acta
geologica
polonica

Vol. 29, No. 3 Warszawa 1979

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Shell adaptation and ecological variability in the pelecypod species *Sphenia anatina* (Basterot) from the Korytnica basin (Middle Miocene; Holy Cross Mountains, Central Poland)

ABSTRACT: The pelecypod species *Sphenia anatina* (Basterot) from the shore facies of the Korytnica basin (Middle Miocene; Holy Cross Mountains, Central Poland) was adopted to live in more or less empty borings produced by diverse pelecypods (*Gastrochaena, Aspidopholas, Jouannetia, Lithophaga*). In result of the tendency to fill the space of the boring tightly to protect the body against the rocking and shaking prevailing all over the biotope, the shell of particular individuals acquired the shape of the occupied boring. In consequence, the four groups of the shell shape may be distinguished, all of them almost strictly counterparting the shape of the primary occupants. These groups, the ecotypes (*gastrochaenicola, aspidopholicola, jouanneticola, lithophagicola*, respectively), although of no taxonomic importance, may be well indicated in the hitherto described specimens from the Neogene deposits of Europe. The revision of taxonomy of all those specimens shows that presumably only one species of the genus *Sphenia* Turton lived in the Neogene of Europe, viz. *Sphenia anatina* (Basterot), and all the shape-deviated and variously called specimens are the ecological variants of this very species. Finally, this extinct species is compared, in the terms of its shell characteristics, taxonomy, and ecological requirements, with the present-day species *Sphenia binghami* Turton which, if taxonomically really separate, has developed directly from its Neogene ancestor, *Sphenia anatina* (Basterot).

INTRODUCTION

The investigated material of the pelecypods *Sphenia anatina* (Basterot, 1825) comes from the Middle Miocene (Badenian) littoral deposits of the Korytnica basin situated on the southern slopes of the Holy Cross Mountains, Central Poland, and being a part of the northernmost outskirts of the Fore-Carpathian Depression (*cf.* Bałuk & Radwański 1977, Text-fig. 1; and 1979, Text-fig. 1). Within this small basin which is filled mostly with the fossiliferous Korytnica Clays that bear the world-famous assemblage of diverse invertebrates, primarily mollusks (*cf.* Radwański 1969; Bałuk 1975; Bałuk & Radwański 1977, 1979), the occurrence site of *Sphenia anatina* (Basterot) is unique. It is confined to a small area of the shorezone (*cf.* Text-

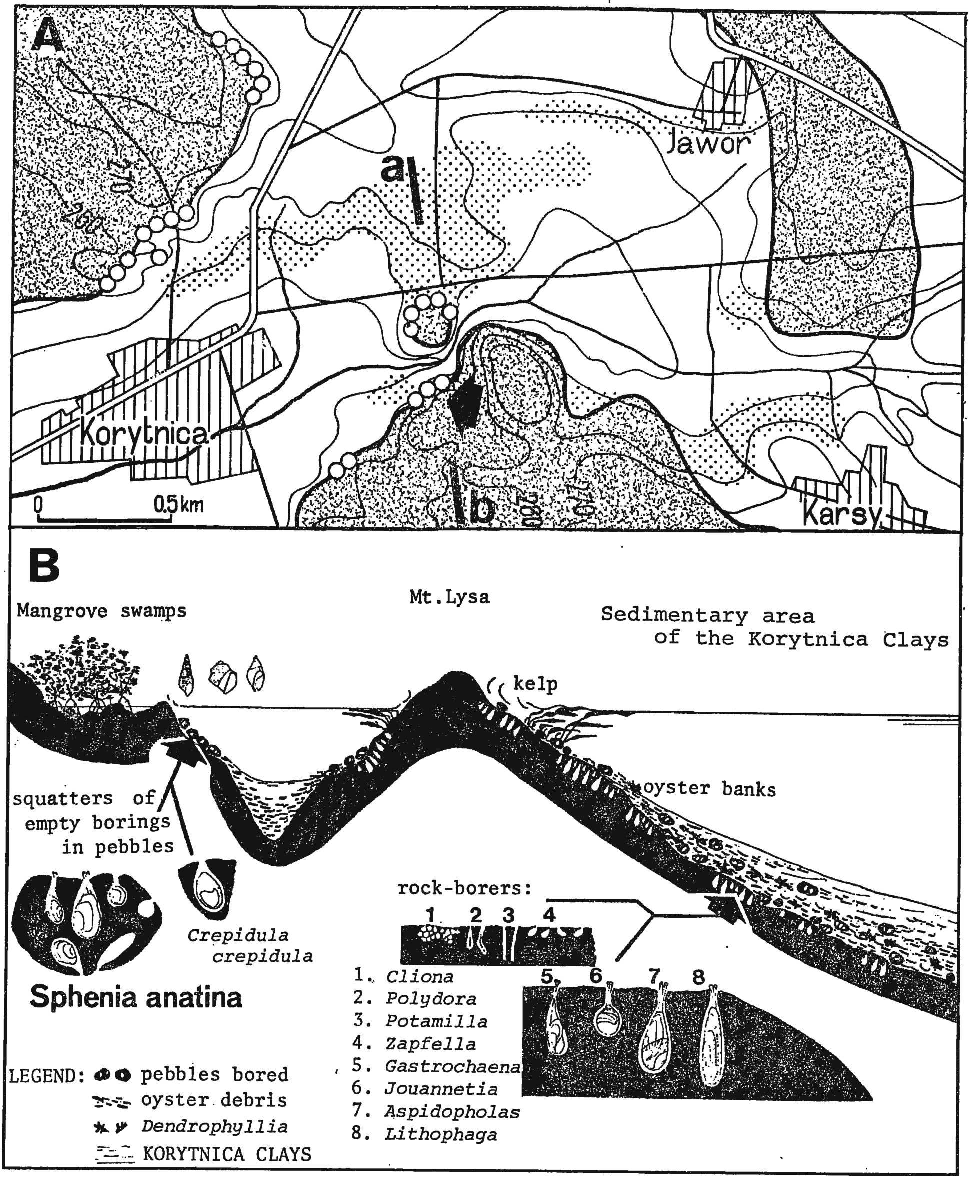


Fig. 1. Paleoenvironmental sketch of the southern part of the Korytnica basin (A) and an idealized section of the shorezone (B) to show the occurrence site of *Sphenia anatina* (Basterot); adopted *from* Bałuk & Radwański (1977, Text-figs 2 and 5)

For the sketch (*A*) indicated are: marine area of the basin during the Middle Miocene (Badenian) transgression (*blank*), present-day outcrops of the Korytnica Clays (*stippled*), preserved fragments of littoral structures (*circled*), and land or island areas along the seashore (*hachured*); leaders (*a* and *b*) indicate the line of the section presented in *B*; arrowed is the occurrence site of *Sphenia anatina* (Basterot) within a littoral rubble (*cf.* section in *B*)

For the section (*B*) indicated are: some elements of the mollusk assemblage of the mangrove swamps (gastropos *Terebralia*, *Neritina* and *Melanopsis*); secondary dwellers ("squatters") of the pelecypod borings within the littoral rubble beneath the swamps, *Sphenia anatina* (Basterot) and *Crepidula crepidula* (Linnaeus); rock-borers and some other elements of the island shore facing an open part of the Korynica basin where the Korytnica Clays were accumulated; for other explanations of the shorescape *see* Bałuk & Radwański (1977)

-figs 1—2) in which all the collected specimens have been found inside borings of the rock-boring pelecypods, and produced within limestone rock-pieces or pebbles. These borings, when domiciled by *Sphenia anatina* (Basterot) were either empty or they still contained the shells of their original occupants. In the latter case, the specimens of *Sphenia anatina* (Basterot) are preserved inside the shells of the rock-boring pelecypods, the isolated valves of which have been pushed aside. Occasionally within a boring, two generations of *Sphenia anatina* (Basterot) are preserved, regardless the being of remains of the previous host, and all the shells are deposited in a "cone-in-cone" manner.

The frequency of *Sphenia anatina* (Basterot) under such conditions is rather low. Within a pebble that usually contains 20—30 or more larger borings, at most a few of them are taken by *Sphenia anatina* (Basterot), and even so many of their shells are damaged either by hydrodynamic agents in their life environment or by diagenesis and/or weathering in the deposit. Consequently, the total number of well preserved specimens, collected by crushing and breaking up the pebbles and emptying the borings does not exceed half a hundred.

