themselves (*see* Pls 6 – 7); (*iv*) the squatting of large damages by the secondary inhabitants (*see* Pl. 7, Fig. 5a-5c).

During their search for biogenic damages in the Korytnica gastropods the Authors have inspected over 30-35,000 larger shells (length or diameter >1 cm). Within the damages identical with those presented by GEARY & *al.* (1991) and PETHER (1995) and subjected to the present study, both the forms typical of the spearing and of the smashing activity of the stomatopods are recognized. To note, such damages are practically absent from shells of other mollusks (chitons, scaphopods, bivalves) common in some parts of, or allover, the Korytnica sequence.

Moreover, similar damages of the stomatopod origin appeared to be easily recognizable in many illustrations of the Miocene gastropods from Europe, monographed by prominent malacologists from various countries. A review of such recognized stomatopod damages will follow the description of the Korytnica material.

SYSTEMATIC REMARKS

The taxonomy of the discussed stomatopod crustaceans is kept in the present paper the same as that used by MOORE & MCCORMICK (1969) and HOLTHUIS & MANNING (1969), supplemented in an earlier publication by SCHRAM (1968).

Phylum **Arthropoda** SIEBOLD & STANNIUS, 1845
Superclass **Crustacea** PENNANT, 1777
Class **Malacostraca** LATREILLE, 1806
Subclass **Eumalacostraca** GROBBEN, 1892
Superorder **Hoplocarida** CALMAN, 1904
Order **Stomatopoda** LATREILLE, 1817
Suborder **Unipeltata** LATREILLE, 1825

Families, to which the activity of stomatopods from the Korytnica Basin is herein ascribed:
Squillidae LATREILLE, 1803
Gonodactylidae GIESBRECHT, 1910

STOMATOPOD DAMAGES IN THE KORYTNICA BASIN

The studied material from the Korytnica Basin contains (*see* Tables 1-3 and Pls 1-9) over twelve hundred gastropod shells bearing the stomatopod damages. All recognized stomatopod damages occur in clean shells, that is those free from any endo- or epizoans.

In the following review, the taxonomy of the indicated gastropod species is the same as that used in the monographic descriptions of the Korytnica gastropods (BAŁUK 1975, 1995, 1997).

MORPHOLOGY OF THE DAMAGES

The morphology of the stomatopod damages in the studied gastropod shells from the Korytnica Basin is much variable. The simplest, but the commonest forms (*see* Tables 1-2) are herein classified as the holes, all of which tend to acquire a more or less circular outline (*see* Pls 1-2 and 4-6).

Circular holes

The circular holes vary in size from tiny punctures (*see e.g.* Pl. 1, Figs 1a-1b, 2a-2b, 4a, 5a-5b) to quite large holes damaging seriously the last whorl of the gastropod shell (*see e.g.* Pl. 1, Figs 1e-1f, 2e, 4e, 5e). In particular gastropod species, a range of the hole diameter is well accentuated in various specimens (Pl. 1, Figs 1-5).

Some circular holes are partly elongated, and then acquiring a keyhole shape (*see e.g.* Pl. 1, Figs 1f, 4d, 5d; Pl. 2, Figs 6 and 13; Pl. 4, Figs 3b-3c). Such holes certainly result from a double injury, the nearby holes of which have fused together, as it is apparent from the shells that bear the two injuries separated (Pl. 2, Figs 14-19), one of which may also be doubled into a keyhole shape (Pl. 2, Fig. 17).

To note, the holes of a less regular outline appear usually in the thinner-walled gastropod shells, for instance of the genera *Clavatula* and *Turritella*. In the thicker gastropod shells the holes are almost ideally circular (*see e.g.* Pl. 2, Figs 2-3 and 7-8; Pl. 6, Figs 3-4).

The smaller circular holes are interpreted as punctures of a spearing stomatopod dactyl that pierced the gastropod shell throughout. The largest holes (*see e.g.* Pl. 7, Figs 1 and 5; Pl. 8, Figs 1e-1g; possibly also those above-indicated in Pl. 1, Figs 1e-1f, 2e, 4e, 5e) fall into the range of damages produced by the smashing stomatopods.

Elongated scars

The elongated scars (*see* Pl. 3) are remarkably less common in the studied material from the Korytnica Basin (*cf.* Tables 1-2). They vary in size and extent from small elongated punctures (Pl. 3, Figs 4-5) to larger fissures or holes that cut the gastropod shell whorl across (Pl.

PLATE 1

Stomatopod injuries (circular holes) in shells of some of the most commonly attacked species (*see* Table 1) of the Korytnica gastropods; all in nat. size

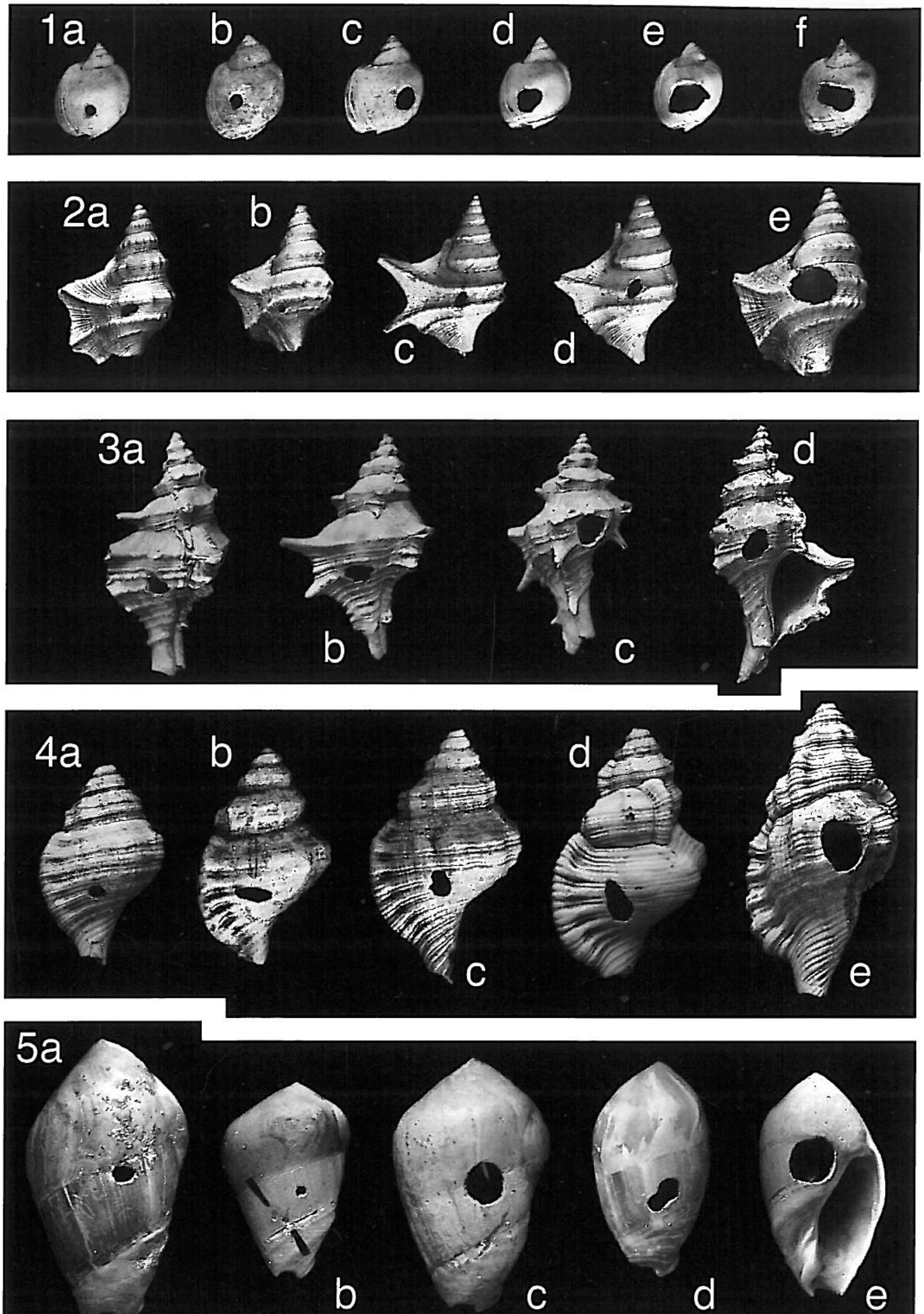
1a-1f — Injuries in *Sphaeronassa schoenni* (HOERNES & AUINGER)

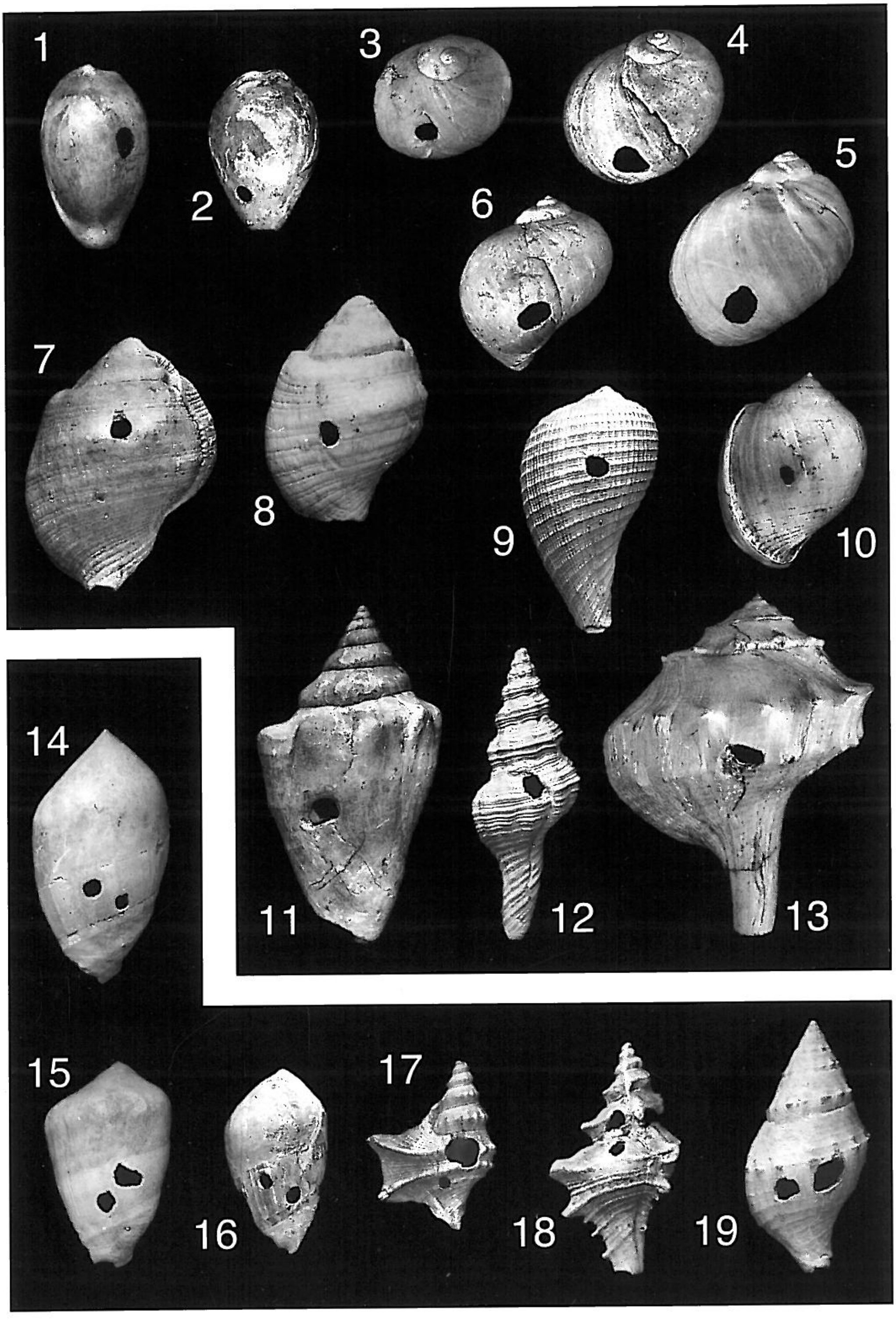
2a-2e — Injuries in *Aporrhais pespelecani* (LINNAEUS)

3a-3d — Injuries in *Murex (Tubicauda) friedbergi* COSSMANN & PEYROT

4a-4e — Injuries in *Cymatium (Lampusia) affine* (DESHAYES)

5a-5e — Injuries in *Ancilla (Baryspira) glandiformis* (LAMARCK); in Fig. 5b indicated by leaders are two initial ("unsuccessful") punctures (*see* Pl. 5)


1a
b
c
d
e
f
2a
b
c
d
e
3a
b
c
d
4a
b
c
d
e
5a
b
c
d
e


1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19

3, Fig. 10). Their setting in shells of particular gastropod species is variable, both as concerns the whole shell (*see* Pl. 3, Figs 4-5), and the last whorl solely (*see* Pl. 3, Figs 6-8 and 9-12). Some of such larger scars continue into a superficial scratch of the shell (*see* Pl. 3, Fig. 6). Moreover, there also occur scratches of the shape and extent comparable to those of scars (*see* Pl. 3, Fig. 1b-1c). Sporadically, two elongated scars occur in a shell (Pl. 3, Fig. 12).

