acta
geologica
polonica

Vol. 24, No. 1 Warszawa 1974

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Predation by muricid and naticid gastropods on the Lower Tortonian mollusks from the Korytnica clays

ABSTRACT: Traces of the predation by boring gastropods, very common on the Lower Tortonian gastropods, pelecypods and scaphopods from the Korytnica clays on the southern slopes of the Holy Cross Mts, Central Poland, have been ascribed to the activity of four muricid and five naticid species. A very strong differentiation of the proneness of particular species to be attacked by predatory boring gastropods has been shown by a statistical analysis of more than 20,000 specimens of over 120 species. In this respect the character of differentation of large taxonomic and ecological groups suggests that it results not so much from the ethology of the predators as from the ecology of their potential prey. The ratio of the numbers of the naticid and muricid prey within the range of large taxonomic and ecological groups indicates divergent interests of the two groups of predatory boring gastropods and an only small extent of their competition.

INTRODUCTION

Traces of the predation by boring gastropods are very common among the abundant and excellently preserved Lower Tortonian mollusks which occur in the Korytnica clays (*cf.* Friedberg 1911—1928, 1934—1936, 1938; Kowalewski 1930; Bałuk & Jakubowski 1968; Radwański 1969, 1970; Bałuk 1971, 1972, 1974). They have been found in gastropods, pelecypods and scaphopods, but never so far in chitons. They are observed in the form of more or less regular, round or elliptic holes, through which the predatory gastropods reached with their proboscides the inside of the shell and the soft flesh of their prey. As the identical traces are well known in the Recent fauna, the authors have undertaken the comparative studies to recognize both the nature of the borings as well as ethology of the predators and ecology of their prey. The particular species that are the prey of predatory gastropods have been examined statistically to obtain as far as possible the most reliable data on general proneness of these species to the attack of predators. The obtained results are regarded to be instructive for paleo--synecological analysis of the mollusk communities that settled in the Lower Tortonian environment yielding the remarkably fossiliferous Korytnica clays.

Acknowledgements. The authors are indebted to Dr. W. Bałuk, University of Warsaw, and Dr. G. Jakubowski, Museum of the Earth (Polish Academy of Sciences), for making available their collections of the Korytnica mollusks and helpful advices. Thanks are also due to Docent A. Radwański, University of Warsaw, for critical reading of the manuscript.

PREDATORY BORING GASTROPODS

Many laboratory studies were undertaken on the ethology and manner of boring in the Recent carnivorous gastropods (Ziegelmeier 1954, Wells 1958, Paine 1963). Almost identical traces, frequently met with in the Tertiary and sporadically in the Cretaceous, are generally considered to be the result of the activity of identical groups of gastropods with the Recent ones, *viz.* Muricacea and Naticacea. On the other hand, Paleozoic traces similar in character probably represent the effects of boring of other animals (Carriker & Yochelson 1968), although sometimes they are ascribed to the activity of gastropods different than Muricacea and Naticacea, *viz.* the genus *Subulites* (*cf.* Cameron 1967).

In ecological and paleoecological literature, there occur frequent ambiguities and often it is not clear whether the authors deal with the predatory gastropods which directly attack the soft body of their prey or with those securing their food by boring the shells. It is beyond any doubt, however, that the latter manner of attacking is observed in various genera of Muricacea (*Murex, Ocenebra, Pteropurpura, Thais, Urosalpinx*) and Naticacea (*Ampullina, Euspira, Natica s.l.*). Fischer (1922, 1966) mentions that also some of the Recent species of *Nassa* are boring predators, but he is very cautious concerning such a possibility in the case of older geological epochs. More explicit in this respect is Milashevich (1916, *fide* Davitashvili & Merklin 1968), who maintains that *Nassa reticulata* (Linnaeus), the species absent at Korytnica, bores the shells of thin-valved pelecypods in search of food. All other species of *Nassa* are, however, treated either as necrophags or predators directly attacking their prey. Not quite clear is the status of such genera as *Columbella, Euthria* and *Fusus,* sometimes mentioned as boring gastropods ((Fischer 1922), but in more recent papers (Ziegelmeier 1954, Carriker & Yochelson 1968, Taylor 1970), there are no suggestions that, except for the Muricacea and Naticacea, any other genera or species are predatory boring gastropods.

Under such circumstances, the authors believe that the borings of this type found in the Korytnica mollusks may be considered as the symptoms of the predation mostly by following most common at Korytnica (*cf.* Friedberg 1911—1928, 1938) species of muricids and naticids: *Murex friedbergi* Cossmann & Peyrot, *Ocenebra crassilabiata* (Hilber), *O. orientalis* Friedberg, *Natica helicina* Brocchi, *N. josephina* (Risso), *N. millepunctata* Lamarck, *N. pseudoredempta* Friedberg, and *N. redemta* Michelotti.

The Recent Muricacea and Naticacea markedly differ from each other in their mode of life and their borings vary morphologically (Carriker & Yochelson 1968, Taylor 1970).

The Muricacea that bore by a rotatory motion of their radulae (*cf.* Carriker & Yochelson 1968) belong to epifauna which explains why at Korytnica their borings are so frequently met with at the outer margin of shallowly burrowing pelecypods. The muricid borings in the Korytnica mollusks are of a cylindrical shape (Pl. 1, Fig. 1), frequently irregular in outline and with jagged margins (Pl. 4, Fig. 1). Failed borings which occur sometimes have markedly concave bottoms. Sometimes, several borings are observed on one and the same prey (Pl. 2, Fig. 5), which seems to result from the muricids' tendency to the attack in groups (*cf.* Paine 1963). Not all species of the muricids secure their food by boring the shell of prey. Moreover, as follows from laboratory studies on the behavior and manner of attacking prey by Recent species of *Murex*, borings are made only by young individuals, while the adults are sufficiently strong to open the shells of pelecypods (Wells 1958).