It is noteworthy that within the Korytnica basin in which the assemblage of pelecypods comprises about 200 species, some of them being very common (*cf.* Bałuk & Radwański 1977), the species *Sphenia anatina* (Basterot) has been recognized only in the discussed littoral environment. Its occurrence at that place has been stated previously (Radwański 1969, p. 89 and Pl. 35, Figs 9—10), and reported subsequently twice more (Radwański 1970, p. 375; Bałuk & Radwański 1977, p. 92, Text-fig. 5 and Pl. 1, Figs 4—5). In the whole Fore-Carpathian basin in Poland this species has as yet been found only at one locality more, namely within the littoral

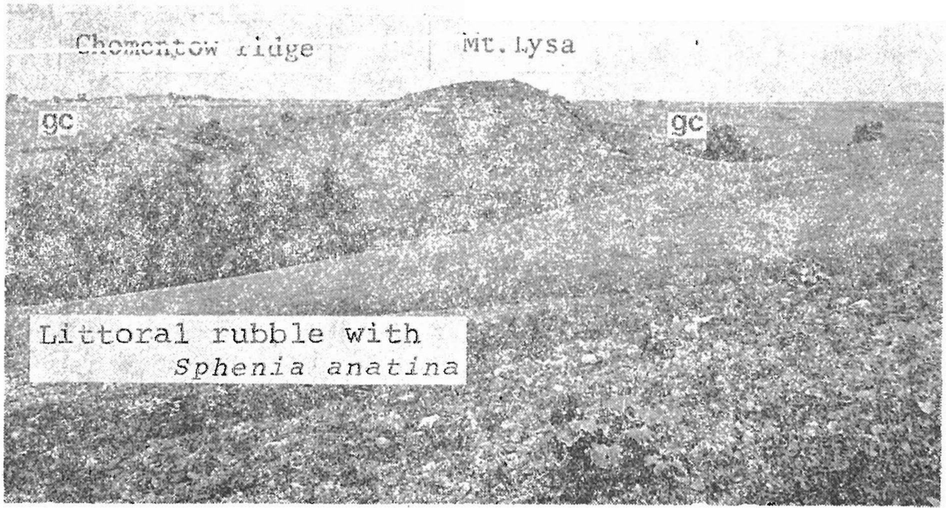


Fig. 2. General view of the locality with the littoral rubble (*in foreground*) being the biotope of *Sphenia anatina* (Basterot); the photo is taken from the place above the littoral rubble, just adjacent to the zone of suggested mangrove swamps (*cf.* Text-fig. 1*B*), and towards Mt. Lysa along the section presented in Text-fig. 1; indicated are areas of the gastropod-bearing Korytnica Clays (*gc*) exposed over the cropland, and the Chomentow ridge bounding the Korytnica basin

cliff and boulders exposed at Małoszów, Miechów Upland (*cf.* Friedberg 1934, 1938; Radwański 1969, p. 89).

THE BIOTOPE OF *SPHENIA ANATINA* (BASTEROT)

The biotope of *Sphenia anatina* (Basterot) was a littoral rubble that developed along rocky shores of the Korytnica basin. This rubble is composed of angular pieces or weakly rounded pebbles of diverse Jurassic limestones derived directly from the neighboring shorezone. It was deposited along slightly inclined shoreslope of the area protected by a small island (see Text-fig. 1*A*—*B*), and within such an environment the action of hydrodynamic agents was relatively low. In result many shells contained within the borings, and belonging either to their rock-boring hosts or to the secondarily dwelling *Sphenia anatina* (Basterot), have been preserved entirely and not crushed and swept away. The pebbles are embedded within yellow, sandy clay that fills many of the borings, both empty or keeping shells of any of the two discussed kinds. Associated mollusks, mostly gastropods *Terebralia bidentata* (Grateloup), *Pirenella tabulata* (Hörnes), *Cerithium* aff. *zelebori* Hörnes, *Neritina picta* Férussac, *Melanopsis aquensis* Grateloup, and others (*cf.* Radwański 1969, p. 90; Bałuk & Radwański 1977, pp. 93—94), much deviated in their ecological character from those of the main area of the Korytnica basin, are comparable to those of the present-day communities of the mangrove facies (*see* Plaziat 1970, 1975a,b; Taylor 1971; Braithwaite & al. 1973). Consequently, they are regarded as indicative of this very type of the shore environment (Radwański 1974, Bałuk & Radwański 1977). Regardless the suggested presence of mangroves, this *Sphenia*-bearing environment situated beneath the coastal swamps (cf. Text-fig. 1*B*) is to be characterized as featured with a rather quaggy bottom on which isolated pebbles were scattered, and generally quiet waters were only temporarily so agitated that were able to disturb the rock-pieces and pebbles dwelled by the pelecypods (*see* reconstruction of the shorescape *in*: Bałuk & Radwański 1977, Text-fig. 5).

THE HABITAT OF *SPHENIA ANATINA* (BASTEROT)

The only habitat of *Sphenia anatina* (Basterot) within the discussed biotope were the borings produced by rock-boring pelecypods, and neither fissures nor holes and other irregularities of the pebble surface were domiciled by them. The latter were certainly able to deliver sufficient room for settling the larvae, but they were not enough chambered to keep and protect the specimens when turning adult.

The borings kept by *Sphenia anatina* (Basterot) were produced by the four pelecypods, viz. *Gastrochaena dubia* (Pennant), *Aspidopholas rugosa* (Brocchi), *Jouannetia semicaudata* (des Moulins), and *Lithophaga lithophaga* (Linnaeus), whose shells are preservable inside the borings and which allow to recognize the producer to its specific rank (*cf.* Text-fig. 3). When studying the morphology of borings (Radwański 1969) it appeared that this morphology matches ideally to the shape of the shells of those pelecypods at their adult stage. Consequently, the producer is recognizable to the specific rank even if the borings have been emptied of the shells. The borings of the discussed species much differ in their shape, primarily in the chamber that contained the shelled animal, while the siphonal necks, being much differentiated within particular species, are not so diagnostic (*cf.* Text-fig. 3).

It is noteworthy that under the same conditions, as secondary dwellers of borings produced by the rock-boring pelecypods, associated are two pelecypods, *Striarca lactea* (Linnaeus) and *Hiatella arctica* (Linnaeus), and one gastropod, the slipper limpet *Crepidula crepidula* (Linnaeus), all of which are also to be found (*see* Radwański 1969, Pl. 35, Fig. 8; Bałuk & Radwański 1977, Pl. 1, Figs 1—3) within the rock-pieces and pebbles domiciled by *Sphenia anatina* (Basterot).

Within the biotope under investigation, the borings occupied by *Sphenia anatina* (Basterot) are often more or less abraded after the life of the original occupant, and before the settlement of these secondary squatters. Consequently, some specimens are stretching almost up to the surface of the inhabited pebble in the exposure (*cf.* Radwański 1969, Pl. 35, Fig. 10), whereas the others are hidden inside the fully preserved borings and are not visible through their small siphonal openings.

TAXONOMY OF THE SPECIES

The genus *Sphenia* to which the investigated species belongs, was founded by Turton in 1822 for a present-day species *binghami* established in the same description. Turton had only shells at his disposal, and this conchologic material was the only one known until Forbes & Hanley reported in 1853 on the soft parts of the animal. The species *Sphenia binghami* Turton is distributed primarily along the Atlantic coasts of Morocco, and of Europe, from Portugal through England, as well as in the Mediterranean (*cf.* Forbes & Hanley 1853, Jeffreys 1865, Smith 1893, Sacco 1901, Younge 1951, Tebble 1966), although it is missing in the Adriatic (*cf.* Starmühlner 1963). Within these areas, the species is known to nestle from just offshore to moderate depths (40—45 m) in crevices or borings to which it adopts its shape (*cf. also* Kühnelt 1933). A similar mode of life is moreover displayed by diverse *Sphenia* species from the America coasts (Abbott 1974).

The ancient forms from the Neogene deposits of Europe has for the first time been recognized by Basterot (1825) in the Miocene of Aquitaine, and named *Saxicava anatina* Basterot. This specific name, *anatina* Basterot, although Basterot himself did not illustrate any specimen, was in common use by the French authors (Grateloup 1838, Benoist 1873, and Fontannes 1876; *cf.* Dollfus & Dautzenberg 1902, Cossmann & Peyrot. 1909), and Fontannes (1876) was the first to include the species into the genus *Sphenia.* The first who illustrated the species was Hörnes (1870) from the Vienna Basin. In Italy however another specific name was used for identical forms, namely *testarum* Bonelli. The latter name was used by Bonelli in his unpublished catalogue of the Zoological Museum in Turin, and the date of the original manuscript is indicated on the cover page by Bonelli's handwriting as 1834; nevertheless, the dates of either 1827 were accepted by some authors (Sacco 1901, Cerulli-Irelli 1909) or 1839 by the others (Dollfus & Dautzenberg 1902, with a statement that it was "*in* Michelotti"). Regardless the validity of the specific name *testarum* which according the *ICZN* Code is a *nomen nudum* (see Articles 8, 9, 12 and 16 of the Code), none of these dates had the priority over the date of *anatina*. At the times the *ICZN* Code has not been established yet, and the priority rule not so apparent, these two names were in use, simultaneously with that of *binghami* to which some of the discussed ancient forms were also attributed (Sacco 1901, Cerulli-Irelli 1909). Finally, the specific names *anatina* and *testarum* were sometimes regarded as denoting diverse species (Dollfus & Dautzenberg 1902).