All the elongated scars are interpreted as caused by deep injuries produced by the sprearing stomatopod dactyl, whereas the scrathes are thought to be initial forms of the former.

The punched plug

The morphology of almost all the circular holes and elongated scars is characterized by their very jagged margins, both on the outer and the inner side of the gastropod shells (*see* Pls 4-5). Strongly jagged, full of spalls, is usually the lower margin formed on the shell interior (*see* Pl. 4, Figs 1c, 2c, 3c, 4c; Pl. 5, Fig. 4b-4c). This indicates that the plug formed when the stomatopod was punching the shell, was also featured by jagged margins on its both sides. It happened that one such a plug was recovered loose in a sifting material from the gastropod shell interior (Pl. 5, Fig. 5a-5b).

Initial punctures

The initial punctures (*see* Pl. 5) embossed usually on the thicker-walled gastropod shells occur either singly (Pl. 5, Figs 1-2), or in pairs (Pl. 1, Fig. 5b; Pl. 5, Figs 3-4). All of them display more or less jagged margins, adorned with a crushed residuum of the shell punched by a

---

PLATE 2

Circular holes in shells of some other species (*cf.* Pl. 1) of the Korytnica gastropods: Figs 1 – 13 single holes, Figs 14 – 19 double holes; all in nat. size

1-2 — Single injuries in the cowries:
- **1** — *Apiocypraea subamygdalum* (D'ORBIGNY),
- **2** — *Monetaria brocchii* (DESHAYES)

3 — Single injury in *Neverita josephinia* RISSO
4-5 — Single injuries in *Polinices redemptus* (MICHELOTTI)
6 — Single injury in *Natica tigrina* RÖDING
7-8 — Single injuries in *Gyrineum (Aspa) marginatum* (MARTINI)
9 — Single injury in *Ficus (Ficus) condita* (BRONGNIART)
10 — Single injury in *Semicassis (Semicassis) miolaevigata* SACCO
11 — Single injury in *Strombus (Strombus) bonellii* BRONGNIART
12 — Single injury in *Latirus valenciennesi* (GRATELOUP)
13 — Single injury in *Tudicla (Tudicla) rusticula* (BASTEROT)
14-16 — Double injuries in *Ancilla (Baryspira) glandiformis* (LAMARCK)
17 — Double injury in *Aporrhais pespelecani* (LINNAEUS)
18 — Double injury in *Murex (Tubicauda) friedbergi* COSSMANN & PEYROT
19 — Double injury in *Euthria puschi* (ANDRZEJOWSKI)

stomatopod. The impressed part of the gastropod shell tended to form a plug, the sole of which, also jagged, is well visible on the innerside of the shell (Pl. 5, Figs 3b, 4b-4c).

The doubled initial punctures (Pl. 5, Figs 3-4) were presumably formed by the stomatopods repeating their attack soonafter the first attempt did not result in a full puncture.

All the initial punctures are interpreted as traces of unsuccessful attacks (*see* Table 3) of the stomatopods which either could not pierce the gastropod shell throughout, or discarded the attacked prey. The frequency of such unsuccessful attacks is, generally, very low (*see* Table 3).

The heaviest damages

The heaviest damages in gastropod shells from the Korytnica Basin, and ascribed to the predatory action of stomatopods (*see* Pls 8-9), realize by the large holes or irregular shapes (Pl. 8, Fig. 1g) which could develop by an enlargement of smaller holes, either single (Pl. 8, Figs 1a-1e) or double (Pl. 8, Fig. 1f), and can continue onwards, up the spire of the shell, and taking half a whorl (Pl. 8, Figs 1h-1m) or more (*see* Pl. 9), up to one and a half whorls (Pl. 9, Fig. 5a-5b).

An interpretation of the heaviest damages is directed to the smashing activity of stomatopods. Although such damages may be arranged in a successive file from small punctures at its beginning (as in Pl. 8, Figs 1a-1m), the first items of such a file must be ascribed to the spearing activity of stomatopods.

An attention is paid that the heaviest stomatopod damages are morphologically very close to those produced by predatory crabs (*see* RADWAŃSKI 1969, 1977; BAŁUK & RADWAŃSKI 1977; VERMEIJ 1978, 1987; and references therein). Some of the collected specimens cannot be precisely classified in this matter. The typical crabs' damages are always adorned with margins tattered regularly into a saw-like manner (*see* Pl. 8, Figs 2a-2d and 3a-3c), that corresponds to successive nipping-off the shell pieces by the cutting claws (*cf.* RADWAŃSKI 1977, pp. 253-254).

Surprisingly, the heaviest damages in the long-spired shells of the genus *Clavatula* are occasionally associated with one, two, or even three

PLATE 3

Elongate scars in shells of the Korytnica gastropods; all in nat. size

1 — Two elongate scars in a shell of *Ancilla* (*Baryspira*) *glandiformis* (LAMARCK); seen in successive adapertural views (**a**, **b**, **c**) to focus the scars, one of which is an initial scratch (indicated by a leader)

Single elongated scars in:

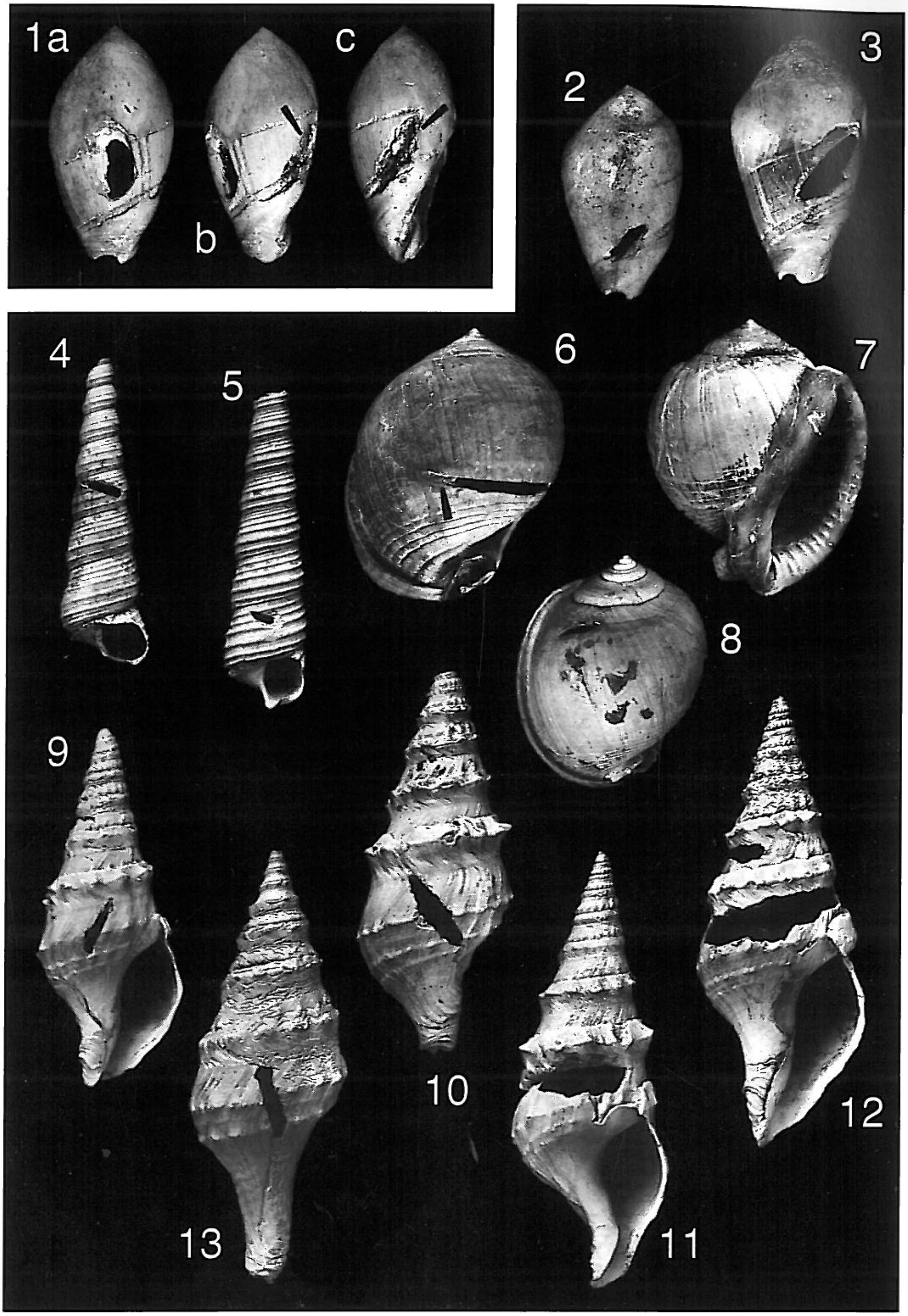
2-3 — Two other specimens of *Ancilla* (*Baryspira*) *glandiformis* (LAMARCK)

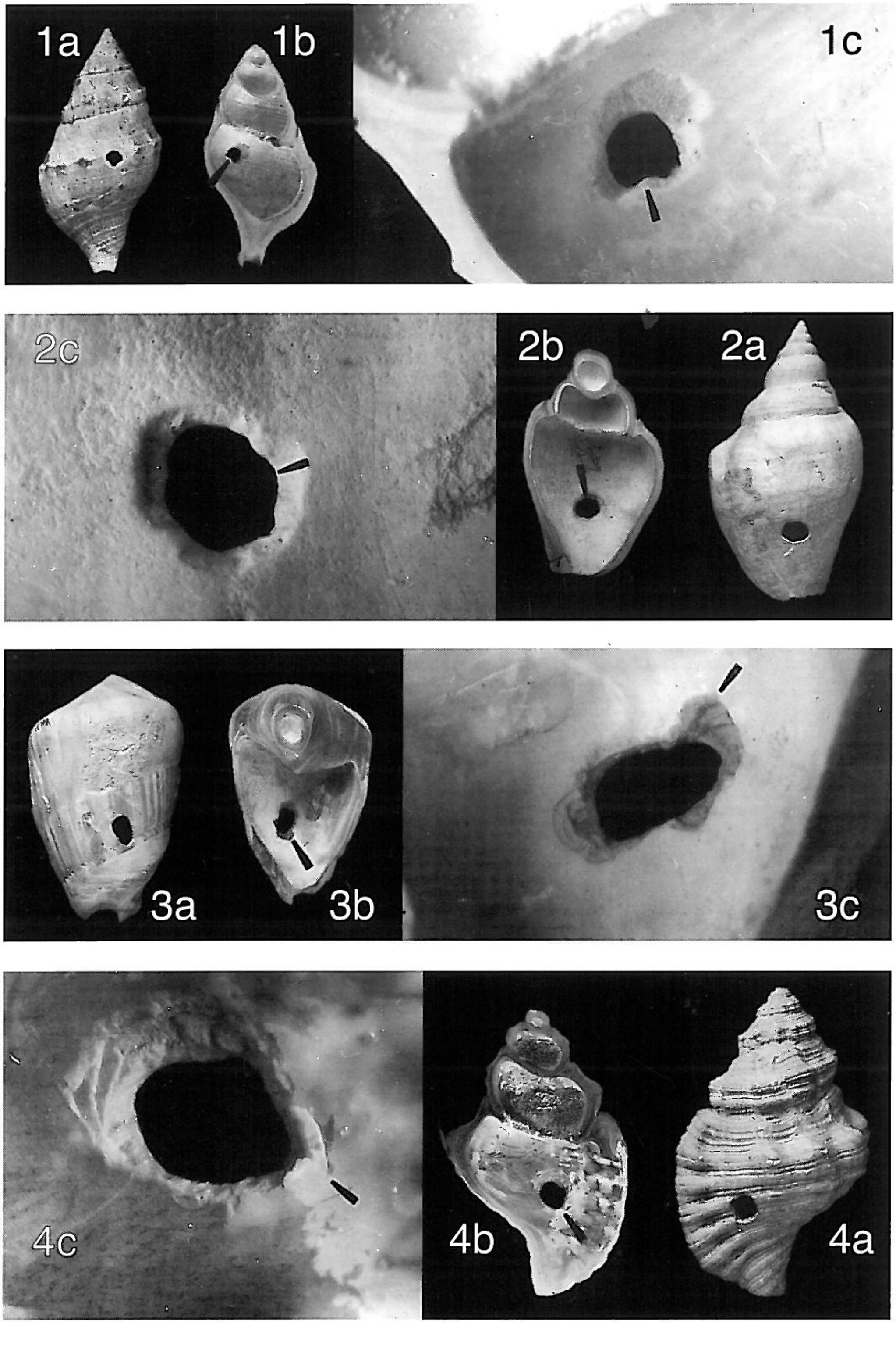
4-5 — *Turritella* (*Haustator*) *badensis* SACCO

6-8 — *Semicassis* (*Semicassis*) *miolaevigata* SACCO; in one of the specimens (Fig. 6) the scar continues into a scratch (indicated by a leader)

9-12 — *Clavatula asperulata* (LAMARCK); one of the specimens (Fig. 12) bears two scars

13 — *Clavatula laevigata* (EICHWALD)


1a
b
c
2
3
4
5
6
7
8
9
10
11
12
13


1a
1b
1c
2c
2b
2a
3a
3b
3c
4c
4b
4a

punctures in the adapical part of the shell (Pl. 9, Figs 1-6), and some of these punctures may be initial (*arrowed* in Pl. 9, Fig. 5a-5b). An interpretation of such damages remains a scientific guess: should this be a result of a combat of one spearer that was catching/holding the shell which was just being effectively broken by one smasher becoming the winner?