The Naticacea, belonging to infauna, look for their food and attack prey in the bottom sediment only, and get out onto the surface only under unfavorable conditions. The strongly developed foot allows them to enfold strongly their prey and to handle it as long as it is necessary to find an appropriate place for boring. Thus far, nobody has been able to answer whether Naticacea choose a definite place on the shell of prey or their borings are distributed at random (Carter 1967, Reyment 1971). They bore by a rotatory motion of their radulae and the participation of the sulfuric acid secretion in this process has not so far been confirmed (Ziegelmeier 1954). The naticid borings in the Korytnica mollusks are very regular, widely conical (Pl. 1, Figs 2 and 4). A characteristic, centrally situated boss (Pl. 1, Fig. 3) is observed on the bottom of failed borings. Sometimes, several borings are met with on one and the same prey (Pl. 2, Figs 1—3 and 6—7), and they supposedly represent either the effect of a prolonged handling of the prey, or it is a matter of pure accident (the group attack is unknown in these gastropods). On the other way, as follows from laboratory studies, the naticids do not distinguish between the alive and dead specimens and they bore each shell they find, sometimes those previously bored including (Ziegelmeier 1954). Thus far, no species of naticids are known which would secure their food in other manner.

BORINGS OF MURICACEA AND NATICACEA

As indicated by the results of studies on the abundant material from Korytnica, the morphological criteria cited above (Carriker & Yochelson 1968), although very helpful in a correct assignment of the borings to an appropriate group of predators, are insufficient and frequently leave a considerable margin of uncertainty. Moreover, determining a distinct boundary seems to be impossible, since in many cases the authors noticed in the borings a gradual passage from the "naticid" type to the "muricid" one, even when the same predator had been evidenced — a distinct preference for the place of boring in e.g. *Sabatia callifera* Boettger or *Nassa schoenni* (R. Hoernes & Auinger) indicates one only type of a predator (*cf.* Pl. 3, Figs 1—10).

Sometimes, the morphology of the borings is so closely correlated with the microstructure of the shell that it completely precludes a correct identification of the borings on the basis of the morphological criteria expressed by Carriker & Yochelson (1968). In this respect, the genus *Corbula* may serve as an example. The valves of these common pelecypods contain a characteristic, very hard "conchioline" mid-layer (Fischer 1963), which distinctly affects the manner of boring and, consequently, the morphology of holes (*cf.* Pl. 4). A complete conformity of Fischer's drawings and borings observed in the Korytnica material (Pl. 4, Figs 3—10) with the description (Ziegelmeier 1954) of the borings of *Lunatia nitida* Donovan has allowed the authors to classify them as indubitably naticid borings. This brings in question the accuracy of Taylor's (1970) determinations, as a vast majority of the borings found in these pelecypods were ascribed by him to the activity of the muricids.

The necessity of an arbitrary assignment of these, in fact rather few, borings, which might be the result of the activity of gastropods different than Muricacea and Naticacea, to these two morphological types, is an additional factor decreasing the reliability of the identification.

All these facts cause a vast variability within the range of the two groups distinguished (borings of Muricacea and Naticacea) and preclude their unequivocal delimitation. It is likely that similar difficulties were faced by other investigators, but all attempts to establish better criteria of identifying borings (*e.g.* the diameter of hole — Reyment 1963, 1966a, b) have so far failed to yield satisfactory results.

PRONENESS OF THE KORYTNICA MOLLUSKS TO THE ATTACK BY MURICIDS AND NATICIDS

The proneness of mollusks most common in the Korytnica clays to the attack by the predatory boring gastropods has been subjected to statistical analysis the results of which are given in Table 1. For each species (sometimes genus) it is shown how many individuals were contained in the sample examined. Here, the authors treat every two pelecypod valves as an equivalent of one individual, assuming that under the sedimentary conditions of the Korytnica clays (no transportation and,

Table 1

Proneness of mollusks to the attack by predatory boring gastropods in the Lower Tortonian of Korytnica

The species listed in Tables 1—3 determined by Dr. W. Bałuk; their taxonomy for archaeogastropods and a part of caenogastropods (Littorinacea, Rissoacea, Cerithiacea, Scalacea) presented *in* Bałuk (1974)