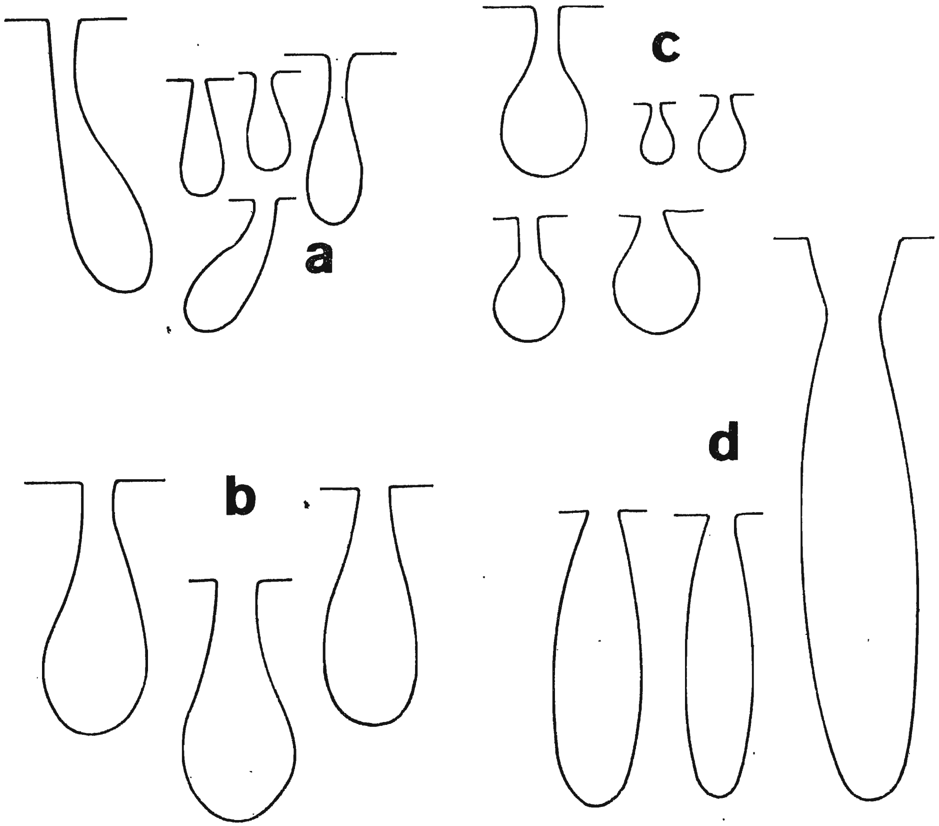


Fig. 3. Morphology of the pelecypod borings domiciled by *Sphenia anatina* (Basterot), to show the variability of shape and size of the borings of particular species (some specimens, especially in *c* and *d* are partly abraded at their tops; *cf.* rock-borers *5—8* in Text-fig. 1*B*); adopted from Radwański (1969, Text-figs 5—6, 8 and 10), slightly reduced

The borings were produced by: **a** — *Gastrochaena dubia* (Pennant), **b** — *Aspidopholas rugosa* (Brocchi), **c** — *Jouannetia semicaudata* (des Moulins), **d** — *Lithophaga lithophaga* (Linnaeus)

Fig. 4. Ecotype *gastrochaenicola* of *Sphenia anatina* (Basterot): **4a** left valve in the boring of *Gastrochaena dubia* (Pennant), **4b** left valve in inner and outer views, **4c** right valve in two views; all ×2, further explanations in the text

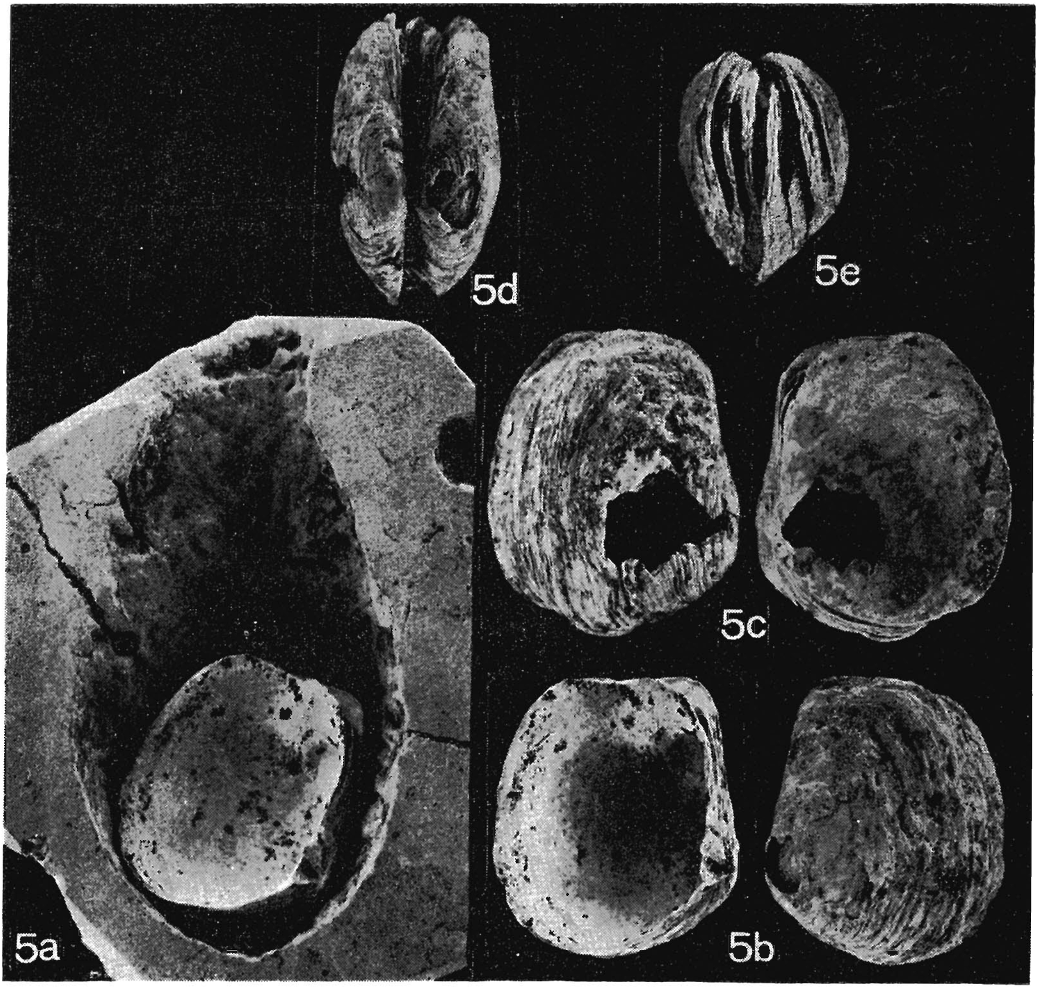


Fig. 5. Ecotype *aspidopholicola* of *Sphenia anatina* (Basterot): **5a** left valve in the boring of *Aspidopholas rugosa* (Brocchi), **5b** left valve in inner and outer views, **5c** right valve in two views, **5d** dorsal view, **5e** posterior view to show the splitting of the shell; all ×2, further explanations in the text