REPARATION OF THE GASTROPOD SHELLS

Some of the studied injuries in gastropod shells from the Korytnica Basin are evidently repaired (*see* Pls 6-7), what clearly indicates that, even if a puncture throughout the shell was formed, some stomatopod attacks remained unsuccessful, that is not fatal to the shell owner that survived and could repair its shell.

To clarify the nomenclature, the term **reparation** is herein understood the same as used by the Authors earlier (BAŁUK & RADWAŃSKI 1984a, p. 215), to denote the process of a repair of the shell by its owner. This term was introduced instead of the formerly used "*regeneration of the shell*" or "*regeneration of damages in shells*". The term **regeneration** is proclaimed to cover the process of a further growth of an animal's fragment which consequently attains, more or less ideally, the shape and size typical of the adult specimens of the species (*see* discussion *in*: BAŁUK & RADWAŃSKI 1984a).

In the studied material of the stomatopod damages in gastropod shells, repaired are holes of variable size and shape. The reparated holes are usually situated near the shell aperture (*see* Pl. 6, Figs 1a, 3-4, 8a, 9a), but some may appear very high along the shell spire (*see* Pl. 6, Figs 2a, 5a, 6-7). If the first group is interpreted as a result of a stomatopod attack upon the gas-

PLATE 4

Detailed anatomy of the circular and/or almost circular holes in shells of the Korytnica gastropods

In all figures: **a** — outside view of the shell, **b** — innerside view, as seen in the sectioned shell, both in nat. size; **c** — close-up of the innerside (leaders refer to the points indicated in **b**, as all close-ups are lightened and/or oriented slightly differently than b), × 5

1 — *Euthria puschi* (ANDRZEJOWSKI): **1a** – outside view, **1b** – innerside view of the sectioned shell, **1c** – close-up of the innerside

2 — *Strombus* (*Strombus*) *bonellii* BRONGNIART: **2a** — outside view, **2b** – innerside view of the sectioned shell, **2c** – close-up of the innerside

3 — *Ancilla* (*Baryspira*) *glandiformis* (LAMARCK): **3a** – outside view, **3b** – innerside view of the sectioned shell, **3c** – close-up of the innerside

4 — *Cymatium* (*Lampusia*) *affine* (DESHAYES): **4a** – outside view, **4b** – innerside view of the sectioned shell, **4c** – close-up of the innerside tropod which was able to withdraw deeply into its shell, and thus to survive, the second group is supposedly a result of attacks by stomatopods which occasionally discarded (or, lost) their "almost sure" catch.

In all cases, the studied gastropod shells were repaired with an additional shell layer, the extent of which often overlaps the margins of a plug formed during the attack. In result, the sole of a plug, covered with an additional shell layer, looks like a small, more or less rounded bump (Pl. 6, Fig. 5b). The effect of reparation becomes more pronounced when the gastropod extended the repaired portion of its shell far down, just to the aperture, inside which a new one was formed to adher firmly to the former one (*see* Pl. 7, Figs 1-3). In these cases, the new aperture was formed during reparation of the shell damage situated near the aperture, but the damages themselves were of much variable size, ranging from small punctures (Pl. 7, Fig. 3a-3b), through larger ones (Pl. 7, Fig. 2a-2b), to quite large holes (Pl. 7, Fig. 1a-1c).

In some elongated, high-spired shells, the stomatopod damages are repaired by an additional shell layer partly, to cut off an access to the shell apex, but without filling up the holes fully (Pl. 7, Fig. 4a-4b).

The total number of the reparated shells in the studied material is very low (*see* Table 3), as it reaches merely the value of 46 per 6 gastropod species.

SETTING OF THE DAMAGES

The setting of the stomatopod damages in gastropod shells from the Korytnica Basin is generelly preferential. In the majority of specimens the

---

PLATE 5

Initial injuries not piercing throughout the shells ("unsuccessful" in Table 3) of the Korytnica gastropods; overall views in nat. size, close-ups × 5

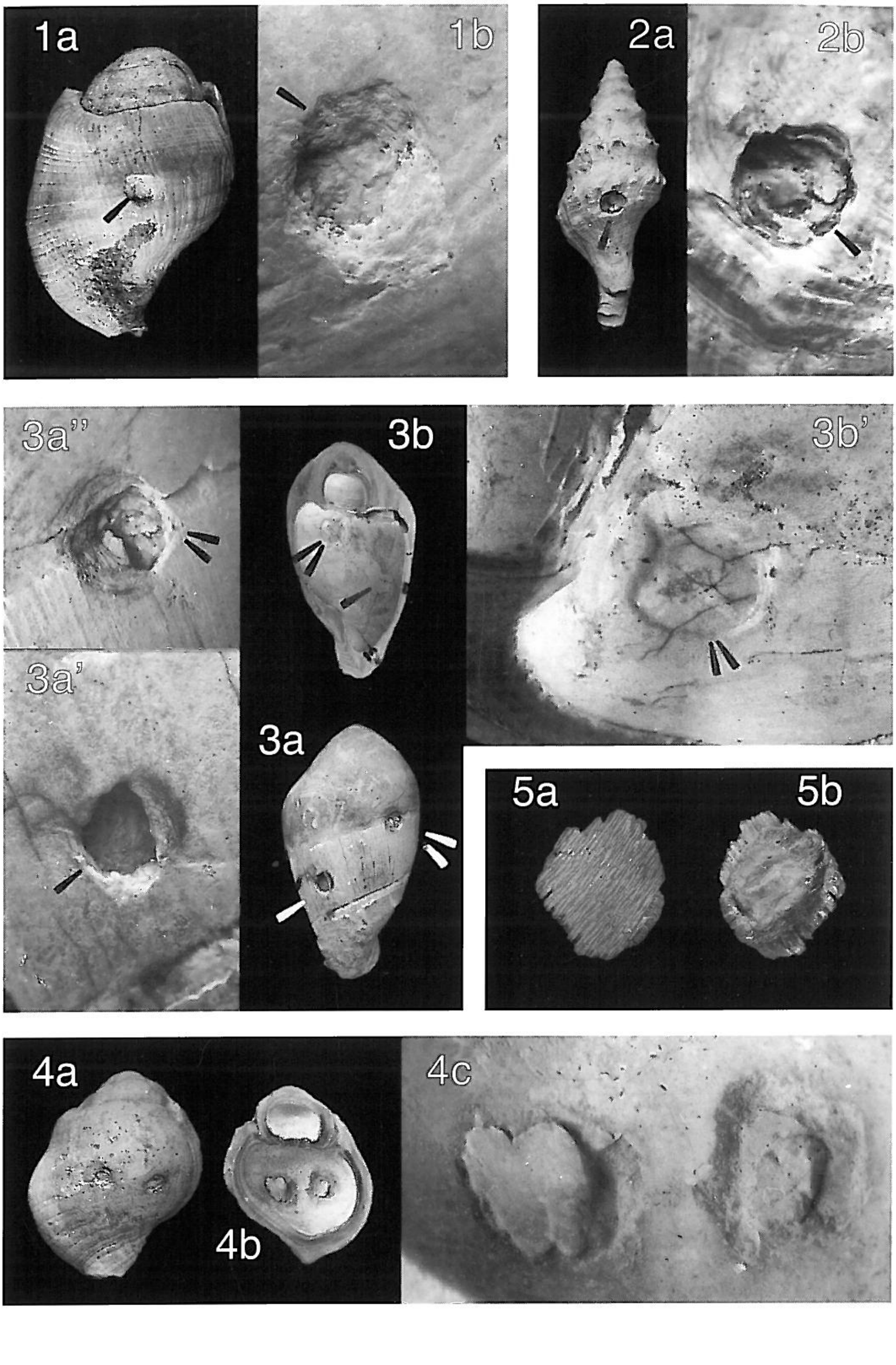
1 — *Gyrineum (Aspa) marginatum* (MARTINI): **1a** – outside view; **1b** – close-up of the unjury (leader indicates the reference point)

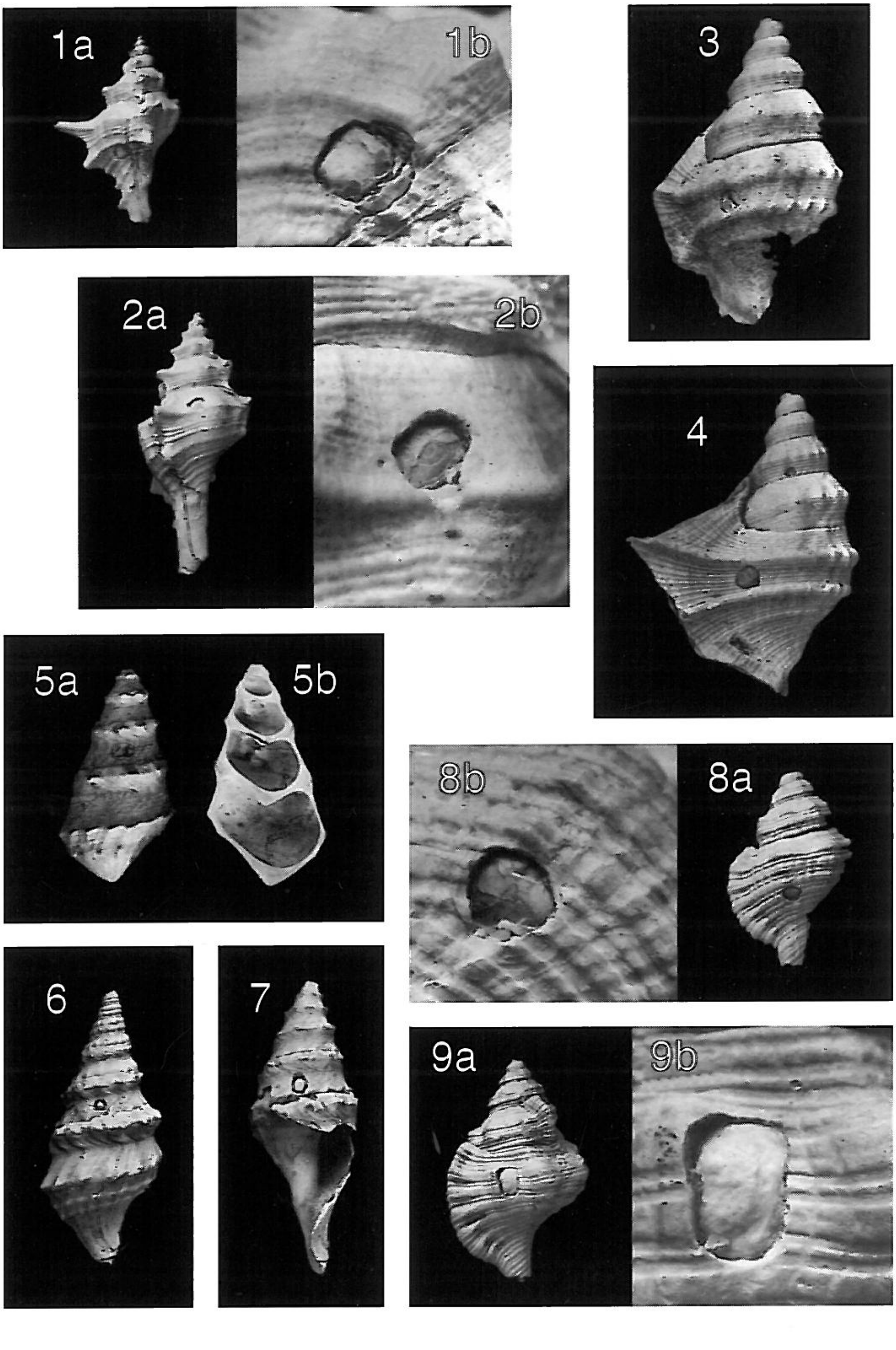
2 — *Clavatula laevigata* (EICHWALD): **2a** – outside view; **2b** – close-up of the injury (leader indicates the reference point)

3 — *Ancilla (Baryspira) glandiformis* (LAMARCK) with two injuries: **3a** – outside view (the reference leaders indicate the injuries shown in close-ups **3a'** and **3a"**); **3b** – innerside view of the sectioned shell (double leader indicates the injury close-uped in **3b'**)

4 — *Gyrineum (Aspa) marginatum* (MARTINI) with two injuries: **4a** – outside view, **4b** – innerside view, **4c** – close-up the innerside

5 — Jagged plug from a puncture piercing the shell throughout, found loose in a clay sifted from the gastropod-shell interior: **5a** – outer view, **5b** – inner view; both × 5


1a
1b
2a
2b
3a''
3b
3b'
3a'
3a
5a
5b
4a
4b
4c


1a
1b
3
2a
2b
4
5a
5b
8b
8a
6
7
9a
9b

stomatopod damage(s) is/are situated in the last whorl of the gastropod shell, usually slightly farther than a quarter of the whorl from the aperture (*see* Text-fig. 1a). The damages more distant to the shell aperture are uncommon (*see e.g.* Pl. 1, Figs 3d, 5e; Pl. 6, Figs 5-7; Pl. 8, Figs 1d-1e).