Species	Number of specimens in the sample	Per cent proportion of the attacked specimens	95% confidence interval	Naticid to muricid prey ratio
GASTROPODS:				
Acrilla subreticulata /d'Orbigny/	31	3	0–9	
A. terebralis /Michelotti/	146	8	4–12	
Actaeon pinguis d'Orbigny	43	12	2–22	
A. reussi Boettger	141	22	15–29	1:23.0
Actaeon sp.	49	4	0–10	
Alvania alexandrae Boettger	115	12	6–18	
A. curta /Dujardin/	89	7	2–12	
A. montagui ampulla /Eichwald/	211	16	11–21	1:10.3
A. perregularis /Sacco/	125	22	15–29	1:26.0
A. venus transiens /Sacco/	164	9	5–13	
Alvania sp.	190	16	11–21	
Ancilla glandiformis /Lamarck/	590	3	2–4	
Aporrhais alatus /Eichwald/	192	2	0–4	
Astraea mehelyi /Boettger/	61	13	5–21	
Atys miliaris /Brocchi/	178	13	8–18	1:0.2
Bittium reticulatum /da Costa/	98	19	11–27	1:8.5
B. spina /Partsch/	228	25	19–31	1:2.9
Caecum glabrum /Montagu/	220	8	5–11	1:0.1
Ceratia striata /Hoernes/	30	13	1–25	
Ceratia sp.	193	15	10–20	
Cerithiopsis tubercularis /Montagu/	201	12	8–16	1:3.2
Cerithium banaticum Boettger	133	9	4–14	
Circulus sp.	209	12	8–16	1:0.6
Clavatula asperulata /Lamarck/	192	2	1–3	
C. evae /R. Hoernes & Auinger/	22	4	0–12	
C. laevigata /Eichwald/	622	3	2–4	
C. styriaca Auinger	25	4	0–12	
Columbella curta /Dujardin/	140	11	6–16	
C. kostejana Boettger	39	23	10–36	
C. subnassoides Friedberg	47	19	8–30	
Conus dujardini Deshayes	33	9	0–19	
Cythara subcylindrata /Boettger/	203	30	24–36	1:0.7
Drillia sp. div.	67	27	16–38	
Erato barrandei /R. Hoernes & Auinger/	44	7	0–14	
Eulima subulata /Donovan/	320	17	13–21	1:0.2
Eulimella conulus /Eichwald/	126	21	14–28	1:0.1
Euthria puschi /Andrzejowski/	81	10	3–17	
Ficus sp. div.	30	0	0–6	
Fusus hoessi Partsch	53	6	0–12	
Genota ramosa elisae /R. Hoernes & Auinger/	24	8	0–19	
G. valeriae /R. Hoernes & Auinger/	24	4	0–12	
Gibbula buchi /Dubois/	87	4	0–8	
G. pseudangulata /Boettger/	101	5	1–9	
Hipponix sulcatus /Borson/	39	17	5–29	
Hyala vitrea /Montagu/	125	3	0–6	
Jujubinus celinae /Andrzejowski/	39	5	0–12	
J. turricula hoernesianus Sacco	85	8	2–14	
Mansonia scalaris /Dubois/	81	15	7–23	
Menestho sp. div.	65	34	22–46	
Merica fenestrata /Eichwald/	42	7	0–15	
Mitra recticosta Bellardi	62	10	3–17	
Murex friedbergi Cossmann & Peyrot	511	5	3–7	
Nassa dujardini /Deshayes/	50	16	6–26	
N. limata /Chemnitz/	115	15	9–21	
N. restitutiana /Fontannes/	547	10	8–12	1:0.4
N. schoenni /R. Hoernes & Auinger/	52	8	1–15	
N. serraticosta /Bronn/	63	10	3–17	
N. striaticosta Boettger	81	7	2–12	
N. toulai /Auinger/	614	8	6–10	1:0.5
Natica helicina Brocchi	189	9	5–13	1:0.1
N. josephina /Risso/	202	11	7–15	1:0.2
N. millepunctata Lamarck	428	11	8–14	1:0.2
N. redempta Michelotti	159	9	5–13	1:0.1
Neritina picta Férussac	246	4	2–6	
Ocenebra crassilabiata /Hilber/	40	8	0–16	
O. orientalis Friedberg	46	13	3–23	
Ocenebra sp.	84	20	11–29	
Peratotoma unica /Boettger/	311	3	2–4	
Potamides sp. div.	31	10	0–20	
Pyramidella digitalis Boettger	273	17	13–21	1:0.7
P. plicosa Bronn	73	29	19–39	1:0.2
Pyrgulina interstincta /Montagu/	120	41	32–50	1:0.0
Ranella marginata /Martin/	32	0	0–6	
Raphitoma hispidula /Jan/	618	12	10–14	1:0.8
Ringicula auriculata buccinea /Brocchi/	1860	2	1–3	1:1.3
Rissoina podolica Cossmann	150	24	17–31	1:3.0
Sabatia callifera Boettger	51	33	20–46	
S. utricula /Brocchi/	33	0	0–6	
Sandbergeria perpusilla /Grateloup/	145	32	26–38	1:0.4
Scala spinosa Bonelli	402	11	8–14	1:14.0
Semibittium multiliratum /Brusina/	58	29	17–41	
Semicassis miolaevigata Sacco	47	0	0–4	
Sveltia dertovaricosa Sacco	80	17	9–25	
S. inermis /Pusch/	25	0	0–8	
Teinostoma woodi /Hoernes/	136	1	0–3	
Teres anceps /Eichwald/	44	27	14–40	
Tornatina heraclitica Berger	154	27	20–34	1:0.9
T. truncatula /Bruguière/	162	40	33–47	1:0.4
Tricolia eichwaldi /Hoernes/	212	5	2–8	
Trigonostoma puschi R. Hoernes & Auinger	39	8	0–20	
Triphora perversa /Linnaeus/	190	14	9–19	1:2.9
Triton affine Deshayes	98	3	0–6	
Triton sp.	24	8	0–19	
Tudicla rusticula /Basterot/	47	4	0–9	
Turbocella acuticosta /Sacco/	266	5	3–7	
Turbonilla scala /Eichwald/	92	17	9–25	
Turritella badensis Sacco	1229	17	15–19	1:1.8
T. bicarinata Eichwald	112	28	20–36	1:1.7
T. erronea Cossmann	120	25	17–33	
PELECYPODS:				
Abra alba /Wood/	34	9	2–16	
Anadara diluvii /Lamarck/	656	7	6–8	1:1.1
Anomia ephippium Linnaeus	43	12	4–20	
Cardita crassa sororcula Mayer	52	15	8–22	
Cardium papillosum Poli	135	2	0–4	
Chama gryphoides Linnaeus	54	4	0–8	
Codakia sp. div.	22	19	7–31	
Corbula gibba /Olivi/	928	27	25–29	1:0.5
Ervilia pusilla /Philippi/	17	12	1–23	
Glycimeris pilosa deshayesi /Mayer/	25	40	27–53	
Hiatella arctica Linnaeus	48	17	7–27	
Limopsis anomala Eichwald	23	4	0–10	
Loripes dentatus niveus /Eichwald/	311	19	16–22	1:0.5
Lutetia nitida /Reuss/	75	17	11–23	
Mactra subtruncata triangula Reuss	36	16	8–24	
Meretrix sp. div.	28	43	30–56	
Montacuta exigua Cossmann	52	6	1–11	
M. ferruginosa Montagu	20	8	0–16	
Myrtea spinifera Montagu	33	22	12–32	
Nucula nucleus /Linnaeus/	84	7	4–10	
Nuculana fragilis /Chemnitz/	111	9	5–13	
Phacoides agassizi Michelotti	60	25	17–33	
Pteromeris scalaris /Sowerby/	113	12	8–16	
Striarca lactea /Linnaeus/	40	18	10–26	
Venus multilamella marginalis Eichwald	920	6	5–7	1:0.6
SCAPHOPODS:				
Dentalium fossile /Schroeter/	552	5	3–7	1:0.6
Fustiaria miocaenica /Boettger/	664	4.	2–6	1:0.6

consequently, no sorting in practice), the probability of finding the right and the left valve is identical. The proneness to the attack by boring gastropods is characterized through the percentage of the individuals attacked which occur in the sample under study. Since, however, the differences in the size of samples of particular species are considerable and the samples themselves fairly small in some cases, the relations in actual populations were described by means of confidence intervals. They were computed on the basis of a binomial probability distribution, since it is the simplest method of statistical analysis of the "either — or" type of data, *viz.* in this case: "an attacked individual — a non-attacked individual". If the confidence level is determined — as usually in biological studies — at 95 per cent, the confidence interval may be computed from the following formula (Reyment 1971):

$$p \pm 1.96 \sqrt{\frac{p(1-p)}{N}}$$

where *p* denotes the percentage of one of the classes (in this case: "the attacked individuals") in the sample, and *N* — the size of the sample.