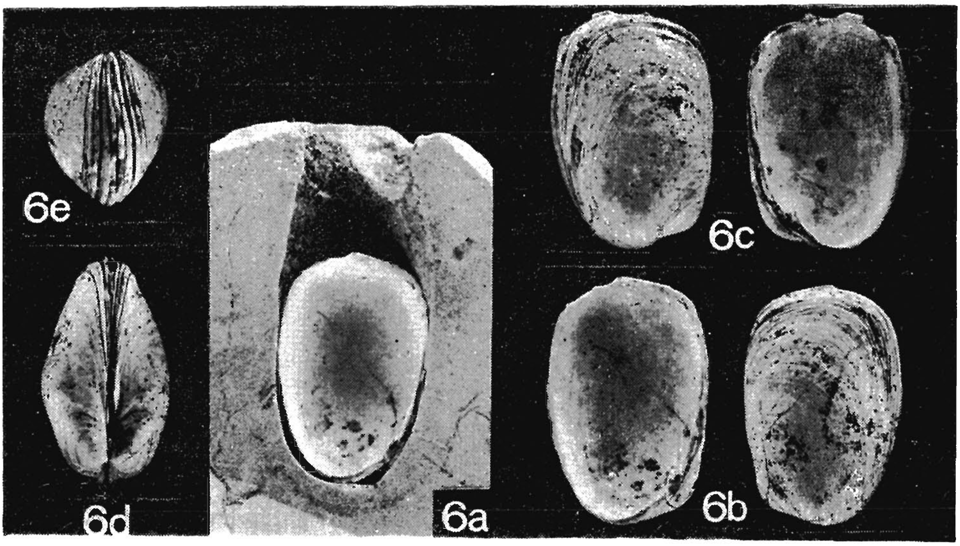


Fig. 6. Ecotype *lithophagicola* of a half-grown specimen of *Sphenia anatina* (Basterot): **6a** left valve in the boring of *Lithophaga lithophaga* (Linnaeus), **6b** left valve in inner and outer view, **6c** right valve in two views, **6d** dorsal view, **6e** posterior view; all ×2, further explanations in the text

Fig. 7. Another example of the ecotype *lithophagicola* of *Sphenia anatina* (Basterot): **7a** left valve in the boring of *Lithophaga lithophaga* (Linnaeus), **7b** left valve in inner and outer views, **7c** right valve in two views (arrowed is a file of incisions within the growth lines), **7d** dorsal view, **7e** posterior view; all ×2, further explanations in the text

To clarify the above review, it is to note that Sacco (1901) regarded *testarum* Bonelli as a variety of *binghami* Turton, and he did not mention *anatina* Basterot at all. On the contrary, Dollfus & Dautzenberg (1902) when regarding *testarum* Bonelli and *anatina* Basterot as diverse species, they used the first name for the forms with elongated and truncated shells, and the latter one for the bulged forms with posteriorly tapering shells; moreover, they did not use the name *binghami* Turton, whilst one of the so-determined Sacco's specimens they synonymized with *anatina* Basterot (sic!).

As apparent from the illustrations and descriptions available, *anatina* Basterot is identical with and has therefore a priority over *testarum* Bonelli.

The relation between *anatina* Basterot and *binghami* Turton remains however not evidently clear. The present authors have no opportunity to study the present-day forms and make such comparisons as did Sacco (1901). In this matter, the present authors are to uphold the opinion expressed by Sacco (1901) as well as by Cossmann & Peyrot (1909) about slight differences between these taxa consisting primarily in the more subtrapezoidal or rectangular shape and smaller size in *Sphenia binghami* Turton (*cf. also* Yonge 1951, Tebble 1966; and discussion in the last chapter of this paper), and regard these taxa as separate but closely related. With this understanding, the species *anatina* Basterot is thought to have been a direct, Neogene ancestor of the present-day species *binghami* Turton, the latter species being not represented in the Neogene deposits of Europe. The present authors guess that such a judgement upon the taxonomy of these two *Sphenia* species may become a subject to discussion or objection.

The discussion upon what the forms distinguished by the previous authors within or closely to the "*binghami-anatina-testarum* triangle" really represent is undertaken in one of the successive chapters. In that discussion omitted are those taxa which have formerly fallen into the "*binghami-anatina-testarum* triangle", e.g. *Sphenia lamellosa* De Stefani & Pantanelli 1880, or *S. brocchii* Dollfus & Dautzenberg 1888 (*cf.* De Stefani & Pantanelli 1880, De Stefani 1889; *and comments by* Sacco 1901, Dollfus & Dautzenberg 1902).

ADAPTATION OF *SPHENIA ANATINA* (BASTEROT) TO THE BORINGS

The investigated specimens of *Sphenia anatina* (Basterot) display diversified morphology (*cf.* Text-figs 4—14). Their shells range is shape from broadly ovoidal (Text-figs 11—14) or subtrapezoidal (Text-figs 5—6), through more or less elongated, usually slightly tapering posteriorly (Text-figs 4 and 7—10). The shells of the specimens preserved entirely, are inequivalve, the right valve being usually the larger (Text-figs 5 and 7), although there are some instances with the left valve larger (Text-fig. 10, elder form); moreover, the forms almost equivalve are also present (Text-figs 4 and 6; and younger form *in* Text-fig. 10). Some specimens are more or less twisted along their axis, being distorted either towards their left (Text-fig. 7*d—e*) or their right valve (Text-fig. 10*d—e*).

The shells are biconvex either almost uniformly throughout their length, in places with small corrugations (Text-figs *5d*, *6d* and *10h*) or, when the specimen is distorted, the smaller valve is posteriorly less convex, almost flat or even slightly concave; in the latter case the smaller valve being, as stated above, either the left (Text-fig. *7d*) or the right one (Text-fig. *10d*). The biconvexity in transverse sections of the shells is usually uniform (Text-figs *5e*, *6e*, *10e* and *12c*), although in some specimens either flat or depressed portions appear (Text-fig. *7e*).

The filling of the space in particular borings occupied by the investigated specimens is diverse. Smaller borings, those of *Gastrochaena* and of *Jouannetia* (see *a* and *c* in Text-fig. 3) are filled almost entirely, with only the siphonal neck of the boring not being taken (*cf.* Text-figs 4 and 11—14). Larger borings, those of *Lithophaga* (see *d* in Text-fig. 3) are filled to smaller extent: the average-sized borings of *Lithophaga* are taken either completely (*cf.* Text-figs 7 and 9), or primarily only at their deeper parts (*cf.* Text-figs 6, 8 and 10). In the latter case, the growing shells were usually enlarging aside to the extent sufficient to fill the available space completely (Text-figs 6 and 8), but some specimens could not reach the walls of larger borings (Text-fig. *10a*). The largest borings, those of *Aspidopholas* (see *b* in Text-fig. 3) are occupied without possibility to fill their space entirely; in such a case the investigated specimens look as if floating within the boring (Text-fig. *5a*).

When the growing *Sphenia anatina* (Basterot) could not fill the whole chamber of the boring to protect itself against rocking and shaking, it was able to produce a special device consisting in the splitting of either the anterior (Text-fig. *7a—c*) or posterior part of the shell (Text-figs *5c—e* and *9b*); this feature resulted from the successive deposition of the younger and younger shell layers gradually more and more inwards, the older layers becoming therefore pushed away or "peeled off". In some specimens the successive layers have been stacked without their distinct splitting (Text-fig. *6d—e*; to some extent also Text-fig. *8a—b*). Anyway, the resulting thickness of the valve at the places of its splitting becomes much larger, and it attains even 3.5 mm (specimen presented in Text-fig. 5).

The growth lines of the valves are usually more or less corrugated, being ideally regular only in a few specimens (Text-figs 6 and 12). The analysis of the growth lines shows that some specimens were growing initially along their length, and afterwards they enlarged themselves ventrally to fill the available space, thus becoming subtrapezoidal in their shape (*see* Text-fig. *5b—c*, to some extent also Text-fig. *6b—c*). The outline of the growth lines often exhibits a distinct incision on the right valve directed apically; it is situated approximately at the one fourth of the valve length (*see* Text-figs *7c* and *9a*; *arrowed*). This is interpreted as a result of the disturbances in the valve growth caused by the byssus which projects from the body just at this very region (*cf.* Yonge 1951, Text-fig. *1B*). A corresponding incision at the valve margin, but much larger, has been observed in a single specimen, within the internal layers of the "split-off" stack (Text-fig. *7b—c*).

In some borings, the two generations of *Sphenia anatina* (Basterot) are observable, the younger shell (*y* in Text-figs 10 and 14) being preserved inside the elder one (*e* in Text-figs 10 and 14; *cf. also* Text-fig. *9a—b*). The shells of the both generations are stacked one into another one in a "cone-in-cone" manner. The younger shell is either much smaller than the elder one (Text-fig. 10), or it may be of almost identical size (Text-fig. 14). In the latter case, the younger shell when enlarging has been projecting with its tips through the ventral gape of the elder shell (slightly visible in Text-fig. 14*a*: the younger shell overlaps the ventral margin of the elder one). In all the discussed instances of that type it may be said that the younger shell adopts its shape not to the boring, but to the shell of its own "mother", taken for settlement after her death.

Finally, some specimens of *Sphenia anatina* (Basterot) have adopted their shell to the room still partly kept by the shell of the original occupant which has been left in the boring. This is well demonstrated in the borings of *Jouannetia semicaudata* (des Moulins) whose shells have especially often remained intact in the investigated biotope (*cf.* Text-figs 12—14; *see also* Radwański 1969, p. 89; and Bałuk & Radwański 1977, pp. 92—93). Most specimens of *Sphenia anatina* (Basterot) have not suffered from the presence of such shells (*see* Text-figs 12 and 14). Some of them however have strongly deformed their shells, especially in the region which contacted with the broad and thick hinge part of the *Jouannetia* shell, and this resulted in the development of a deeply incised notch in the ventral margin of the growing valves (*see* Text-fig. 13; *cf. also* remarks on the taxon "*parvinflata*" established by Sacco, 1901).