The elongated scars occur in any part of the preyed gastropod shell, and are distributed from the apertural part (*see* Pl. 3, Fig. 8) up to the mid-height of the spire (*see* Pl. 3, Figs 4 and 12).

Nevertheless, in several common gastropod species the setting pattern of the stomatopod damages was investigated more detaily, to recognize their distribution over the shell, when the damages were counted in sectors of every 15° of the shell spire (Text-fig. 1).

Of these selected gastropod species that bear more numerous stomatopod damages, *Ancilla* (*Baryspira*) *glandiformis* (LAMARCK) displays the injuries located preferentially at the above-indicated place (Text-fig. 1a), whereas *Clavatula laevigata* (EICHWALD) at the sector opposite to the former, that is situated almost a whorl far from the aperture (Text-fig. 1b). Such settings are interpreted as resulted from a different shape and/or balance (weight) of the body-containing gastropod shell inspected by a stomatopod catching the prey and willing to attack. In the muricid species with shells featured by prickly varices, *Murex* (*Tubicauda*) *friedbergi* COSSMANN & PEYROT, preferentially exposed to stomatopod attacks were the intervarical sectors of the shell (Text-fig. 1c).

The presented examples show that many factors influenced the position of the stomatopod attack upon diverse gastropod species living in the Korytnica Basin.

PLATE 6

Repaired injuries in shells of the Korytnica gastropods; overall views in nat. size, close-ups × 5

1-2 — *Murex* (*Tubicauda*) *friedbergi* COSSMANN & PEYROT: **1a**, **2a** – outside views; **1b**, **2b** – close-ups (lightened and/or oriented slightly differently, to focus the injuries)

3-4 — *Aporrhais pespelecani* (LINNAEUS)

5 — *Clavatula laevigata* (EICHWALD): **5a** – outside view, **5b** – innerside view of the sectioned shell

6 — *Clavatula asperulata* (LAMARCK)

7 — *Clavatula laevigata* (EICHWALD)

8-9 — *Cymatium* (*Lampusia*) *affine* (DESHAYES): **8a**, **9a** – outside views, **8b**, **9b** – close-ups (lightened and/or oriented slightly differently, to focus the injuries)

FREQUENCY OF THE DAMAGES

The stomatopod predatory frequency in shells of particular gastropod species from the Korytnica Basin is much variable, as it ranges from less than one up to 54.4%, that is it may concern over a half of the population of a given species. The average values range from 2 up to 11-13% (*see* Tables 1 – 2).

In the presented account of the stomatopod damages, the gastropod shells featured by the circular holes are counted separate (Table 1) to those bearing the elongated scars (Table 2). In both cases counted are the attacked gastropod specimens regardless the number of damages they bear on their shells.

For some of the most common gastropod species presented is also a variability range of damages, to exemplify their number (up to four in several specimens), character (initial, or completed), and possible reparation (Table 3).

PLATE 7

Examples of the more complex repairs, and of the squatting the heavily injured shells of the Korytnica gastropods

1 — *Cymatium* (*Lampusia*) *affine* (DESHAYES): three successive views (**1a**, **1b**, **1c**) of the heavily injuried shell, healed, and repaired with an additional inner layer continuing onwards into an additional varical aperture (*double leader*) set up inside the primary varical aperture (*single leader*); nat. size

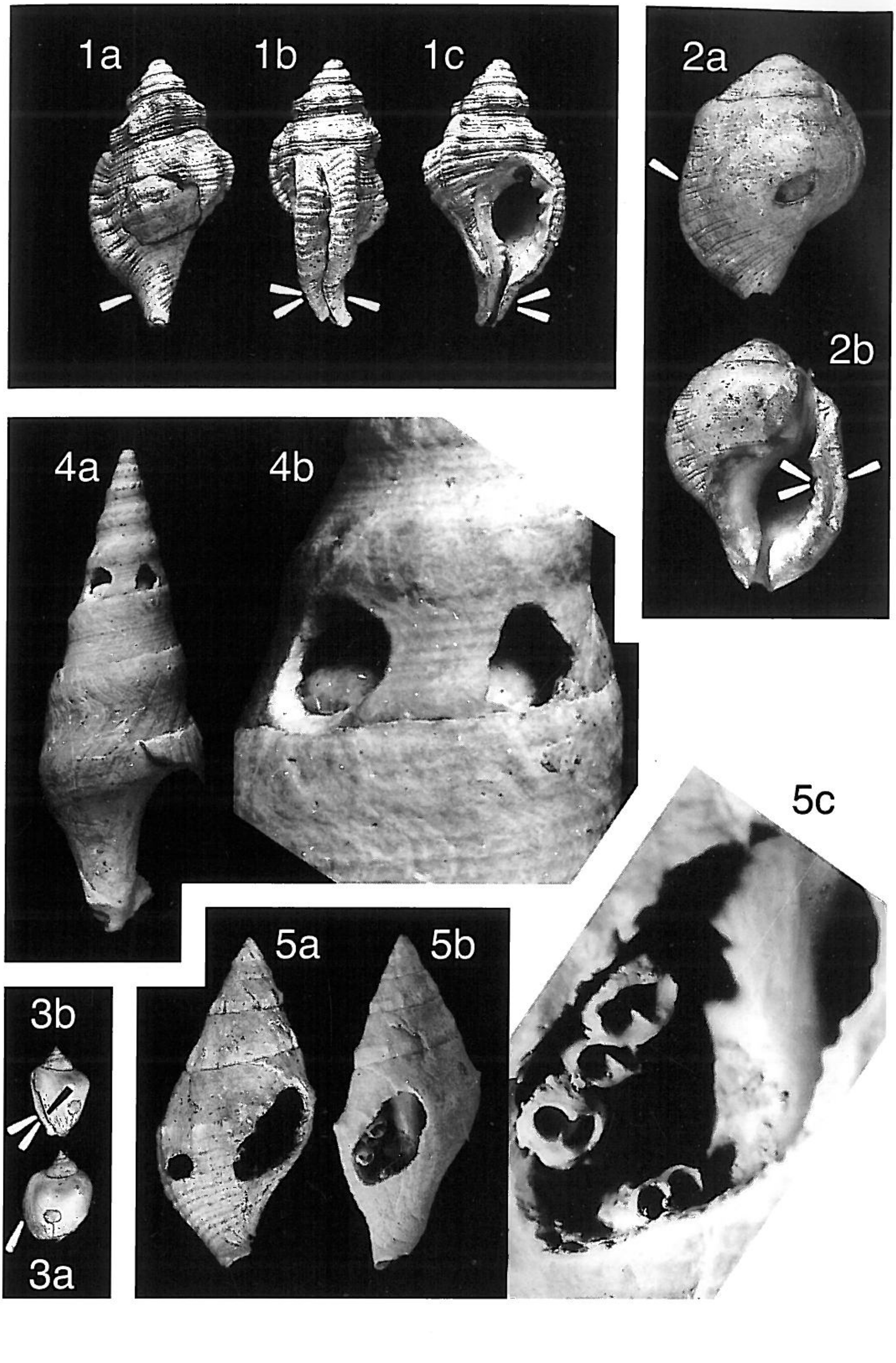
2 — *Gyrineum* (*Aspa*) *marginatum* (MARTINI): two views (**2a**, **2b**) of the shell with a healed injury, and repaired with an additional inner layer continuing onwards (*see* apertural view in Fig. 2b) into the aperture terminated with an additional varix (*double leader*) set up inside the primary varix (*single leader*); nat. size

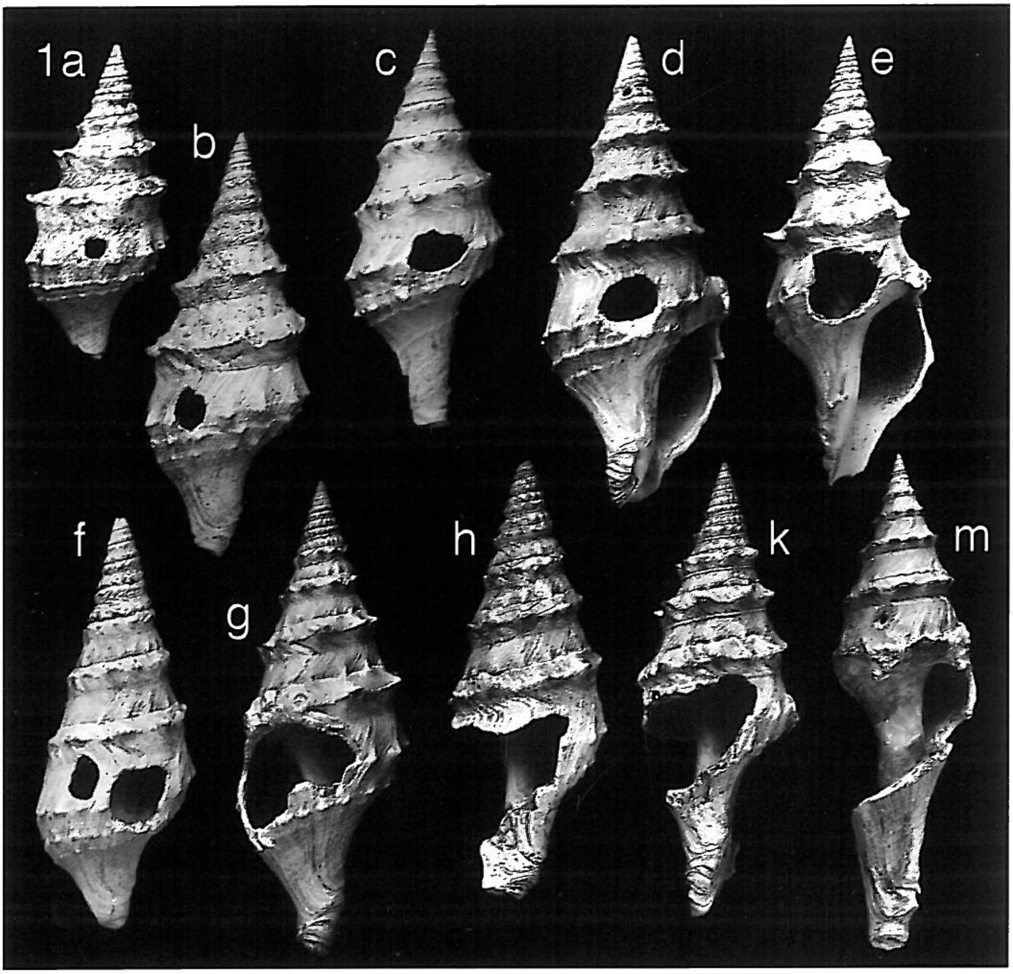
3 — *Sphaeronassa schoenni* (HOERNES & AUINGER): two views (**3a**, **3b**) of the shell with a healed small puncture, and repaired with an additional inner layer continuing onwards (*see* apertural view in Fig. 3b) into the aperture terminated with an additional outer lip (*double leader*) inside the primary lip (*single leader*); nat. size