For particular species, the authors sought to determine the numerical ratio of the individuals attacked by the naticids and the muricids (naticid to muricid prey ratio), but due to the difficulties mentioned above concerning the identification of borings and the size of the confidence interval, this value was given only in the cases in which the number of the individuals attacked was sufficiently high to assure an appropriate accuracy.

The values given in Table 1 enable the determination of a mean value for the main area of the Korytnica clays, of the proneness of particular species to the attack, since the assemblage under study was collected at various exposures and stratigraphical levels of these clays. If, however, the samples examined come from definite localities, the deviation from the mean value may be considerable. As an example, the locality from which comes a sample markedly enriched in the naticids (locality *I* of littoral facies *in* Radwański 1969, Fig. 31), but considerably impoverished in the species (Dr. W. Bałuk's oral communication), is characterized by the percentage of the attacked individuals of *Nassa schoenni* (R. Hoernes & Auinger) distinctly higher (Table 2) than in the main area of the Korytnica clays (*cf.* Table 1). A similar difference takes place for *Natica pseudoredempta* Friedberg, found only in this locality, when compared with mean values for the other species of this genus (*cf.* Tables 2 and 1).

As follows from a perfunctory analysis of the obtained data (*cf.* Table 1), the proneness to the attack by boring gastropods is subject to considerable fluctuations within one superfamily (*e.g.* Cardiacea), family (*e.g.* Bullidae) and even genus (e.g. *Actaeon, Alvania, Sveltia*), which probably may be explained by the occupation by particular species of sowewhat different ecological niches or by their special adaptations. In this respect, a fairly good example is offered by Cardiacea of various age (*cf.* Table 3) some species of which may quickly jump by means of their foot and thus escape the attackers (Davitashvili & Merklin 1966).

Table 2

Proneness of local populations to the attack by predatory boring gastropods in the Lower Tortonian of Korytnica (locality *I*, *cf.* the text)

Species	Number of specimens in the sample	Per cent proportion of the attacked specimens	95% confidence interval
Nassa schoenni /R. Hoernes & Auinger/	120	32	24–40
Natica pseudoredempta Friedberg	81	18	10–26

Table 3

Proneness of Cardiacea to the attack by predatory boring gastropods in various geological epochs

Species	Per cent proportion of the attacked specimens	95% confidence interval
A: Lutetian, Paris Basin /based on Taylor, 1970/		
Loxocardium bouei /Deshayes/	8	4–12
Venericardia imbricata Deshayes	0	0–2
Venericardia serrulata Deshayes	30	28–32
B: Lower Tortonian, Korytnica /cf. Table 1/		
Cardita crassa sororcula Mayer	15	8–22
Cardium papillosum Poli	2	0–4
C: Recent, Niger Delta /based on Reyment, 1971/		
Cardium kobelti v. Maltzan	10	10
Cardium lacunosa Reeve	14	14
Cardium papillosum Poli	26	26

Table 4

Proneness of mollusk classes or groups to the attack by predatory boring gastropods in the Lower Tortonian of Korytnica

Class or group	Number of specimens in the sample	Per cent proportion of the attacked specimens	95% confidence interval
Gastropoda /total/	17273	11	11
including: muricids	681	5	3–7
naticids	1059	11	9–13
Pelecypoda	3244	11	10–12
Scaphopoda	1216	4	3–5

As follows from the comparison of the habitat and mode of life of Muricacea and Naticacea, they could not meet each other and, consequently, nearly all borings found in their shells (Pl. 1, Figs 3—4; Pl. 2, Figs 3, 4) should be considered as symptoms of cannibalism (although it is obviously impossible to ascertain whether or not it is an intraspecific cannibalism). Only small number of borings may possibly come from the naticids, which incidentally have bored already empty shells buried in the bottom deposit. The percentage of attacked naticids in a population is exactly equal to the values computed for gastropods and pelecypods already treated as entire classes (Table 4). This indicates that the object of attack was selected by the naticids rather at random and without any preference. The level of cannibalism among the muricids is markedly lower than a mean value of the proneness to attack computed for all gastropods (Table 4), which suggests that the muricids distinguished themselves when looking for prey. Such a suggestion is, as a matter of fact, confirmed by laboratory studies (Wells 1958) showing that *Murex fulvescens* Sowerby recognizes and it almost does not attack at all *Ostrea equestris*, a pelecypod most common in its natural environment, and its main food consists of *Crassostrea*.

As seen from previous studies (Wells 1958, Paine 1963, Taylor 1970), the main food of the muricids usually consists of a few common species, primarily of oysters and Cardiacea. However, in the Korytnica clays, it is difficult to distinguish any group as a fundamental food for Muricacea, which probably results from the scantiness of oysters and Cardiacea with a simultaneous abundance of other pelecypods and gastropods.

The percentage of the attacked individuals in the Korytnica mollusks may sometimes exceed even 40% (Table 1), as *e.g.* in *Meretrix* sp. div., *Pyrgulina interstincta* (Montagu), *Glycimeris pilosa deshayesi* (Mayer), *Tornatina truncatula* (Bruguière), in both the listed pelecypods being confined mostly to young individuals. The predatory boring gastropods might, therefore, pose a serious biological danger to some species and it is not unlikely that sometimes they might also become the main cause of the extinction of their local populations (*cf.* Fischer 1966). In all probability, the formation of the "conchioline" mid-layer in the valves of *Corbula* might, therefore, play the role of a defensive mechanism. The efficiency of such a mechanism may be shown by the fact that, in the Recent populations of *Corbula,* less than one per cent of the individuals fall a victim to the boring gastropods, although they attack them not less violently than in the geological past (Fischer 1963). It is also the thickness of the shell of *Meretrix,* which causes that only less than a half of the individuals attacked perishes, that may serve, among other functions, as a defence against the boring gastropods.