The size of the investigated specimens of *Sphenia anatina* (Basterot) varies from some 3 mm in length of the tiny specimens from juvenile borings of *Lithophaga*, to about or slightly over 21 mm in the largest forms (*see* Text-figs 7—8; and elder form in Text-fig. 10). Some specimens which fill the boring tightly with their anterior part, but did not enlarge along with the boring length, are interpreted here as half-grown in size, but adult individuals (*see* Text-fig. 6). The specimens with a strong splitting of their shells represent either the adult individuals more advanced in their age, or gerontic (*see* especially Text-fig. 5; moreover, Text-fig. 7).

When comparing the investigated specimens with the present-day and other Neogene forms, it may be noted that the shell asymmetry and its distortion have commonly been reported both in *Sphenia binghami* Turton (*cf.* Turton 1822, Jeffreys 1865, Smith 1893, Yonge 1951) and in the forms included in the below presented synonymy into *Sphenia anatina* (Basterot) (*cf.* Hörnes 1870, Cossmann & Peyrot 1909, Friedberg 1938). This has been recognized as resulting from the mode of the shell attachment by byssus within the crevices or borings (Yonge 1951), the right valve then becoming the larger due to asymmetry in the hinge mechanism (Yonge 1951). Instances with the left valve larger have not as yet been recorded in the present-day forms.

Generally, the shell adaptation in the investigated *Sphenia anatina* (Basterot) to the borings is of the same character as the adaptation of other pelecypods either to the borings or to any crevices or holes within the littoral stones and rocks, as it is exemplified primarily by the extant genera *Saxicava* (*Hiatella*) and *Arca* (*Barbatia*, *Striarca*) (*cf.* Kühnelt 1930, 1933; Hunter 1949; Yonge 1951; Starmühlner 1963). Within the littoral zone of the Korytnica basin such an adaptation is apparent not only in the species *Striarca lactea* (Linnaeus) (*cf.* Bałuk & Radwański 1977), and *Hiatella arctica* (Linnaeus), but also in some specimens of the gastropod species *Crepidula crepidula* (Linnaeus) (*cf.* Radwański 1969, 1970, 1974; Bałuk & Radwański 1977). In the latter gastropod species, a splitting of the shell and the resulting anchorage device is recorded in some specimens (*cf.* Bałuk & Radwański 1977, Pl. 1, Fig. 2) whose adaptational deviation in shell morphology becomes therefore highly comparable to that in *Sphenia anatina* (Basterot).

As apparent from the above description and discussion, as well as from the comparison with the present-day species *Sphenia binghami* Turton, all the investigated specimens (*cf.* Text-figs 4—14) belong to one species, *Sphenia anatina* (Basterot). Their variable morphology results evidently from their adaptation to live inside the diverse pelecypod borings. Some specimens, as indicated by the growth lines, were changing their shape during ontogeny to fill better the available room (*e.g.* Text-fig. 5), and the same happened during their adult or gerontic stages when splitting of the shells have led to the same result (*cf.* Text-figs 5 and 7). Consequently, the investigated specimens may be grouped into four morphological classes, the final shape of which depended on the shape of the borings produced by their primary occupants. These ecological variants are called here the *ecotypes*, the names of which are derived from the generic names of the boring pelecypods, as follows:

ecotype *gastrochaenicola* (Text-fig. 4) which comprises the forms nestled inside borings of *Gastrochaena*,
ecotype *aspidopholicola* (Text-fig. 5) which comprises the forms nestled inside borings of *Aspidopholas*,
ecotype *jouanneticola* (Text-figs 11—14) which comprises the forms nestled inside borings of *Jouannetia*,
ecotype *lithophagicola* (Text-figs 6—10) which comprises the forms nestled inside borings of *Lithophaga*.

An average shape of the investigated species, if the final shape of particular ecotypes is not taken into account, should be imaginated as more or less oblong, certainly very close to that displayed by the younger form that lived within the shell of the elder one (*see* Text-fig. 10*f*—*h*).

DISCUSSION ON THE NEOGENE REPRESENTATIVES OF *SPHENIA ANATINA* (BASTEROT)

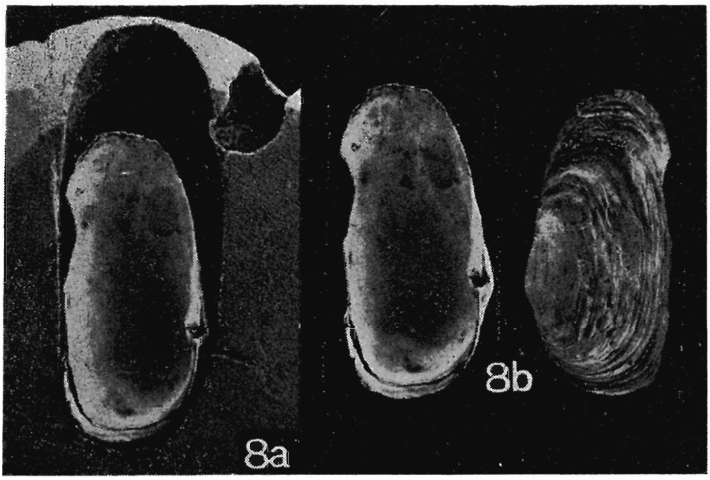
As indicated in discussion on the taxonomy of the investigated species, *Sphenia anatina* (Basterot) within the Neogene deposits of Europe has long been known from both the Mediterranean (Tethys and Paratethys) and Atlantic realms, although it nowhere occurs commonly. When its taxonomic assignation had long been un-

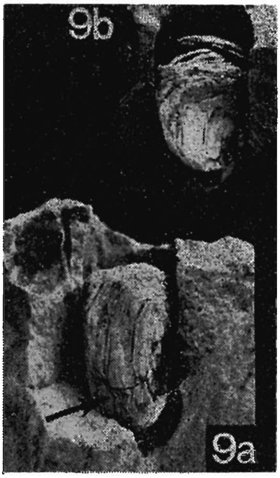
TEXT-FIGURES 8—10 (*see opposite page*)

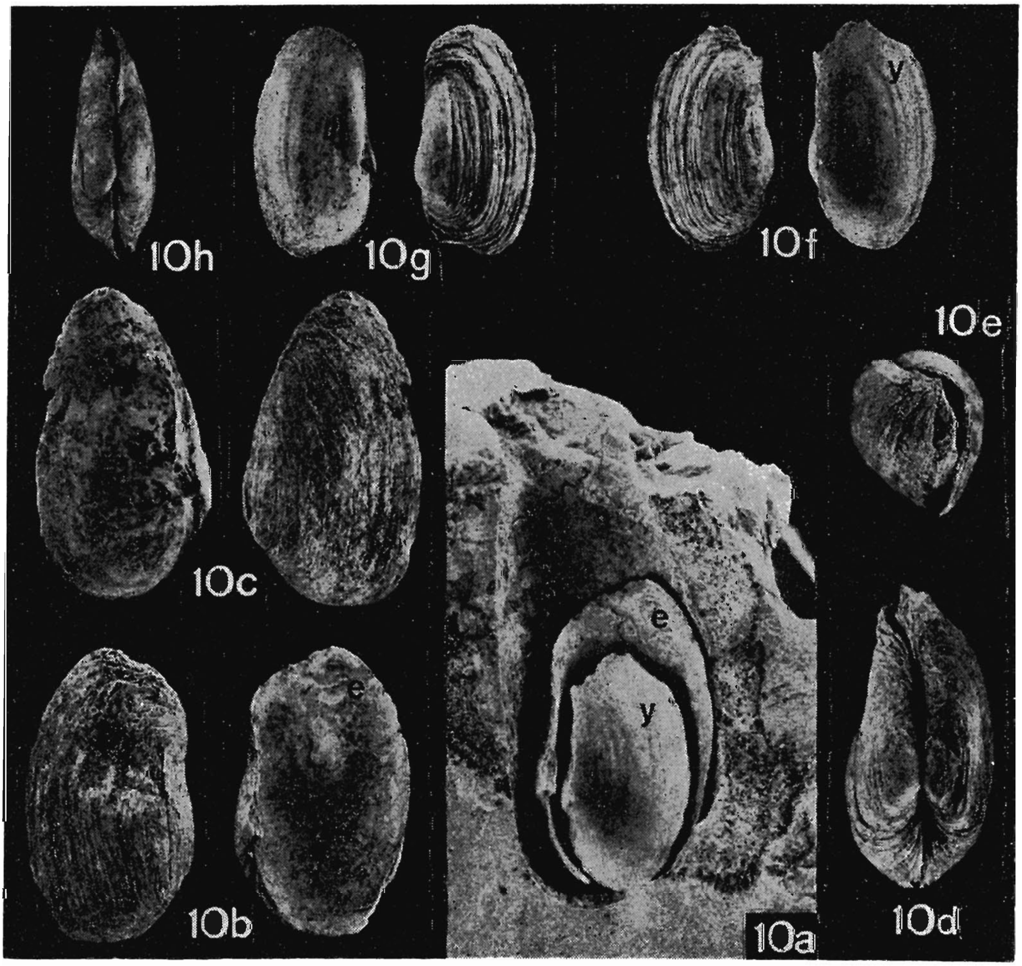
8a Left valve of *Sphenia anatina* (Basterot) in the boring, **8b** left valve in inner and outer views