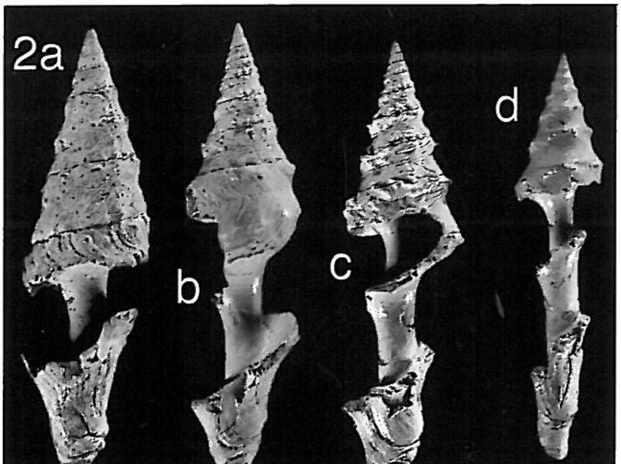
4 — *Clavatula pretiosa* (BELLARDI): two injuries repaired with an additional inner layer of the shell, to form a kind of an "apical operculum" known in present-day turritellas (*see* CHARLES 1977, Pl. 7, Fig. 3a-3b); overall view (**4a**) in nat. size, close-up (**4b**) taken × 5

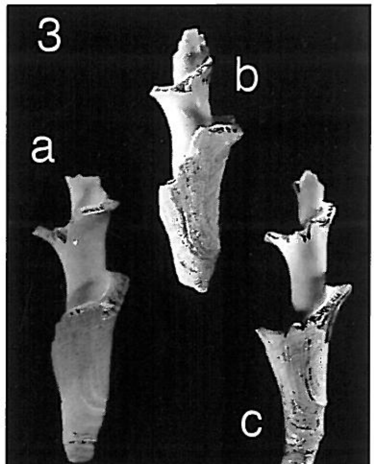
5 — *Euthria puschi* (ANDRZEJOWSKI): shell with two injuries, the larger of which evidences its being (*i.e.* origin) in the sedimentary environment of the Korytnica Clays: this injury was squatted by a group of four bivalves *Gastrochaena dubia* (PENNANT) as a refuge spot, to keep apertures of their crypts ("agglutinaceous tubes"; *cf.* RADWAŃSKI 1969, Fig. 5c) steadily with the margin of the injury; the same specimen as illustrated in BAŁUK & RADWAŃSKI (1984a, Pl. 1, Fig. 3)

5a, **5b** – Two successive views, to focus the injuries, × 1.5; **5c** – close-up, × 5


1a
1b
1c
2a
2b
4a
4b
5c
5a
5b
3b
3a


1a
b
c
d
e
f
g
h
k
m


2a
b
c
d


3
a
b
c

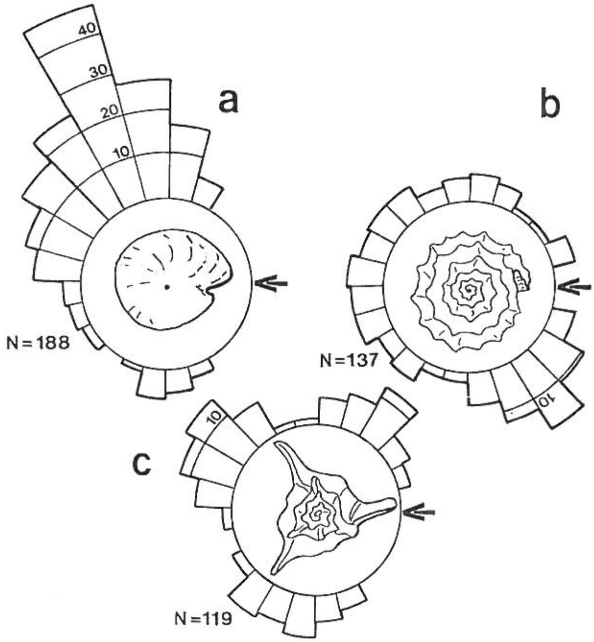


Fig. 1

Rose diagrams showing distribution of the stomatopod injuries (single circular holes, *see* Table 1) in shells of some gastropod species from the Korytnica Basin; the shells are outlined in their apical view, position of the aperture is arrowed; the number of the counted items is indicated with circles at every 10 specimens

a – *Ancilla (Baryspira) glandiformis* (LAMARCK)
b – *Clavatula laevigata* (EICHWALD)
c – *Murex (Tubicauda) friedbergi* COSSMANN & PEYROT

PLATE 8

1a-1m — A series of clavatulid shells, to show the size range of injuries ascribed to predatory attacks of the stomatopods in the Korytnica Basin; all in nat. size

1a-1b, **1d-1m** — *Clavatula asperulata* (LAMARCK); **1c** — *Clavatula laevigata* (EICHWALD)

2-3 — Comparative series of clavatulid shells from the Korytnica Basin, to show successive stages of the destruction by hermit crabs (*cf.* RADWAŃSKI 1969, 1977; BAŁUK & RADWAŃSKI 1977) and/or calappid crabs (*cf.* SHOUP 1968; VERMEIJ 1978, Fig. 2.13); all in nat. size

2a-2d — *Clavatula* sp. div., heavily damaged ("successfully") by a chipping-off the shell up to the last three whorls

3a-3c — *Clavatula* sp. div.: crab's "kitchen-middens" composed of shells the most heavily chipped-off (*cf.* Fig. 2d of this Plate) and their columellas broken into halves

Table 1

Predatory attacks of stomatopods upon particular gastropod species from the Korytnica Basin

Counted are the specimens bearing circular holes of diameter >1 mm, both unhealed (*see* Pls 1-2 and 4-5) and/or repaired (*see* Pls 6-7)

Gastropod species	attacked specimens	of total	percentage of attacked
Sphaeronassa dujardini (DESHAYES)	49	90	**54.4**
Sphaeronassa schoenni (HOERNES & AUINGER)	69	146	47.6
Clavatula jouanneti (DESMOULINS)	11	**40**	27.5
Clavatula styriaca (AUINGER)	8	60	13.3
Ancilla (Baryspira) glandiformis (LAMARCK)	229	**1750**	13.1
Murex (Tubicauda) friedbergi COSSMANN & PEYROT	144	**1200**	12.0
Ficus (Ficus) condita (BRONGNIART)	4	35	11.4
Aporrhais pespelecani (LINNAEUS)	41	**370**	**11.1**
Cymatium (Lampusia) affine (DESHAYES)	26	270	9.6
Clavatula laevigata (EICHWALD)	169	**1780**	9.4
Gyrineum (Aspa) marginatum (MARTINI)	10	110	**9.1**
Purpura (Tritonalia) erinacea (LINNAEUS)	3	35	8.7
Clavatula camillae (HOERNES & AUINGER)	19	235	8.1
Pyrene (Alia) polonica (PUSCH)	14	185	7.6
Semicassis (Semicassis) miolaevigata SACCO	7	105	6.7
Strombus (Strombus) bonellii BROCCHI	2	**30**	**6.6**
Clavatula asperulata (LAMARCK)	73	**1200**	6.1
Monetaria brocchii (DESHAYES)	2	35	5.7
Ficus (Ficus) cingulata (BRONN *in* HÖRNES)	2	35	5.7
Turritella (Haustator) badensis SACCO	125	**2300**	**5.4**
Euthria puschi (ANDRZEJOWSKI)	7	150	4.7
Tudicla (Tudicla) rusticula (BASTEROT)	8	**180**	4.2
Neverita josephinia RISSO	9	240	3.7
Hexaplex (Phyllonotus) pomiformis (EICHWALD)	2	55	3.6
Latirus valanciennesi (GRATELOUP)	1	30	3.3
Polinices redemptus (MICHELOTTI)	7	**225**	**3.1**
Polinices protractus (EICHWALD)	9	**350**	**2.7**
Narona (Sveltia) varricosa (BROCCHI)	5	200	2.5
Euthriofusus virgineus (GRATELOUP)	3	120	2.5
Narona (Sveltia) inermis (PUSCH)	1	50	2.0
Natica tigrina RÖDING	19	**3000**	**0.6**

Bold-faced are values commented hereafter

Table 2

Predatory attacks of stomatopods upon particular gastropod species from the Korytnica Basin

Counted are the specimens bearing elongated scars (*see* Pl. 3), all of which are unhealed (not repaired)

Gastropod species	attacked specimens	of total	percentage	total percentage (values of Tables 1 and 2 summarized)
Clavatula laevigata (EICHWALD)	78	1780	4.4	**13.8**
Clavatula camillae (HOERNES & AUINGER)	8	235	3.4	11.5
Sphaeronassa schoenni (HOERNES & AUINGER)	5	146	3.4	**51.0**
Semicassis (Semicassis) miolaevigata SACCO	3	105	2.9	9.6
Clavatula jouanneti (DESMOULINS)	1	40	2.5	**30.0**
Clavatula styriaca (AUINGER)	1	60	1.7	15.0
Clavatula asperulata (LAMARCK)	19	1200	1.6	**7.7**
Murex (Tubicauda) friedbergi COSSMANN & PEYROT	14	1200	1.2	**13.2**
Ancilla (Baryspira) glandiformis (LAMARCK)	12	1750	0.7	**13.8**
Tudicla (Tudicla) rusticula (BASTEROT)	1	180	0.6	**4.8**
Cymatium (Lampusia) affine (DESHAYES)	1	270	0.4	10.0
Polinices redemptus (MICHELOTTI)	1	225	0.4	3.5

Bold-faced are values commented hereafter

Table 3

Variability of the stomatopod damages in shells of some most common Korytnica gastropods

Number and character of damages (all are circular holes, as in Table 1)	*Ancilla (Baryspira) glandiformis* (LAMARCK)	*Murex (Tubicauda) friedbergi* COSSMANN & PEYROT	*Clavatula laevigata* (EICHWALD)	*Turritella (Haustator) badensis* SACCO
Number of specimens	1750	1200	1780	2300
1S	142	103	123	107
2S	19	15	11	11
3S	-	2	7	-
4S	-	-	-	1
1S + 1U	14	6	9	-
1S + 2U	2	-	-	-
1S + 3U	-	-	1	-
2S + 1U	1	-	3	-
2S + 2U	1	-	-	-
1U	42	5	6	-
2U	3	-	-	-
1U + 1Ur	-	1	1	-
1Ur	3	-	6	-
1Sr	1	11	2	6
1Sr + 1Ur	1	1	-	-
Total number of damages (as *in* Table 1)	229=13.1%	144=12.0%	169=9.4%	125=5.4%

S – hole throughout the shell: "successful" for the stomatopod, **U** – hole not piercing the shell: "unsuccessful" for the stomatopod, **r** – scar repaired by the gastropod

The most common of the studied species, the moon shell *Natica tigrina* RÖDING, is omitted, as its stomatopod-predation frequency is less than 1.0% (*see* Table 1)

Of the counted taxa of the Korytnica gastropods (*see* Tables 1 – 2), some results of the stomatopod attacks are to be commented as follows.

(*i*) The highest percentage of attacked specimens is displayed by the two species of the small-sized genus *Sphaeronassa*, viz. *S. dujardini* (DESHAYES) and *S. schoenni* (HOERNES & AUINGER). The percentage of the attacked specimens within these two species much exaggerates (54.4, and 51.0, respectively) all other values. This may be interpreted as a result either of keeping the same, possibly restricted, ecospace by these two spheronassids and the mantis shrimps, or of the prey, that is of the food, preference of the mantis shrimps.

(*ii*) Of the most common and showy gastropods, the clavatulids (formerly, the broad genus *Pleurotoma*, that implied the name of the Korytnica Clays as the Pleurotoma Clays – *see* BAŁUK & RADWAŃSKI 1977, p. 96), the most seriously preyed (30.0%) is a rather rare (40 specimens collected) species *Clavatula jouanneti* (DESMOULINS), to which the circumstances indicated above (as in *i*) may be applied.

(*iii*) Of the two commonest species of the genus *Clavatula*, viz. *C. laevigata* (EICHWALD) and *C. asperulata* (LAMARCK), studied in the great number of specimens (1780, and 1200, respectively), the first one, featured by a relatively weak ornamentation and slightly thinner shell, was preyed by the stomatopods more easily (13.8%) than the second one (7.7%), adorned with heavy and prickly nodes.

(*iv*) The higher percentage values are displayed also by some very common species, such as almost smooth, but thicker-shelled *Ancilla glandiformis* (LAMARCK), or prickly ornamented, but rather thin-shelled *Murex* (*Tubicauda*) *friedbergi* COSSMANN & PEYROT (13.8, and 13.2, respectively). This indicates that, generally, neither the moderate thickness nor ornamentation (as in *iii*) of the shells were effective protections against the stomatopod attacks.