Several mollusks which in practice are not attacked by the predatory boring gastropods at all (*cf.* Table 1) have also been found in the Korytnica clays. To a considerable extent, as in e.g. *Semicassis miolaevigata* Sacco, *Ficus* sp. div., *Ranella marginata* (Martin), as well as in *Ancilla glandiformis* (Lamarck), *Clavatula asperulata* (Lamarck) and *C. laevigata* (Eichwald) this probably results from the size of specimens available to the authors [1], since the correlation between the proneness to the attack and the size of a specimen is very distinct (*cf.* Table 5). The larger the prey the larger was obviously the attacker (Reyment 1971) and it should be remembered that the number of large predators among the

Table 5

Relationship between proneness to the attack by predatory boring gastropods and size of the prey in the Lower Tortonian of Korytnica

Group	Number of specimens in the sample	Per cent proportion of the attacked specimens	95% confidence interval
Greatest gastropods	3940	5	4–6
Smallest gastropods	4632	15	14–16

Korytnica gastropods is strongly limited (*cf.* Friedberg 1911—1928, 1938). Not all of course may be explained by the interdependence between the proneness to the attack and the size of potential prey, as among the almost not attacked Korytnica species there are also small ones (*cf.* Table 1), such as e.g. *Cardium papillosum* Poli, *Hyala vitrea* (Montagu), *Peratotoma unica* (Boettger), *Ringicula auriculata buccinea* (Brocchi) and *Teinostoma woodi* (Hoernes). Their security might have most likely resulted from a small probability of meeting predatory boring gastropods, the feature caused by their settlement in different ecological niches. As shown by the example of the genus *Ringicula*, which was not attacked as early as in the Lutetian of the Paris Basin (Taylor 1970), such a situation may persist fairly long, but, on the other hand, the fact that the species almost not attacked at all at Korytnica, that is, *Cardium papillosum* Poli, makes up at present a main food of the naticids in the Niger Delta (Reyment 1966a, b), indicates a possibility of fundamental changes.

As shown by the tabularized data on the numerical ratio of the naticid and muricid prey among large taxonomic groups (Table 6), the interests of the two groups of the predators strongly differ from each other: the naticids mostly attack pelecypods and scaphopods, as well as some of the gastropods, while the muricids are primarily interested in gastropods. Thus, the former confine themselves in principle to the infauna and the latter to the epifauna. Noteworthy is, however, the fact that the

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[1] Mostly adult specimens have been collected in the soil of arable fields at Korytnica.

Korytnica clays also contain mollusks, e.g. *Anadara diluvii* (Lamarck), which make up the object of competition of predatory boring gastropods

Table 6

Naticid to muricid prey ratio in particular mollusk classes in the Lower Tortonian of Korytnica

Class	Naticid to muricid prey ratio
Gastropoda	1:1.2
Pelecypoda	1:0.6
Scaphopoda	1:0.6

(*cf.* Table 1). This fact results from their mode of life transitional between the epi- and infauna.

The soundness of the suggestion concerning different interests of the naticids and muricids is confirmed by the results presented in Table 7: small (less than 3 mm), ribbed gastropods are mostly attacked by the muricids and smooth ones primarily by the naticids. It is obvious when considering that the smoothness of the shell of small gastropods is a feature important to the adaptation to the life in sediment, while the sculpture — to the life on the surface.

Table 7

Naticid to muricid prey ratio in gastropods of various shell ornamentation; Lower Tortonian of Korytnica

Group	Naticid to muricid prey ratio
Small ribbed gastropods	1:1.7
Small smooth gastropods	1:0.4

Contrary to Ziegelmeier's (1954) and Boekschoten's (1966) suggestions, no interdependence between the degree of ornamentation of a shell and the percentage of the individuals attacked by all the predatory boring gastropods has ever been found among the Korytnica mollusks (Table 8). This is the reason why precisely such a justification of the character of the strong differentiation of the proneness of the Upper Cretaceous and Paleocene ostracods from Nigeria to the attack (Reyment 1963, 1966a) seems to the authors to be insufficient. One could rather suppose that a decisive role herein was probably played by the ecology of potential prey and not by the resistance of their more or less sculptured carapaces to the attack by the boring gastropods.

Table 8

Relationship between the degree of shell ornamentation of the prey and proneness to the attack by predatory boring gastropods in the Lower Tortonian of Korytnica

Group	Per cent proportion of the attacked specimens	95% confidence interval
Ribbed gastropods	15	14–16
Smooth gastropods	15	13–17

Interesting is the comparison of muricid and naticid predation activities in different geological epochs. There is a 10 times greater number (*based on* Taylor 1970) of prey for each muricid specimen than for naticid one, in the Lutetian of the Paris Basin. In the Lower Tortonian Korytnica clays this proportion is even higher: a number of prey is for each muricid specimen 20 times greater than for naticid one. This growth of muricid activity may be regarded as being related to the enlarging of their body size, a feature so characteristic in the evolution of Muricacea since the Eocene through the Upper Pliocene (*cf.* Fischer 1922).

CONCLUSIONS

Analysis of the traces of the predation by the Muricacea and the Naticacea found in the assemblage of the Lower Tortonian mollusks at Korytnica allows one to state that at least since that geological epoch and, as shown by the comparison with the data from the Paris Basin presented by Taylor (1970), even since the Lutetian the ecology and ethology of these groups have not been the subject to any fundamental changes. Despite a similar manner of securing their food the competition between the two groups is rather small and limited only to a narrow transitional zone, which facilitates the coexistence of great populations of the muricids and naticids. On the other hand, this division of interests of the muricids and naticids causes that the numerical ratio of their prey in a population may be of importance to the determination of the ecology of the species being the prey.

The great size of the samples studied precludes with a considerable degree of reliability any chance character of the results obtained and subsequently used as a basis for ecological and paleontological considerations, although it is true that small samples require the application for this purpose at least the simplest statistical analysis. One may suppose that the computation of the confidence intervals, used in the present paper, assures a sufficient justification of ecological conclusions. It also seems that this may considerably facilitate any possible comparisons of the data from Korytnica with those coming from other areas and other geological epochs.