9a Complete shell of *Sphenia anatina* (Basterot) not removed from the boring (arrowed is a file of incisions within the growth lines), **9b** oblique posterior view to show the two generations of the shells, the younger one being turned in relation to the elder, and a slight splitting of the shell layers

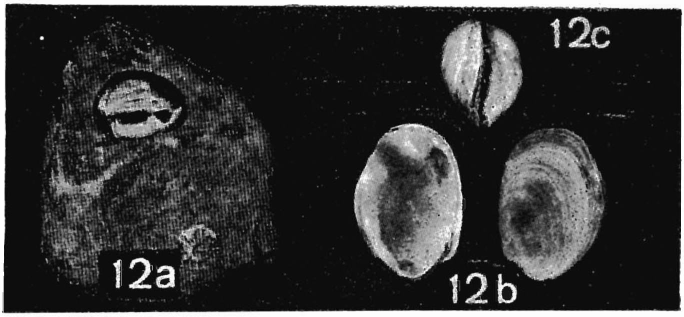
10a Two generations of right valves (e elder, y younger) of *Sphenia anatina* (Basterot) in the boring; **10b** – **10e** elder shell (*10b* right valve in two views, *10c* left valve in two views, *10d* dorsal view, *10e* posterior view), **10f** – **10h** younger shell (*10f* right valve in two views, *10g* left valve in two views, *10h* dorsal view)

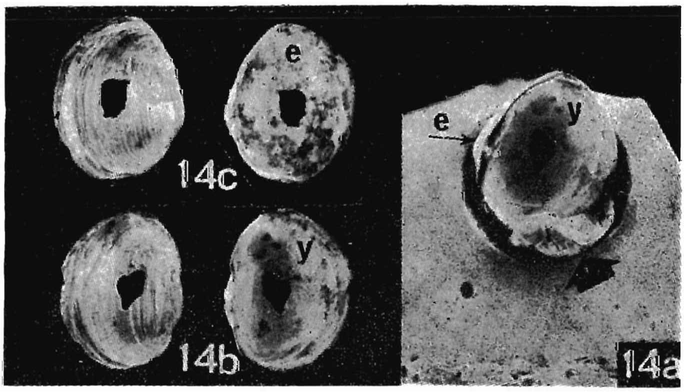






Figs 8—10 .Other examples of the ecotype *lithophagicola* of *Sphenia anatina* (Basterot) that lived in the borings of *Lithophaga lithophaga* (Linnaeus); all ×2, for explanatons more detailed than on the opposite page see the text





Figs 11—14. Examples of the ecotype *jouanneticola* of *Sphenia anatina* (Basterot) that lived in the borings of *Jouannetia semicaudata* (des Moulins); all ×2 (except of *12a*), for explanations more detailed than on the opposite page *see* the text

clear, its ecological variability was almost completely overlooked. This certainly resulted, partly at least, in creation of new species and/or varieties of the subspecific rank. As it is apparent from the illustrations, many of these forms are strictly comparable to the ecotypes distinguished in the Korytnica basin. In this respect, the following discussion will be presented to indicate the forms the morphological features of which resulted from their adaptation to live presumably within the empty borings of particular pelecypods. In the discussed literature there usually are no indications about the mode of the *Sphenia* occurrence, the same as within the collections, and any informations about their finding in the borings are sporadic (Grateloup 1838, p. 68; Hörnes 1870; Benoist 1873, p. 19; De Stefani & Pantanelli 1880, p. 63; De Stefani 1889, p. 16; Friedberg 1938; Goretski 1957; Vialov & Goretski 1965, p. 44).

The presented discussion is organized in the mode of the synonymy of particular ecotypes, by the end of which the list of the unrecognizable forms is also given. Considered are all the forms attributed by the previous authors either to the "*binghami-anatina-testiarum* triangle" or to the associated species, and only the most representative monographs from diverse Neogene basins are taken into account (Hörnes 1870, Fontannes 1881, Sacco 1901, Dollfus & Dautzenberg 1902, Cossmann & Peyrot 1909, Cerulli-Irelli 1909, Friedberg 1934). Of the other papers only those are listed which contain undoubted illustrations (Brocchi 1814, Friedberg 1938, Goretski 1957).

Within the referenced Neogene basins, the recognized ecotypes are attributable to these genera of the rock-boring pelecypods which have been distributed in the Fore-Carpathian basin (*cf.* Radwański 1969, Bałuk & Radwański 1977). It is highly possible however that in the regions others than the latter, different rock-boring genera of pelecypods were responsible for making the borings. The below presented synonymies therefore offer an attempt to the recognition of the four at least, diverse ecotypes which can be attributed either directly to the same genera of the rock-borers as in the Fore-Carpathian basin, or to those (related or not-related) which produced the borings of a very similar morphology (*cf.* Text-fig. 15).

TEXT-FIGURES 11—14 (*see opposite page*)

11a Right valve of *Sphenia anatina* (Basterot) in the boring, **11b** right valve in outer and inner views

12a Complete shell of *Jouannetia semicaudata* (des Moulins) still projecting from the boring inhabited later by *Sphenia anatina* (Basterot); the photo taken *from* Radwański (1969, Pl. 35, Fig. 4), the specimen is the only one presented in its actual size; **12b** left valve (inner and outer views) of *Sphenia anatina* (Basterot) that lived inside the shell of the original occupant shown in *12a*; **12c** posterior view of the complete shell of *Sphenia anatina* (Basterot)

13a Right valve of *Sphenia anatina* (Basterot) in the boring with preserved shell of its original occupant, *Jouannetia semicaudata* (des Moulins), the left valve of which (*arrowed*) disturbed the shell of the squatter; **13b** right valve (outer and inner views) with a deeply incised notch at the place disturbed

14a Two generations of right valves (e elder, y younger) of *Sphenia anatina* (Basterot) in a larger boring with preserved shell of its original occupant, *Jouannetia semicaudata* (des Moulins), the shell of which (visible is its left valve, *arrowed*) did not disturb the squatter; **14b** right valve of the younger generation (outer and inner views), **14c** right valve of the elder generation (outer and inner views)

RECOGNIZABLE ECOTYPES

Ecotype *Gastrochaenicola*

(1) 1901. *Sphenia* cfr. *Binghami* Turt. var. *testarum* (Bonn.) (es. deform.); F. SACCO, p. 33 and Pl. 5, Fig. 34. [This specimen is really not deformed.]

(2) 1902. *Sphenia anatina* Basterot; G.-F. DOLLFUS & P. DAUTZENBERG, p. 70 and Pl. 2, Figs 5—9.

(3) 1909. *Sphenia Paulina* Mayer; M. COSSMANN & A. PEYROT, p. 90 and Pl. 2, Figs 46 and 48.

(4) 1909. *Sphenia anatina* (Basterot); M. COSSMANN & A. PEYROT, p. 88 and Pl. 2, Figs 49—52.

(5) 1909. *Sphenia testarum* Bonelli sp.; S. CERULLI-IRELLI, p. 146 and Pl. 16, Figs 9—10.

(6) 1934. *Sphenia anatina* Bast.; W. FRIEDBERG, p. 22 and Pl. 3, Fig. 8.

(7) 1957. *Sphenia* sp.; V. A. GORETSKI, p. 273 and Pl. 2, Fig. 2.

Ecotype *Aspidopholicola*

(8) 1901. *Sphenia* cfr. *Binghami* Turt. var. *lamellosa* De Stef. & Pant.; F. SACCO, p. 33 and Pl. 5, Fig. 30.

(9) 1902. *Sphenia anatina* Basterot; G.-F. DOLLFUS & P. DAUTZENBERG, p. 70 and Pl. 2, Figs 1—4.