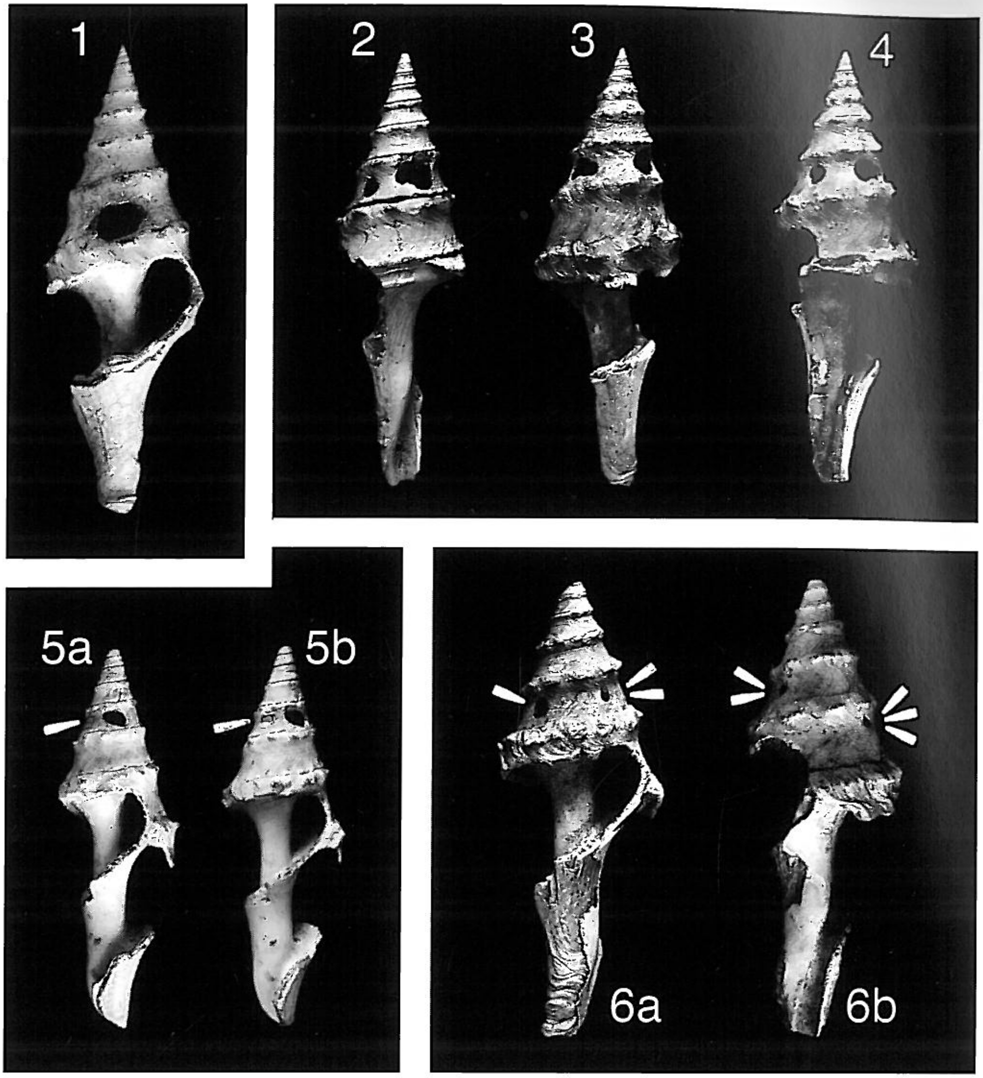
(*v*) A low percentage value for the common turritellid species, *Turritella* (*Haustator*) *badensis* SACCO (5.4% of 2300 counted specimens) may be interpreted as a result of their being, by their highly elongated slender shells, not an easy tidbit for the stomatopods. To note, however, that all the collected shells have their apertural parts broken-out; it cannot therefore be excluded that such damages were caused, partly at least, if not in majority, by the stomatopod predation.

(*vi*) As concerns the infaunal species, it may be inferred that the stomatopods could attack the shallow infaunal forms, such as *Aporrhais pespelecani* (LINNAEUS) more easily (11.1% of 370 specimens) than those burrowing deeply, as diverse species of the moon shells, *Polinices* and *Natica*, the latter of which, *Natica tigrina* RÖDING, displays the lowest percentage value (0.6%) against its being of the largest number (3,000) of specimens counted in this study.

(*vii*) Finally, it is noteworthy, that the showy-shelled species *Tudicla* (*Tudicla*) *rusticula* (BASTEROT) is damaged to a very low extent (4.8% of 180 specimens) as compared to its damage by the hermit crabs, to whose activity the destruction in most of the specimens collected is ascribed (BAŁUK & RADWAŃSKI 1977, p. 112 and Pl. 11; RADWAŃSKI 1977, pp. 253-254 and Pl. 11b).

To generalize, it is apparent that within the studied specimens the stomatopod injuries in the form of circular holes (Table 1) predominate pronouncedly those realized as elongated scars (Table 2).

Surprisingly, for the strombid gastropod from Korytnica, the species *Strombus* (*Strombus*) *bonellii* BRONGNIART, the stomatopod-predation frequency is of the same order (6.6%, *see* Table 1) as for the Pliocene



Examples of the heaviest damages in shells of the Korytnica gastropods, caused by predatory attacks of the stomatopods; all in nat. size

All examples concern large shells of *Clavatula laevigata* (EICHWALD), chipped-off up to one and a half whorls (compare Pl. 8, Fig. 1h-1m), and bearing one or more (up to three) circular injuries in their apical part; interpreted as a result of the combat of two mantis shrimps competing for a tidbit

1 — Specimen chipped-off up to one whorl, with one larger hole

2-4 — Specimens chipped-off up to one whorl, with two smaller circular holes

5 — Two views of the specimen chipped-off the most deeply, up to one and a half whorls, with two smaller circular holes, one of which (indicated by a leader) is an initial ("unsuccessful") puncture

6 — Two views of the specimen chipped-off up to 1.2 whorls, with three circular holes (indicated by leaders: single, double, and triple, respectively) strombid (*S. floridanus*) of Florida (*see* GEARY & *al.* 1991, Table 2: range 8.0 - 13.1 in particular localities); no further comments are possible as that species belongs to the rarities in the assemblage studied (30 specimens, *see* Table 1).

Not apparent from the counted damages (Table 1), but evident from the studied specimens, is a conclusion that the thick-walled shells of some gastropods could occasionally be an effective protection against the stomatopod attacks. Namely, in the ranellid species *Gyrineum* (*Aspa*) *marginatum* (MARTINI), featured by the thickest shells of all the studied Korytnica gastropods, the predation although of high frequency (9.1% in Table 1), was often completely unsuccessful for the predators: a half of the attacked specimens survived an attack and repaired their scarred shells (*see* Pl. 5, Figs 1a-1b and 4a-4c; Pl. 7, Fig. 2a-2b), whereas the other half did certainly fall (*see* Pl. 2, Figs 7-8).

GENERAL REMARKS ON THE STOMATOPOD DAMAGES IN THE KORYTNICA BASIN

The studied gastropod shell damages evidence both the spearing and smashing methods of predatory attacks by the stomatopods living in the Korytnica Basin. The results of the first type of damages (by spearing; *see* Pls 1-6) predominate (*see* Table 1), and the second (by smashing; *see* Pls 7-9) are subordinate. It cannot be, however, estimated unequivocally whether one or more stomatopod species were responsible for these damages, since there are referenced reports on the hunting with diverse methods by a given present-day stomatopod species (CALDWELL & DINGLE 1975, 1976; BERTNESS 1982; GEARY & *al.* 1991). Moreover, there appear transitional forms within the studied material (Pl. 8, Figs 1a-1m).

In the present-day smasher, *Gonodactylus chiragra* (FABRICIUS, 1781), a wide range of predatory behavior is known (CALDWELL & DINGLE 1976; GEARY & *al.* 1991, p. 355), but this concerns rather heavy damages (breaking-off the shell apex, chipping the lip, shearing-off the whorls). No such variety of predatory methods is reported in the spearers, to which the majority of the studied shell damages from Korytnica belong. This may implicate the presence of at least two species of stomatopods in the Korytnica Basin: one spearer, more common, and responsible for shell punctures, and one smasher whose attacks realized in heavy shell damages. To the latter type of damages included are these in larger shells of the genus *Clavatula* which were progressively broken (*see* Pl. 8, Figs 1h-1m) up to one and a half whorls (*see* Pl. 9, Figs 1-6). Such damages are produced by the present-day smasher, *Gonodactylus oerstedi* HANSEN, which hunts for the hermit crabs that can easily retreat deeply into the shell when attacked (BERTNESS 1982, p. 180). These extensive damages are really uncommon in the studied material (a dozen or so specimens), and thus it is inferred that the stomatopod attacks in the Korytnica Basin were performed, in majority, upon live gastropods, and not upon any squatters of their emptied shells.

When the hunting for the squatters is taken into account, a suggestion may be offered of even cannibalistic attacks of some stomatopod upon the others that could occupy the emptied gastropod shells in the same manner as the present-day forms do (*see* GEARY & *al.* 1991, p. 355 and 358). A similar case of the crustacean inquilinism has recently been reported for Jurassic lobsters living in the emptied ammonite shells (FRAAYE & JÄGER 1995).

As concerns the Korytnica Basin, a conclusion on the stomatopod predatory attacks upon live gastropods, and not upon hermit crabs, is confirmed by the fact that gastropod shells bearing various endo- and epizoans commensal to the hermit crabs (*see* BAŁUK & RADWAŃSKI 1991, pp. 26-28) are devoid of the stomatopod damages.

An extremely high percentage of the shells injuried by stomatopods in the two nassid species (*see* Table 1), the smallest of all the studied gastropods (*see* Pl. 1, Fig. 1a-1f and Pl. 7, Fig. 3a-3b), suggests that not only the architecture of their shells (a lack of protective sculpture), but also the size could facilitate the stomatopod predatory pressure, involved either by the smaller-sized species, or by the larval forms of the others, and more numerous than the adults (?!).

As the reparated gastropod shells within the studied material are of a very subordinate number (*see* Table 3), it is considered that the stomatopod attacks in the Korytnica Basin were generally successful, that is almost every puncture was fatal to the gastropod having been stabbed with the raptorial claw of a spearing stomatopod, and extracted from the shell with another technique.

Finally, it is also thought that all the studied damages ascribed to the predatory activity of stomatopods in the Korytnica Basin represent only a part of all the executed attacks, of which those battering the gastropod shells into pieces escape from any recognition.

STOMATOPOD PREDATION UPON GASTROPODS IN OTHER MIOCENE SEQUENCES OF EUROPE

As given afore, an insight into classical monographs of the Miocene gastropods of Europe, both of the Tethys/Paratethys as well as of the Atlantic

Gulfs and the North Sea Basin (*see* BAŁUK & RADWAŃSKI 1977; and Text-fig. 2 herein) reveals quite a lengthy list of the shell damages well comparable and/or identical with those from Korytnica, and thus referred to as the predatory damages caused by the stomatopods. Into the coming account, only monographs containing photographic documentation will be taken.

When checking-up the referenced monographs, it becomes apparent that the recognized damages in gastropod shells concern usually the rarely occurring species. This certainly results from the fact that the rare species (often endemic), or selected specimens (*e.g.* holotypes, *see* FERRERO MORTARA & *al.* 1982), have been illustrated regardless their state of preservation. For common species, any biogenic damages

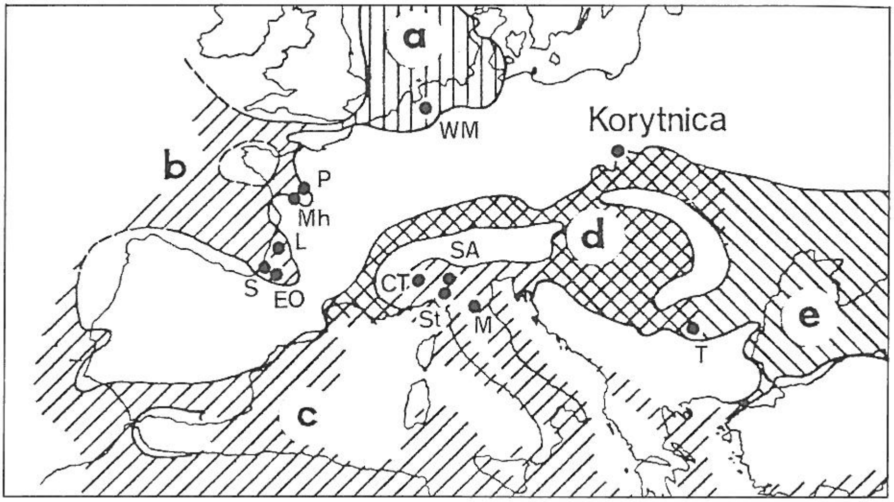


Fig. 2

Paleogeographic setting of the Miocene basins yielding gastropod shells with predation damages ascribed to the activity of stomatopods in the Korytnica Basin on the southern slopes of the Holy Cross Mountains, Central Poland, and in other classical localities in Europe (*adopted from*: BAŁUK & RADWAŃSKI 1977, Fig. 1A)

a – North Sea Basin; **b** – Atlantic Gulfs: Loire Basin (Touraine and Anjou), Aquitaine Basin, Lisbon Basin; **c** – Western Mediterranean Basin (= Tethys Basin); **d** - Paratethys basins (symbol *d* covers the area of the Vienna Basin, and the western part of the Pannonian Basin with localities Szob and Várpalota), **e** – Euxinian Basin

LOCALITIES INDICATED: **WM** – Winterswijk-Miste (*see* JANSSEN 1984); **P** – Pontlevoy (*see* GLIBERT 1952); **Mh** – Manthelan (*see* GLIBERT 1952); **L** – Léognan (*see* COSSMANN & PEYROT 1924, PEYROT 1927); **EO** – Saint-Étienne-d'Orthe (*see* COSSMANN & PEYROT 1919, PEYROT 1927); **S** – Saubrigues (*see* COSSMANN & PEYROT 1919); **CT** – Colli Torinesi (*see* FERRERO MORTARA & *al.* 1982); **SA** – Santa Agata dei Fossili (*see* FERRERO MORTARA & *al.* 1982); **St** – Stazzano (*see* HALL 1964); **M** – Montegibbio (*see* DAVOLI 1977); **T** – Tarnene (*see* KOJUMDGIEVA 1960) caused the shell was classified as of inferior value and taken off their picturing (!).