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Warsaw, June 1973

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PRZEJAWY DRAPIEŻNICTWA MURICIDÓW I NATICIDÓW WŚRÓD DOLNOTORTOŃSKICH MIĘCZAKÓW Z IŁÓW KORYTNICKICH

(Streszczenie)

Przedmiotem pracy jest analiza przejawów drapieżnictwa ślimaków drążących wśród mięczaków występujących w dolnotortońskich iłach korytnickich. Bardzo pospolite tutaj drążenia na muszlach ślimaków, małżów i łódkonogów (pl. 1—4) przypisano czterem gatunkom Muricacea i pięciu gatunkom Naticacea. Poddano krytycznej analizie kryteria rozróżniania drążeń muricidów i naticidów podane przez Carrikera i Yochelsona (1968). Przeprowadzono statystyczną analizę przeszło 20 000 okazów należących do ponad 120 gatunków, wykazując silne zróżnicowanie podatności poszczególnych gatunków, a także większych grup taksonomicznych na atak drapieżnych ślimaków drążących (tab. 1—4). Charakter tego zróżnicowania (tab. 5—8) wskazuje, że wynika ono nie tyle z etologii drapieżników, co z ekologii ich potencjalnych ofiar. Na podstawie stosunku ilości ofiar naticidów i muricidów w obrębie poszczególnych gromad mięczaków oraz poszczególnych grup ekologicznych wśród ślimaków (tab. 6—7) stwierdzono rozbieżność zainteresowań obydwu grup drapieżnych ślimaków drążących i niewielki tylko stopień konkurencji między nimi.