Ecotype *Jouanneticola*

(10) 1881. *Sphenia Tournouëri*, Fontannes; F. FONTANNES, p. 20 and Pl. 1, Fig. 24.

(11) 1901. *Sphenia* cfr. *Binghami* Turton var. *parvinflata* Sacc.; F. SACCO, p. 33 and Pl. 5, 35. [The taxon *parvinflata* was established on this very specimen, regarded by Sacco as probably juvenile or anormal. Dollfus & Dautzenberg (1902, p. 71) regarded it as an accidentally deformed *S. testarum*. According to the present authors' interpretation, a deeply incised notch within this specimen presumably originated due to the presence of a *Jouannetia* shell in the boring when *Sphenia* was growing (*cf.* Text-fig. 13 in this paper).]

(12) 1909. *Sphenia testarum* Bonelli sp.; S. CERULLI-IRELLI, p. 146 and Pl. 16, Fig. 11 (valva sinistra, *deformazione*). [This specimen is really not deformed.]

(13) 1938. *Sphenia anatina* Bast. nova var.; W. FRIEDBERG, p. 19 and Text-fig. 3. [The bivalved specimen is strongly swollen ("*stark gewölbt*" of Friedberg) and ideally matching the shape of the chamber in the *Jouannetia* boring (*cf.* Text-fig. 3*c* in this paper).]

Ecotype *Lithophagicola*

(14) 1814. *Fistulana echinata* Lam.; G. BROCCHI, p. 272 and Pl. 15, Figs 4—5.

(15) 1870. *Saxicava anatina* Bast.; M. HÖRNES, p. 26 and Pl. 3, Fig. 2.

(16) 1901. *Sphenia* cfr. *Binghami* Turt. var. *testarum* (Bon.); F. SACCO, p. 33 and Pl. 5, Figs 31—33.

(17) 1902. *Sphenia testarum* Bonelli mss. sp.; G.-F. DOLLFUS & P. DAUTZENBERG, p. 71 and Pl. 2, Figs 10—13.

(18) 1909. *Sphenia panopaeoides* Mayer; M. COSSMANN & A. PEYROT, p. 91 and Pl. 2, Figs 57—60.

(19) 1909. *Sphenia myacina* Desh. *in coll.*; M. COSSMANN & A. PEYROT, p. 92 and Pl. 2, Figs 66—68. [These two specimens probably represent the half-grown individuals; *cf.* Text-fig. 6 in this paper.]

(20) 1909. *Sphenia Paulina* Mayer; M. COSSMANN & A. PEYROT, p. 90 and Pl. 2, Fig. 47. [This specimen probably also represents an individual half-grown within the boring; *cf.* Text-fig. 6 in this paper.]

(21) 1957. *Sphenia paulini* Mayer; V. A. GORETSKI, p. 272 and Pl. 2, Fig. 3.

UNRECOGNIZABLE FORMS

A remarkable number of the specimens figured by the previous authors are unrecognizable both as to their type of ecological adaptation (ecotype) and even their taxonomic position. These are primarily small specimens, badly illustrated and therefore not displaying any diagnostic features. Some of them certainly belong to other genera. The list of the unrecognizable forms comprises:

1881. *Sphenia Tournouëri*, Fontannes; F. FONTANNES, Pl. 1, Fig. 26.
1901. *Sphenia* cfr. *Binghami* Turt. var. *lamellosa* De Stef. & Pant.; F. SACCO, p. 33 and Pl. 5, Figs 28—29.
1909. *Sphenia Paulina* Mayer; M. COSSMANN & A. PEYROT, p. 90 and Pl. 2, Fig. 45.
1909. *Sphenia Binghami* Turt.; S. CERULLI-IRELLI, p. 145 and Pl. 16, Figs 7—8.
1909. *Sphenia parva* n. sp.; S. CERULLI-IRELLI, p. 147 and Pl. 16, Figs 12—13. [These are probably *Hiatella arctica* (Linnaeus).].
1909. *Sphenia subtriangularis* n. sp.; S. CERULLI-IRELLI, p. 147, and Pl. 16, Fig. 14.

CONCLUDING REMARKS

All the four presented ecotypes of *Sphenia anatina* (Basterot) from the Neogene deposits of Europe, viz. *gastrochaenicola*, *aspidopholicola*, *jouanneticola* and *lithophagicola*, should be regarded as typical representatives of this very species, and they consequently take the four parts of its synonymy. The morphological differences in particular ecotypes are interpreted as resulting only from their adaptation to diverse nestling places, i.e. diverse pelecypod borings they presumably inhabited. A pictured review of the forms included into synonymies of the particular ecotypes (Text-fig. 15) shows their great resemblance to the specimens collected in the Korytnica basin (*cf.* Text-figs 4—14). The distinguished ecotypes, although very distinct in their morphology, resulted only from the environmental adaptation, and have therefore no significance in the taxonomy of the stock which wholly belongs to one paleontological species, *Sphenia anatina* (Basterot).

A similar adaptational diversity takes presumably place also in some at least present-day forms of the genus *Sphenia*. As an example, of the species living along the American coasts, *Sphenia ovoidea* Carpenter is postulated (Abbott 1974) to be an ecologic form of *Sphenia fragilis* (H. & A. Adams).

The specimens of the *Sphenia anatina* stock from the European Neogene, noted as deformed or anormal by the previous authors (Sacco 1901, Pl. 5, Figs 34—35; Cerulli-Irelli 1909, Pl. 16, Fig. 11; Friedberg 1938, Fig. 3) deviate in their shape from typical (average) forms due to their ontogenetic adaptation to the available space within the more or less empty borings left by their original occupants. Such a "deformation" has nothing in common with any destruction either by mechanical agents and/or postburial events.

In consequence, it is stated that in the Neogene deposits of Europe presumably there were occurring no species of *Sphenia* different than *Sphenia anatina* (Basterot). The genus *Sphenia* seems therefore to have been then represented solely by this very species.

The frequency of the particular ecotypes of *Sphenia anatina* (Basterot) within the Neogene deposits of Europe is featured by the dominance of the ecotypes *gastrochaenicola* and *lithophagicola* (see the above synonymies). This is in a good correspondence to the pronounced superior number of *Gastrochaena* and *Lithophaga* amongst the rock-boring pelecypods, as it was recognized in many instances within the littoral zone of the Fore-Carpathian basin (*cf.* Radwański 1969).

COMPARISON WITH THE PRESENT-DAY SPECIES, *SPHENIA BINGHAMI* TURTON

When considering *Sphenia anatina* (Basterot) and *S. binghami* Turton as separate species, it is important to note these similarities of differences which may be decisive for further discussion on the taxonomy and ecology of the both species.

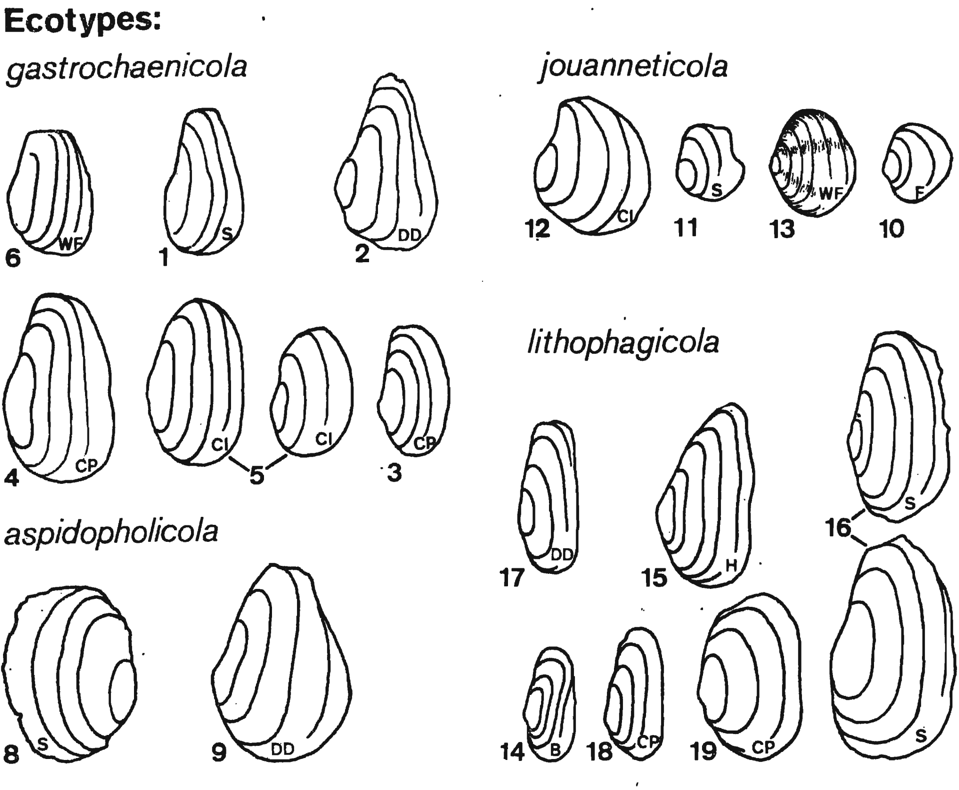


Fig. 15. Comparison of the referenced specimens of *Sphenia anatina* (Basterot) from the Neogene deposits of Europe, to show the four diverse ecotypes of this species (*redrawn from*: Brocchi 1814; Hörnes 1870; Fontannes 1881; Sacco 1901; Dollfus & Dautzenberg 1902; Cossmann & Peyrot 1909; Cerulli-Irelli 1909; Friedberg 1934, 1938)