The recognized stomatopod damages are listed hereafter, with the taxonomy of the gastropod species the same as used by the referenced authors.

To note, none of the recognized damages have been noticed and/or commented by the referenced authors, except of those presented by DAVOLI (1977) who ascribed them to the predatory activity of the supposed crabs.

The list of the recognized damages in gastropod shells, and ascribed herein to the predatory attacks of stomatopods, contains the following items:

(1) The **Tethys Realm**: northern Italy, primarily the classical site of the Turin Hills (Italian: *Colli Torinesi*), and the area of Modena (**c** in Text-fig. 2):

DAVOLI (1977, Pl. 4, Fig. 9; close-up in Fig. 15) in *Terebra* (*Myurellina*) *cingulata* FORESTI, from Montegibbio;

idem (Pl. 4, Fig. 20) – puncture in a specifically undetermined terebrid, from Montegibbio;

These two items were interpreted by DAVOLI (1977) as of predatory attacks of invertebrates other than carnivorous gastropods, supposedly of crabs;

HALL (1964, Pl. 25, Fig. 10) in *Conus elongatus* BORSON, from Stazzano;

FERRERO MORTARA & *al.* (1982, Pl. 3, Fig. 7b) in *Murex patulus* BELLARDI, from the Colli Torinesi;

idem (Pl. 3, Fig. 11b) in the holotype of *Murex danconai* BELLARDI, from the Colli Torinesi;

idem (Pl. 21, Fig. 2b) in *Nassa crassilabris* BELLARDI, from Tetti Borelli;

idem (Pl. 22, Fig. 1b) in the holotype of *Nassa consobrina* BELLARDI, from Santa Agata dei Fossili;

idem (Pl. 22, Fig. 4b) in *Nassa confundenda* BELLARDI, from Stazzano;

idem (Pl. 28, Fig. 4b) in *Nassa inaequalis* BELLARDI, from Tetti Borelli;

All injuries in the above four *Nassa* species are well comparable to punctures from Korytnica (*see herein* Pl. 1, Figs 1a-d).

(2) The **Atlantic Gulfs** (**b** in Text-fig. 2)

(2a) The **Aquitaine Basin**:

COSSMANN & PEYROT (1919, Pl. 11, Figs 39-40) in *Natica* (*Lunatia*) *helicina* BROCCHI, from Saubrigues;

idem (Pl. 12, Figs 31-33) in *Ampullina sanctistephani* COSSMANN & PEYROT, from Saint-Étienne-d'Orthe: Fig. 31 presents a puncture, on the shell inner wall, evidently the same as those from Korytnica (*see herein* Pl. 4, Figs 1c, 2c, 3c and 4c);

COSSMANN & PEYROT (1924, Pl. 8, Figs 8-9) in *Strombus* (*Dilatilabrum*) *trigonus* GRATELOUP, from Léognan;

PEYROT (1927, Pl. 1, Fig. 50) in *Dorsanum veneris* FANJAS var. *bicornata* PEYROT, from Saucats;

idem (Pl. 10, Fig. 2) in *Volutilithes (Athleta) ficulina* LAMARCK, from Léognan;

idem (Pl. 10, Fig. 21) in *Lyria aturensis* PEYROT, from Saint-Étienne-d'Orthe: large injury, comparable to one of those from Korytnica (*see herein* Pl. 8, Fig. 1e);

(2b) The **Loire Basin** (Touraine and Anjou):

GLIBERT (1952, Pl. 2, Fig. 5d) in *Polynices redempta* (MICHELOTTI), from Manthelan;

idem (Pl. 4, Fig. 7) in *Pirula burdigalensis* SOWERBY, from Manthelan;

idem (Pl. 8, Fig. 10b) in *Cantharus pontileviensis* (PEYROT), from Pontlevoy.

(3) The **North Sea Basin** (**a** in Text-fig. 2), exclusively the classical locality Winterswijk-Miste in Holland:

JANSSEN (1984, Pl. 48, Fig. 9) in *Haustator (Haustator) goettentrupensis* (COSSMANN), from Winterswijk-Miste: double injury, comparable to those from Korytnica (*see herein* Pl. 2, Figs 14-16);

idem (Pl. 53, Fig. 4) in *Murex (Haustellum) inornatus inornatus* BEYRICH, from Winterswijk-Miste.

(4) The so-called **Paratethys Realm**, to which the Korytnica Basin also belongs (**d** in Text-fig. 2)

(4a) The **Pannonian Basin** in Hungary:

CSEPREGHY-MEZNERICS (1956, Pl. 4, Fig. 22) in *Murex (Bolinus) subtorularius* HOERNES & AUINGER, from Szob;

STRAUSZ (1966, Pl. 30, Fig. 2) in *Cymatium (Lampusia) affine* DESHAYES, from Szob: injury repaired, comparable to those from Korytnica (*see herein* Pl. 6, Figs 8a-b and 9a-b);

idem (Pl. 45, Fig. 3) in *Cancellaria cancellata dertonensis* BELLARDI, from Szob;

idem (Pl. 57, Fig. 6) in *Pirula condita* BRONGNIART, from Várpalota: an elongate injury;

(4b) Bulgaria (local basins along an isthmus off the Pannonian, to the Euxinian Basin; *see* **e** in Text-fig. 2):

KOJUMDGIEVA (1960, Pl. 34, Fig. 15a) in the cowrie *Monetaria bulgarica* KOJUMDGIEVA, from Tarnene;

idem (Pl. 57, Fig. 16b) in *Fasciolaria (Pleuroploca) tarbelliana* (GRATELOUP), also from Tarnene.

The presented review shows that the stomatopods may be ascertained as not uncommon components of diverse shallow-marine communities in the Miocene epoch of Europe. This recognition enlarges greatly the data known from the stomatopod body remains. To the Authors' knowledge, the only stomatopod species reported so far from the Miocene sequences of Europe is *Squilla miocenica* LOVISATO, 1894, established by LOVISATO (1894) upon isolated raptorial dactyli from Sardinia (Italy), and noted also from Catalonia (Spain) by VIA (1949); its generic identity is, however, regarded as uncertain (HOLTHUIS & MANNING 1969, pp. *R*541-*R*542; SECRETAN 1975).

The other records of the Tertiary stomatopods in Europe concern only the Eocene forms coming from England (H. WOODWARD 1879, QUAYLE 1987), Germany (FÖRSTER 1982, LIENAU 1985), and Italy (MÜNSTER 1839, SECRETAN 1975), supplemented recently by those from the Oligocene of Italy (DE ANGELI & MESSINA 1992, 1996).

CONCLUSIVE REMARKS

A very high percentage of the investigated damages in shells of particular gastropod species (*see* Tables 1 – 2) indicates that the stomatopods were an important component of the Korytnica communities composed of very diverse, and much ubiquitous invertebrates and vertebrates (*see* BAŁUK & RADWAŃSKI 1977, pp. 96-103; HOFFMAN 1977, pp. 242-267; RADWAŃSKA 1992, pp. 147-149 and 311-315; BAŁUK 1995, pp. 160-161).

In majority, the predatory attacks of stomatopods are thought to have been performed upon live gastropods that sometimes could survive and repair their shells (*see* Pls 6-7), and not upon the hermit crabs or other inhabitants occupying the emptied gastropod shells.

The highest percentage of stomatopod damages in three species of Korytnica gastropods, with the values much exaggerating (up to 54.4; *see* Tables 1-2) the maximum figure (13.1%) given by GEARY & *al.* (1991) evidences the role of the mantis shrimps as one of the most serious predators within the Korytnica communities. Their share in the predatory pressure upon the gastropods was of the same extent as that of the hermit crabs (*cf.* RADWAŃSKI 1977, BAŁUK & RADWAŃSKI 1977) and of the carnivorous gastropods, precisely the muricids and naticids (*cf.* HOFFMAN & *al.* 1974, KOWALEWSKI 1990) to which cannibalistic activities were not strange (*see* HOFFMAN & *al.* 1974, Pl. 2, Figs 3-4).

To note, it was formerly reported, by HOFFMAN & *al.* (1974, p. 253 and Table 2), that locally in the Korytnica Basin the predatory attacks of the carnivorous gastropods realized preferably upon the species *Sphaeronassa schoenni* (HOERNES & AUINGER) that is the second in order of these attacked by stomatopods (*see* Table 1 *herein*). Another, small-sized nassid (not included into this study), *Hinia restitutiana* (FONTANNES) [= *Nassa hoernesi* auct.], from the same site (locality *1* in BAŁUK & RADWAŃSKI 1977, Fig. 2) was recognized as an important component of the naticid diet in that habitat (KOWALEWSKI 1990, p. 201 and Table 5).

Consequently, it is assumed that such a predatory pressure of stomatopods, combined with that of other invertebrate predators (hermit and other crabs, carnivorous gastropods) could have involved an ecological response of the increasing reproduction rate of at least some gastropod species to ensure their survival in the Korytnica ecospace. This may explain an enormous ubiquity of some gastropods in the Korytnica Bay encroaching upon the Holy Cross shores in Central Poland at the Middle Miocene time.

An almost complete lack of stomatopod damages in the bivalve shells from the Korytnica Basin is easily understood, because the two dominating species, that is a small-sized, but enormously common *Corbula* (*Aloides*) *gibba* (OLIVI) (*see* BAŁUK & RADWAŃSKI 1977, p. 95) and a larger-sized *Venus multilamella marginalis* EICHWALD, are deeply infaunal forms. A deep burrowing has almost fully protected them from any attacks of the stomatopods, although it has not from hunting of the carnivorous gastropods (*see* HOFFMAN & *al.* 1974, Pls 1-2 and 4).

A fact that, of the deeply infaunal forms, neither gastropods nor bivalves are preyed by stomatopods, implicates that the Miocene stomatopods, those living in the Korytnica Basin at least, have not yet displayed the ability to hunt on the deeply burrowing prey. Such an ability, being perhaps a result of behavioral evolution, becomes typical of the Holocene spearer, *Pterygosquilla armata capensis* MANNING of South Africa, as reported by PETHER (1995, p. 179).

The predatory activity of stomatopods recognized in other Miocene sequences of Europe, although evidences a widespread distribution of these crustaceans in all marine basins of that time, does not allow to estimate as yet their frequency in particular regions to make quantitative comparisons with the Korytnica Basin.

The presence of the stomatopods in the Korytnica Basin itself supplements the formerly known data on the tropical and/or subtropical influences, with distinct Indo-Pacific affinities, within all the Korytnica communities, and both as concerns the invertebrates and vertebrates (*see* review *in*: BAŁUK & RADWAŃSKI 1977, pp. 116-117; RADWAŃSKA 1992, p. 315).

The Indo-Pacific influences in the European seaways during the Miocene epoch may possibly be advocated by the presence of the stomatopods themselves, as their numerous body remains have recently been reported from Korea (YUN 1985) and Japan (KARASAWA & NAKAGAWA 1992, KARASAWA 1996).

Institute of Geology
of the University of Warsaw,
Al. Żwirki i Wigury 93,
02-089 Warszawa, Poland

REFERENCES

BAŁUK, W. 1975. Lower Tortonian gastropods from Korytnica, Poland; Part I. *Palaeont. Polon.*, **32**, 1-186. Warszawa – Kraków.

— 1995. Middle Miocene (Badenian) gastropods from Korytnica, Poland; Part II. *Acta Geol. Polon.*, **45** (3/4), 153-255. Warszawa.

— 1997 *(in press)*. Middle Miocene (Badenian) gastropods from Korytnica, Poland; Part III. *Acta Geol. Polon.*, **47** (1/2). Warszawa.

— & RADWAŃSKI, A. 1977. Organic communities and facies development of the Korytnica Basin (Middle Miocene; Holy Cross Mountains, Central Poland). *Acta Geol. Polon.*, **27** (2), 85-123. Warszawa.