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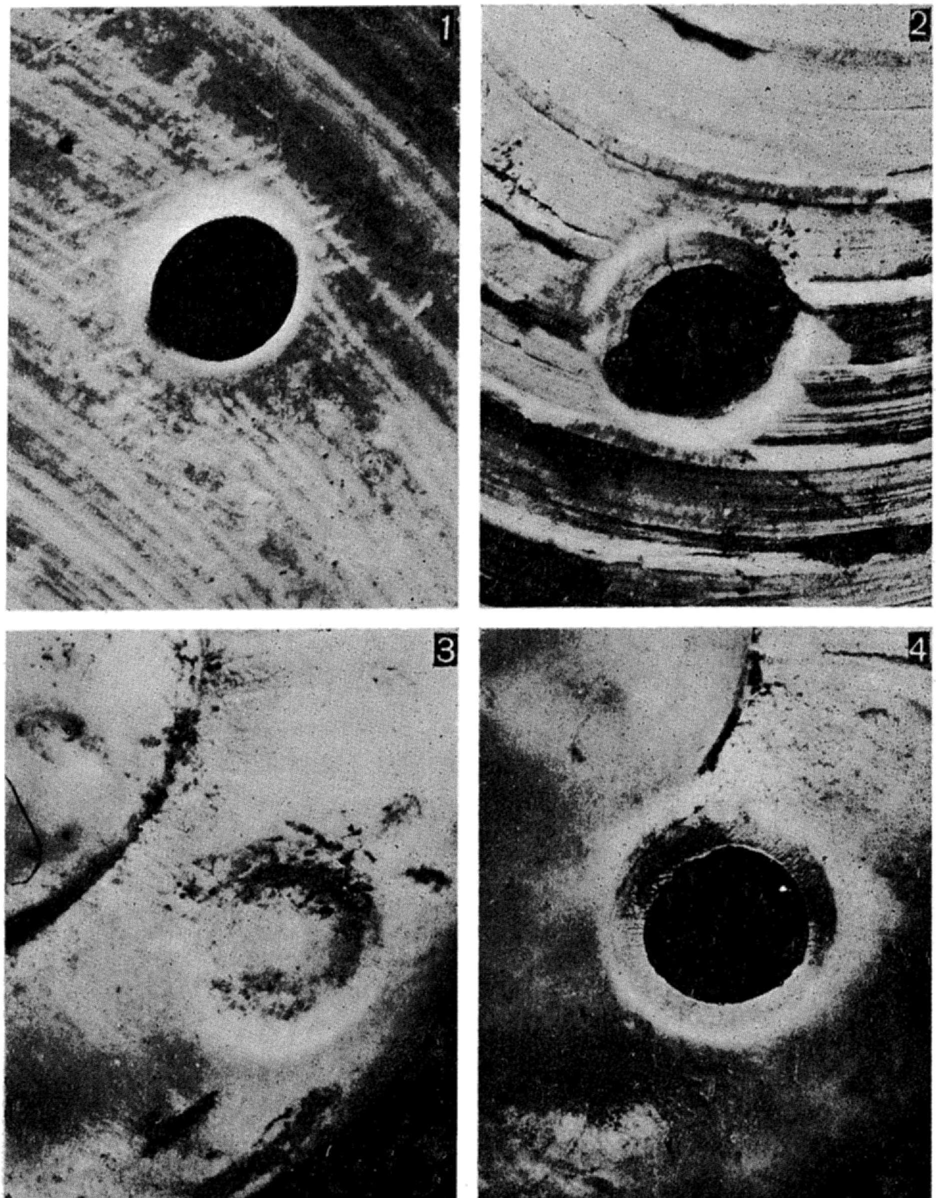
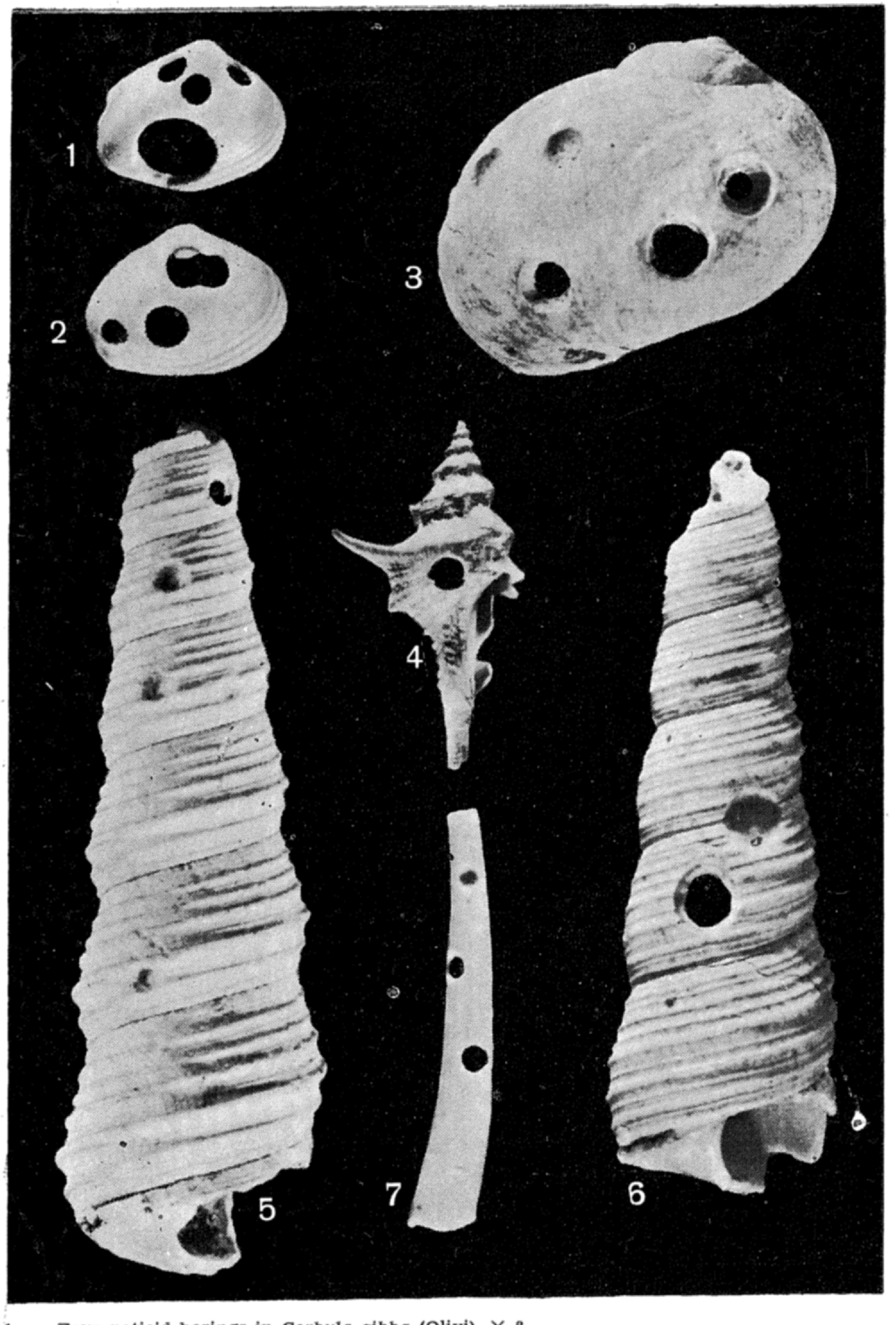
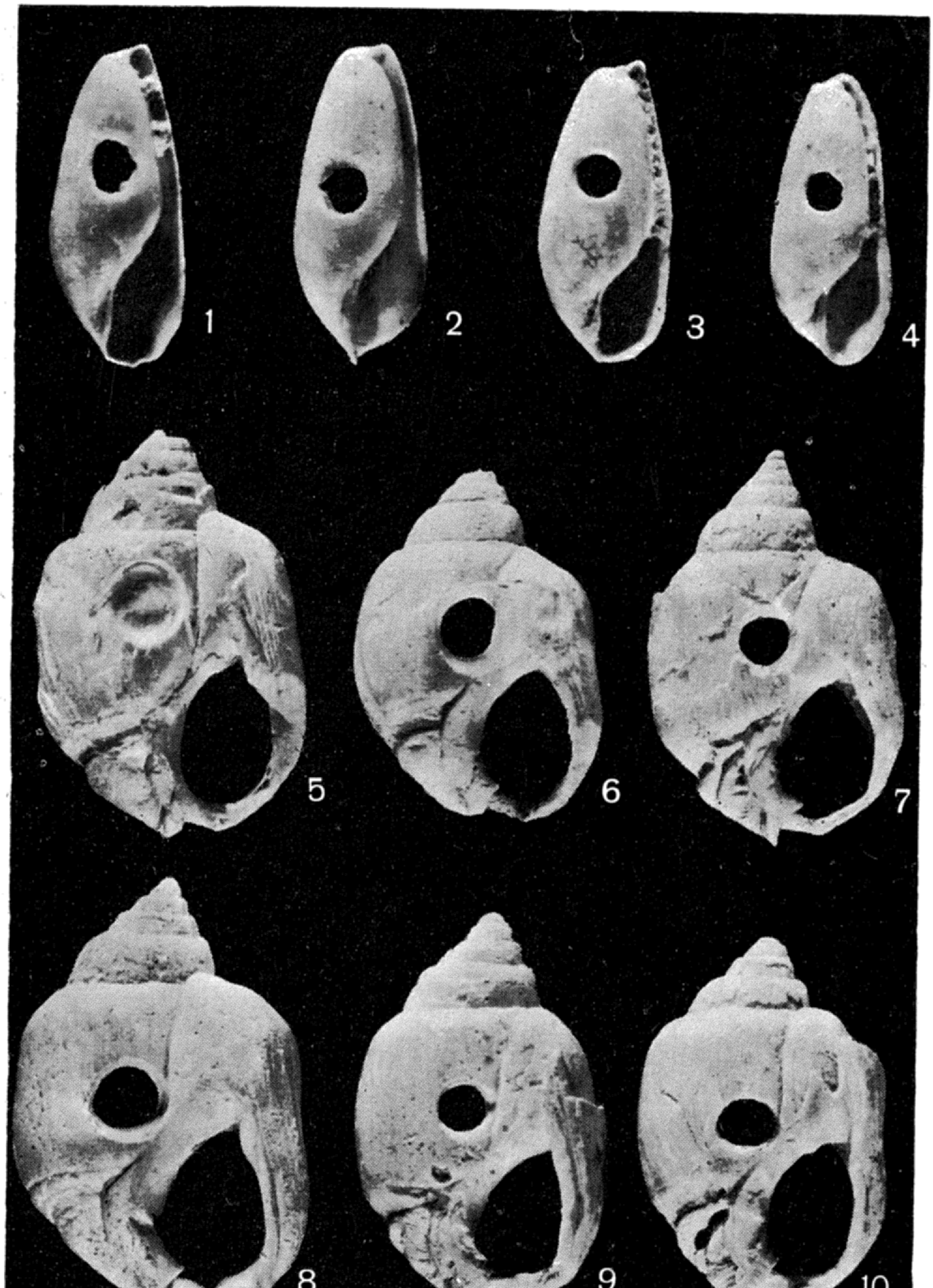