The numbers are the same as used in the synonymies of particular ecotypes; moreover, the abbreviations for the names of the referenced authors are inserted as follows: **B** — Brocchi, **H** — Hörnes, **F** — Fontannes, **S** — Sacco, **DD** — Dollfus & Dautzenberg, **CP** — Cossmann & Peyrot, **CI** — Cerulli-Irelli, **WF** — Friedberg

The size of the specimens in this figure is the same as used in illustrations to the referenced monographs, except of the item (*13*) which is reduced to its actual dimensions

For comparison of the general shape of particular ecotypes and of the attributable borings *see* Text-fig. 3

The morphological features which could differ *Sphenia anatina* from *S. binghami* Turton are only a few, as follows: shape, sculpture, shell distortion, and size.

The general shape of *Sphenia binghami* Turton is usually characterized as somewhat irregular, but tending to be rectangular or broadly oval (*cf.* Yonge 1951, Tebble 1966). This matches well to many of the investigated specimens of *Sphenia anatina* (Basterot), although more elongated forms of the ecotype *lithophagicola*, and all the forms of the ecotype *jouanneticola* do not fall into such characteristics. For *Sphenia binghami* Turton however there are no data about its adaptation to the borings or crevices they inhabit, and it is therefore difficult to judge which shape is primary and which one results from ecological adaptations of that type as in the Korytnica basin.

Of the sculpture of *Sphenia binghami* Turton, the only feature which has not been recognized in the investigated material is a low ridge that runs from the umbones to the posterior ventral corner; this feature is indicated in some illustrations (Turton 1822, Pl. 3, Fig. 4) and/or descriptions (Tebble 1966), but it is missing in the others (Yonge 1951).

The shell distortion in *Sphenia binghami* Turton is characterized (*cf.* Yonge 1951, Tebble 1966) as displayed by the right valve being the larger and more convex than the left one. A case of the left valve being the larger, as it happens in some of the investigated specimens of *Sphenia anatina* (Basterot), has not hitherto been recorded.

The size of *Sphenia binghami* Turton is generally regarded as small; the largest shells are usually about 10 mm and rarely they reach more, up to the half of an inch in length (Yonge 1951, Tebble 1966). The investigated specimens from the Korytnica basin appear therefore (*see* above) to be larger almost twice. In comparison with the other Neogene specimens from Europe, those from Korytnica are however only slightly larger, and this is with an exception of some of the largest specimens from Italy (*cf.* Sacco 1901, Cerulli-Irelli 1909), and from France (*cf.* Dollfus & Dautzenberg 1902, Cossmann & Peyrot 1909). Of the European Neogene forms, regardless their ecotypes, the largest are those from the Loire Basin (*cf.* Dollfus & Dautzenberg 1902). On the other hand, the maximum size, up to 23—26 mm in length is realized in the two forms included by the present authors into the ecotype *aspidopholicola*, and coming both from the Loire Basin and from Italy (*cf.* Sacco 1901, Dollfus & Dautzenberg 1902: items *8* and *9* in the synonymies and Text-fig. 15 of this paper). It should be noted that all the Neogene forms, those from Korytnica including, lived under a strong influence of tropical and/or subtropical climatic conditions (*cf.* Bałuk & Radwański 1977, 1979), and therefore much warmer than those prevailing in the distribution zone of the present-day *Sphenia binghami* Turton being, moreover, the most commonly investigated exclusively from the British waters (*cf.* Yonge 1951, Tebble 1966).

None of the above presented morphological features cannot be consequently regarded as diagnostic for any of the two *Sphenia* species under discussion.

Another feature mentioned only in *Sphenia binghami* Turton is that the posterior part of the shell is weakly calcified (Yonge 1951). It is difficult to recognize whether this feature was pronounced in *Sphenia anatina* (Basterot) when the specimens were alive, but is to note that a frosting appearance observable in the posteriors in some of the investigated shells (*see* Text-figs 7*b*—*c*, 8*b*, 10*b*, and 11*b*) might have been of such an origin.

Finally, there is also a feature of the splitting of shells which is displayed only by some of the investigated *Sphenia anatina* (Basterot), either in their anterior (*cf.* Text-fig. 7*a*; to some extent also 8*a*) or posterior parts (*cf.* Text-fig. 5*a*; to some extent also 6*a* and 9*b*). This feature, interpreted as indicative of the specimens more advanced in age and/or gerontic, has obviously resulted from the necessity to protect both the shell and body against the rocking and shaking that prevailed all over the biotope. The mechanism of its formation was certainly identical with that one observed in the present-day pelecypods (*cf.* Beedham 1958, Mutvei 1964).

This mechanism realized during the ontogeny of the discussed specimens of *Sphenia anatina* (Basterot) in temporary cassations of the shell secretion at the anterior or posterior parts of the both valves. At these moments the mantle must have stuck off the valves, and the secretion of the new shell, slightly distant to the former one, has successively progressed. The mantle has stuck off from the valve margin as far as the pallial line, the periostracum being then broken somewhere at the periostracal groove, and the new shell has become secreted by the epithelium of the outer mantle surface (*cf.* Beedham 1958, Text-fig. 1; Mutvei 1964, Text-figs 2 and 9). The new originated shell layer remained therefore split in relation to the former shell margin. This temporary secretion of the shell margins is comparable to the regeneration of the damaged parts of the shell (*cf.* Mutvei 1964, Text-fig. 6) and, to some extent, to the formation of the pearls (*cf.* Mutvei 1964, Text-fig. 7). The stronger splitting of the posterior part in the investigated shells (*cf.* Text-fig. 5) resulted simply from the pallial line being there the more distant to the valve margin than in the anterior part. Anyway, the process of the shell enlarging by its splitting could have lasted as long as the specimen filled the available room in the boring either completely, or to the extent sufficient to anchorage itself tightly in the deeper parts of the boring (*cf.* Text-figs 5—9).

It is to note that the discussed splitting of the shells, in result of which the valves at their posteriors are contacting closely (*see* Text-figs 5*e* and 6*e*), is responsible for the disappearance of the shell gap, the feature being typical (*cf.* Yonge 1951, Tebble 1966) of the present-day *Sphenia binghami* Turton. It is therefore thought that in the investigated biotope the specimens of *Sphenia anatina* (Basterot) were so well adopted to live within the borings that they could open the whole shells safely to project their siphons. This may be a general rule for those *Sphenia* which live in undamaged borings, the space of which due to their small apertures is almost fully protected against unfavourable environmental conditions. Such as ecological influence for the present-day *Sphenia binghami* Turton has not been studied as yet.

The general ecological requirements of both *Sphenia anatina* (Basterot) and *S. binghami* Turton remained however the same. The investigated *Sphenia anatina* (Basterot) lived in the Korytnica basin just offshore, and this is the zone from which *S. binghami* Turton ranges down to moderate depths, the latter having been missed along these parts of the Korytnica shores (*cf.* Bałuk & Radwański 1977, 1979). As noted by Yonge (1951), *Sphenia binghami* Turton occupies the same biotope as *Hiatella arctica* (Linnaeus), and an identical situation happened in the Korytnica basin.

The recognition of the other relations and of the ecological heritage in the present-day species *Sphenia binghami* Turton which has directly developed from the investigated Neogene species *Sphenia anatina* (Basterot) needs a separate study.

Acknowledgements. Warm thanks are offered to Dr. D. Mori, Torino, for supplying xerox-copies from the manuscript by Bonelli (1834) and some older Italian papers, as well as for associated information; to Dr. P. L. Cook, British Museum (Natural History), for making a copy from the monograph by Turton (1822); to Dr. J.-C. Plaziat, University Paris-Sud, for making a similar copy from the monograph by Basterot (1825) and from some older French papers, always with careful information included. Mrs. K. Zielińska is acknowledged for making photos of the investigated specimens (Text-figs 4—14).

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