— & — 1979a. Additional data on the organic communities and facies development of the Korytnica Basin (Middle Miocene; Holy Cross Mountains, Central Poland). *Acta Geol. Polon.*, **29** (3), 225-238. Warszawa.

— & — 1979b. Boring ctenostomate bryozoans from the Korytnica Clays (Middle Miocene; Holy Cross Mountains, Central Poland). *Acta Geol. Polon.*, **29** (3), 243-252. Warszawa.

— & — 1984a. New data on the Korytnica Basin, its organic communities and ecological relationships between species (Middle Miocene; Holy Cross Mountains, Central Poland). *Acta Geol. Polon.*, **34** (3/4), 179-194. Warszawa.

— & — 1984b. The regeneration in some caryophyllid corals from the Korytnica Clays (Middle Miocene; Holy Cross Mountains, Central Poland). *Acta Geol. Polon.*, **34** (3/4), 213-221. Warszawa.

— & — 1991. 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*. *Acta Geol. Polon.*, **41** (1/2), 1-36. Warszawa.

BARTHEL, K.W. 1978. Solnhofen; Ein Blick in die Erdgeschichte, pp.1-393. *Ott Verlag*; Thun.

BERTNESS, M.D. 1982. Shell utilization, predation pressure, and thermal stress in Panamanian hermit crabs: an interoceanic comparison. *J. Exp. Marine Biol. Ecol.*, **64**, 159-187.

— & CUNNINGHAM, C. 1981. Crab shell-crushing predation and gastropod architectural defense. *J. Exp. Marine Biol. Ecol.*, **50**, 213-230.

BRAITHWAITE, C.J.R. & TALBOT, M.R. 1972. Crustacean burrows in the Seychelles, Indian Ocean. *Palaeogeogr., Palaeoclim., Palaeoecol.*, **11** (4), 265-285. Amsterdam.

CALDWELL, R.L. 1977. Variation in agonistic behavior between populations of the stomatopod, *Haptosquilla glyptocercus*. *Evolution*, **31**, 220-223.

— & DINGLE, H. 1975. Ecology and evolution of agonistic behavior in stomatopods. *Naturwissenschaften*, **62**, 214-222. Berlin.

— & — 1976. Stomatopods. *Scientific American*, **234**, 80-89.

CHARLES, C. 1977. Variabilité de *Turritella communis* en relation avec l'environnement. *Centre d'Etudes et de Recherches de Paléontologie Biostratigraphique*, Contrib. **14**, 1-111. Orsay.

CORNELISSE, F.B. 1996. Paleontology of the Falaises Des Vaches Noires, Normandy, France, pp. 1-25. *Faculty of Earth Sciences, Free University*; Amsterdam.

COSSMANN, M. & PEYROT, A. 1919, 1924. Conchologie néogénique de l'Aquitaine, **3** (2), 385-695; **4** (2), 323-608. *Acta Soc. Linn. Bordeaux*, **70**, **74**. Bordeaux.

CSEPREGHY-MEZNERICS, I. 1956. Die Molluskenfauna von Szob und Letkés. *A Magyar Áll. Föld. Int. Évk. (Ann. Inst. Geol. Publ. Hung.)*, **45** (2), 361-477. Budapest.

DAVOLI, F. 1977. Terebridae (Gastropoda) in E. Montanaro Gallitelli (ed.). Studi monografici sulla malacologia miocenica modenese. Parte I. – I Molluschi tortoniani di Montegibbio. *Palaeontographia Italica*, **70** (*N. Ser.* **40**), 136-169. Pisa.

DE ANGELI, A. & MESSINA, V. 1992. *Upogebia perarolensis* nuova specie di Crostaceo del Terziario del Veneto (Italia). *Lavori Soc. Ven. Sci. Nat.*, **17**, 183-191. Venezia.

— & — 1996. *Pseudosquilla berica*, nuova specie di Stomatopoda del Terziario Veneto (Italia Settentrionale). *Studi e Ricerche, Associazione Amici Museo Civico "G. Zannato" Montecchio Maggiore*, 5-10. Montecchio Maggiore.

FERRERO MORTARA, E. & *al.* 1982. Catalogo dei tipi e degli esemplari figurati della collezione Bellardi e Sacco, Parte I. *Cataloghi Mus. Reg. Sci. Nat.*, **6**, 1-327. Torino.

FÖRSTER, R. 1982. Heuschreckenkrebse (Crustacea, Stomatopoda) aus dem Alttertiär von Helmstedt und Handorf (Niedersachsen) und der Oberkreide von Nigeria. *N. Jh. Geol. Paläont. Mh.*, 1982, (6), 321-335. Stuttgart.

FRAAYE, R.H.B. & JÄGER, M. 1995. Decapods in ammonite shells: examples of inquilinism from the Jurassic of England and Germany. *Palaeontology*, **38** (1), 63-75. London.

GEARY, D.H., ALLMON, W.D. & REAKA-KUDLA, M.L. 1991. Stomatopod predation on fossil gastropods from the Plio-Pleistocene of Florida. *J. Paleont.*, **65** (3), 355-360. Lawrence, Kansas.

GLIBERT, M. 1952. Gastropodes du Miocène moyen du Basin de la Loire. *Mém. Inst. Royal Sci. Natur. Belg., Sér. 2*, **46**, 241-450. Bruxelles.

HALL, C.A. 1964. Middle Miocene *Conus* (class Gastropoda) from Piedmont, northern Italy. *Boll. Soc. Paleont. Ital.*, **3** (2), 111-171. Modena.

HERTWECK, G. 1972. Georgia coastal region, Sapelo Island, U.S.A.: sedimentology and biology; V. Distribution and environmental significance of lebensspuren and in-situ skeletal remains. *Senckenberg. Marit.*, **4**, 125-167. Frankfurt a.M.

HOFFMAN, A., PISERA, A. & RYSZKIEWICZ, M. 1974. Predation by muricid and naticid gastropods on the Lower Tortonian mollusks from the Korytnica Clays. *Acta Geol. Polon.*, **24** (1), 249-260. Warszawa.

HOLTHUIS, L.B. & MANNING, R.B. 1969. Stomatopoda. *In*: R.C. MOORE (*Ed.*), *Treatise on Invertebrate Paleontology*, Part **R** – Arthropoda, Vol. **4** (2), pp. *R*535-*R*552. Lawrence, Kansas.

JANSSEN, A.W. 1984. Mollusken uit het Mioceen van Winterswijk-Miste. *Stichting Uitgeverij Koninklijke Nederlandse Natuurhistorische Vereging*, **36**, 1-451. Leiden.

JOHNSON, M.E. 1988a. Hunting for ancient rocky shores. *J. Geol. Education*, **36** (3), 147-154.

— 1988b. Why are ancient rocky shores so uncommon? *J. Geol.*, **96** (4), 469-480. Chicago.

KABAT, A.R. 1990. Predatory ecology of naticid gastropods with a review of shell boring predation. *Malacologia*, **32** (1), 155-193.

KARASAWA, H. 1996. *Shako*, a new Miocene stomatopod Crustacea from Japan. *Trans. Proc. Palaeont. Soc. Japan, N.S.*, **182**, 413-418. Mizunami.

— & NAKAGAWA, T. 1992. Miocene crustaceans from Fukui and Ishikawa Prefectures, Central Japan. *Bulletin of the Japan Sea Research Institute Kanazawa University*, **24**, 1-18. Kanazawa.

KERN, J.P. 1979. The ichnofossil *Helicotaphrichnus commensalis* in the Korytnica Basin (Middle Miocene; Holy Cross Mountains, Central Poland). *Acta Geol. Polon.*, **29** (3), 239-242. Warszawa.

KOJUMDGIEVA, E. 1960. Le Tortonien du type viennois. *In*: E. KOJUMDGIEVA & B. STRACHIMIROV, *Les fossiles de Bulgarie*; **7**, Tortonien, pp. 13-246. Sofia.

KOWALEWSKI, M. 1990. A hermeneutic analysis of the shell-drilling gastropod predation on mollusks in the Korytnica Clays (Middle Miocene; Holy Cross Mountains, Central Poland). *Acta Geol. Polon.*, **40** (3/4), 183-213. Warszawa.

— 1993. Morphometric analysis of predatory drillholes. *Palaeogeogr., Palaeoclim., Palaeoecol.*, **102** (1), 69-88. Amsterdam.

LIENAU, H.-W. 1985. Heuschreckenkrebse aus dem Geschiebe. *Der Geschiebesammler*, **19** (1), 1-8. Hamburg.

LOVISATO, D. 1894. Avanzi di *Squilla* nel miocene medio di Sardegna. *Rendiconti della R. Accad. dei Lincei, Classe Sci. Fis., Mat. e Nat.*, **3** /1° Sem. (4), 205-209. Roma.

MARTINI, E. 1977. Calcareous nannoplankton from the Korytnica Basin (Middle Miocene; Holy Cross Mountains, Central Poland). *Acta Geol. Polon.*, **27** (2), 125-133. Warszawa.

MOORE, R.C. & MCCORMICK, L. 1969. General features of Crustacea. *In*: R.C. MOORE (*Ed.*), *Treatise on Invertebrate Paleontology*, Part **R** – Arthropoda, Vol. **4** (1), pp. *R*57-*R*120. Lawrence, Kansas.

MÜNSTER, G. Graf zu, 1839. Über die fossilen langschwänzigen Krebse in den Kalkschiefern von Bayern. *Beitr. Petrefaktenkunde*, **3** and **5**.

PETHER, J. 1995. *Belichnus* new ichnogenus, a ballistic trace on mollusc shells from the Holocene of the Benguela region, South Africa. *J. Paleont.*, **69** (1), 171-181. Lawrence, Kansas.

PEYROT, A. 1927. Conchologie néogénique de l'Aquitaine, **5** (1), 1-206. *Acta Soc. Linn. Bordeaux*, **77**. Bordeaux.

QUAYLE, W.J. 1987. English Eocene Crustacea (lobsters and stomatopod). *Palaeontology*, **30** (3), 581-612. London.

RADWAŃSKA, U. 1992. Fish otoliths in the Middle Miocene (Badenian) deposits of southern Poland. *Acta Geol. Polon.*, **42** (3/4), 141-328. Warszawa.

RADWAŃSKI, A. 1969. Lower Tortonian transgression onto the southern slopes of the Holy Cross Mts. *Acta Geol. Polon.*, **19** (1), 1-164. Warszawa.

— 1970. Dependence of rock-borers and burrowers on the environmental conditions within the Tortonian littoral zone of Southern Poland. *In*: T.P. CRIMES & J.C. HARPER (*Eds*), Trace Fossils (*Geol. J. Spec. Issues*, **3**), 371-390. Liverpool.

— 1977. Present-day types of trace in the Neogene sequence; their problems of nomenclature and preservation. *In*: T.P. CRIMES & J.C. HARPER (*Eds*), Trace Fossils **2** (*Geol. J. Spec. Issues*, **9**), 227-264. Liverpool.

— 1996. The predation upon, and the extinction of, the latest Maastrichtian populations of the ammonite species *Hoploscaphites constrictus* (J. SOWERBY, 1817) from the Middle Vistula Valley, Central Poland. *Acta Geol. Polon.*, **46** (1/2), 117-135. Warszawa.

SCHRAM, F.R. 1968. *Paleosquilla* gen.nov. – a stomatopod (Crustacea) from the Cretaceous of Colombia. *J. Paleont.*, **42** (5), 1297-1301. Menasha, Wisconsin.

SECRETAN, S. 1975. Les Crustacés du Monte Bolca. *Miscellanea Paleont. Mus. Civ. St. Nat. Verona*, 315-388. Verona.

SHOUP, J.B. 1968. Shell opening by crabs of the genus *Calappa*. *Science*, **160** (No. 3830), 887-888. Washington.

STRAUSZ, L. 1966. Die miozän-mediterranen Gastropoden Ungarns, pp. 1-692. *Akadémiai Kiadó*; Budapest.

VERMEIJ, G.J. 1978. Biogeography and adaptation: Patterns of marine life, pp. 1-332. *Harvard University Press*; Cambridge, Massachusetts – London, England.

— 1987. Evolution and escalation: An ecological history of life, pp. 1-527. *Princeton University Press*; Princeton, New Jersey.

VIA, L. 1949. Un resto de estomatopodo (*Squilla miocenica* Lovisato) en las margas tortonienses de Montjuich. *Bull. Inst. Catal. Hist. Nat.*, **37**, 99-101. Barcelona.

WOODWARD, H. 1879. Contributions to the knowledge of fossil Crustacea; I. On a fossil *Squilla* from the London Clay of Highgate – part of the "Wetherell Collection" in the British Museum. *Quart. J. Geol. Soc. London*, **35**, 549-556. London.

YUN, H. 1985. Some fossil Squillidae (Stomatopoda) from the Pohang Tertiary basin, Korea. *Journal of the Paleontological Society of Korea*, **1**, 19-31.