1 — Muricid boring in *Merctrix* sp.
2 — Naticid boring in *Venus multilamella marginalis* Eichwald.
3 — Failed naticid boring in *Natica josephina* (Risso).
4 — Naticid boring in *Natica josephina* (Risso).

All figures × 10; taken by B. Drozd, M. Sc.



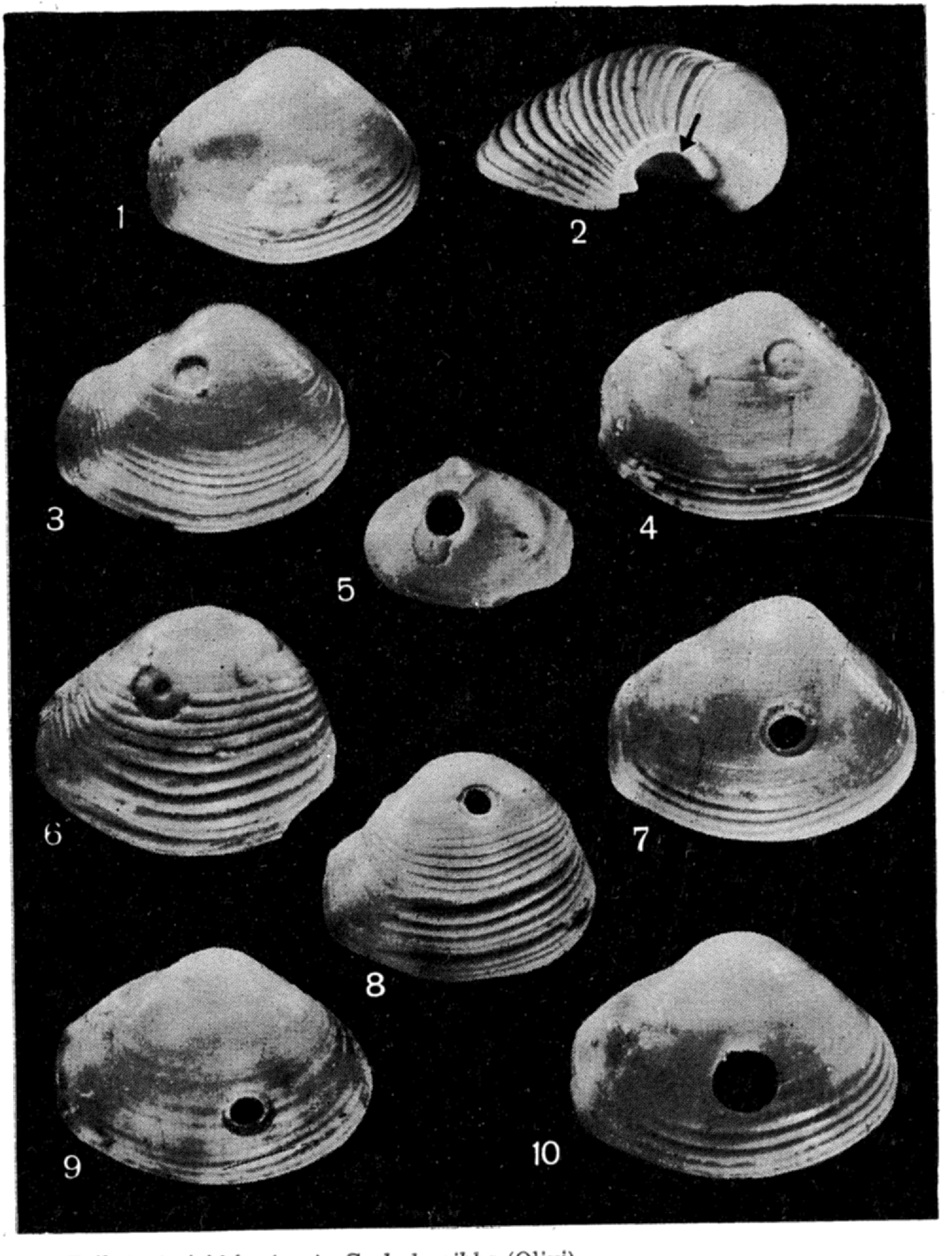
1 — Four naticid borings in *Corbula gibba* (Olivi), × 8.
2 — Four naticid borings in another valve of *Corbula gibba* (Olivi), × 8.
3 — Five naticid borings (two of them failed) in a predatory gastropod, *Natica millepunctata* Lamarck; × 3.
4 — Muricid boring in a predatory gastropod, *Murex friedbergi* Cossmann & Peyrot; × 3.
5 — Five muricid borings (four of them failed) in *Turritella badensis* Sacco, × 3.
6 — Two naticid borings (one of them failed) in *Turritella badensis* Sacco, × 3.
7 — Three naticid borings in *Dentalium fossile* (Schroeter), × 5.
All figures taken by B. Drozd, M. Sc.



1-4 — Naticid borings in *Sabatia callifera* Boettger, × 15.

5-10 — Naticid borings in *Nassa schoenni* (R. Hoernes & Auinger), first of them failed; × 5.

All figures taken by B. Drozd, M. Sc.



1 — Failed muricid boring in *Corbula gibba* (Olivi).
2 — "Conchicline"mid-layer (arrowed) in the valve of *Corbula gibba* (Olivi).
3-10 — Naticid borings in *Corbula gibba* (Olivi); "conchioline" mid-layer visible in most of the borings, some of them failed.

All figures × 8; taken by B. Drozd, M. Sc.