Mesozoic Brachiopods of Alpine Europe
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PYGOPID BRACHIOPODS AND TETHYAN MARGINS

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ABSTRACT—Paleogeographic distribution patterns of four perforated species of the Upper Jurassic–Lower Cretaceous Pygopidae (Brachiopoda) were studied in the Alpine–Carpathian–Balkan region. *Pygope catulloi* and *P. diphya,* bearing small perforations near their umbones lived in the southern margin of Tethys, while *Pygope janitor* and *Pygites diphyoides* with large, central perforations lived on the northern margin. Their separation was caused either by a wide Penninic ocean acting as a barrier, or rather by the adaptation of the forms with smaller perforations to the nutrient-poor environment of the southern margin.

INTRODUCTION

Peculiar forms of brachiopods are contained in the family Pygopidae MUIR-WOOD 1965. Adult specimens bear perforations in the centre of valves. This conspicuous feature considerably helped their identification and provides great support for paleogeographic studies. Mere listing of faunas can be considered as reliable data, thus significantly increasing the number of localities available for paleogeographic study.

Four species of two genera have been considered in the present study (Text-fig. 1):

Pygope diphya (VON BUCH, 1834),
Pygope catulloi (PICTET, 1867),
Pygope janitor (PICTET, 1867), and
Pygites diphyoides (D'ORBIGNY, 1849).

Recently these four species have been revised by DIENI and MIDDLEMISS (1981), listing most figured specimens in synonym lists. Since these publications provide few data compared to the large number of paleogeographic units and to the size of the area discussed, a number of specimens in lists or mentioned in descriptive texts were also considered. Some of the latter have been revised by GEYSSANT (1966), probably after extensive revision of localities and museum material.

Although both AGER (1971) and MIDDLEMISS (1973) have expressed skepticism towards the use of lists of faunas for paleogeographic studies, we think that perforate pygopids are highly conspicuous, therefore their mentioning by non-paleontologist field geologists should be considered reliable.

The present review is limited to two groups established by JARRE (1962): the *Pygope janitor* + *Pygites diphyoides* group, bearing large, central perforations, and the *Pygope catulloi* + *Pygope diphya* group, bearing minor perforations displaced towards the umbo. Ranges of these species are shown in Text-fig. 2.

An early version of the present paper has been published in Hungarian (KÁZMÉR 1990).

PREVIOUS STUDIES

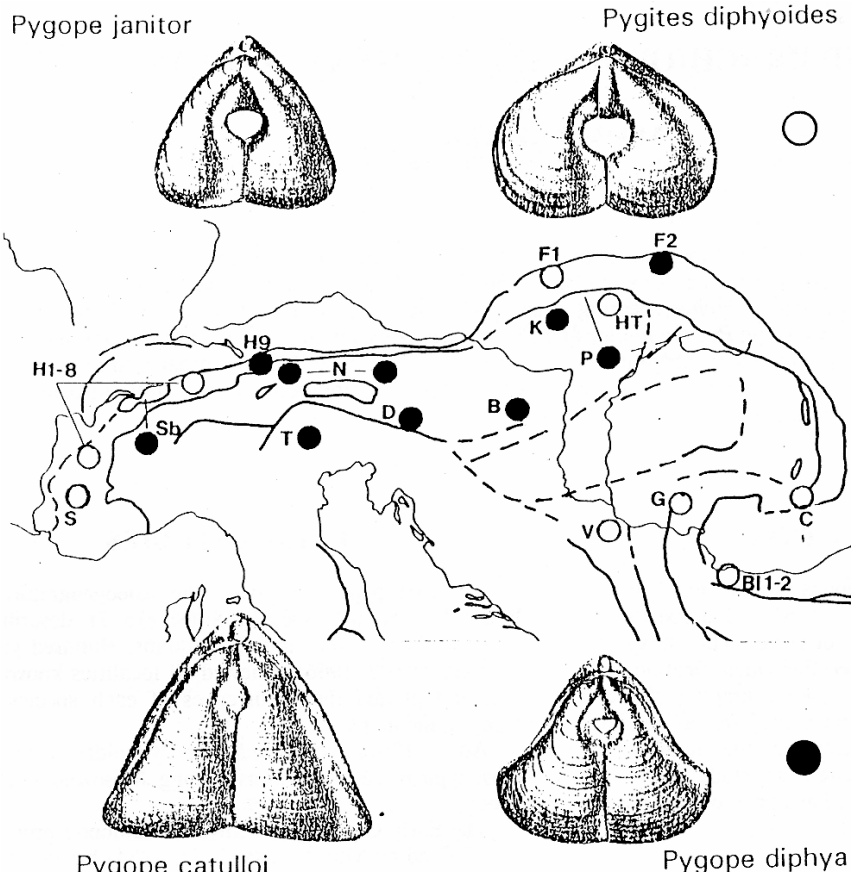
The first paper discussing the paleogeography of Pygopidae was published by SUESS (1867), describing localities in the Alps and Carpathians. Hundred years later GEYSSANT (1966) reviewed all localities known to her, and plotted the occurrences of each species on topographic maps.

AGER (1967) recognized that Pygopidae were the most typical Tethyan forms among Mesozoic brachiopods.

The Early Cretaceous Tethyan brachiopod province was defined by MIDDLEMISS (1973, 1984) based on the following forms: *Pygope, Pygites, Antinomia* (later regarded as *Pygope,* see DIENI and MIDLEMISS 1981), *Nucleata* and undescribed species belonging to the groups *"Terebratula" subsella* and *"Terebratula" moutoniana.* He recognized that the Early Cretaceous provinces in Europe were arranged more or less parallel to the northern margin of Tethys; their location was determined by the distribution of land and sea as well as the paleoclimate (temperature, salinity). He showed the connection between Tethyan faunas and the Alpine fold belt, and recognized that their northernmost occurrences follow the northern boundary of the Alpine fold belt (with some exceptions) from the Betic Cordillera to the Kopet Dagh.

The disjunct areas of *janitor* vs. *diphya* + *catulloi* were clearly observable on the map series of GEYSSANT (1966). VÖRÖS (*in* SANDY 1988) provided an interpretation, based on earlier studies with plate tectonic approach (VÖRÖS 1977, 1980, 1982, 1987): *diphya* occupied the southern, Apulian margin of Tethys (the Mediterranean microcontinent), while *janitor,* originating from there, dispersed on the northern margin.

This novel idea, published by SANDY (1988), is extended here for the species groups *diphya* + *catulloi* and *janitor* + *diphyoides*. SANDY (1988) listed 24 localities ranging from the Massif Central to the Caucasus; in the present paper 62 localities between the Subalpine chains and the Balkans are discussed.



Text-fig. 1—Distribution of four pygopid species in the Alpine-Carpathian-Balkan region.
Brachiopods in the top bear large, central perforations, while the two at the bottom have smaller, umbonal ones (after KÁZMÉR 1990).

METHODS

Most localities from the Subalpine chains in France through the Alps and Carpathians to the Balkan Mountains in Bulgaria, containing published pygopid faunas are listed below. The localities were assigned to tectonic units – mostly nappes or nappe systems – (as indicated by geological and tectonic maps, regional monographs, rarely by the paleontological paper itself), then the tectonic units were assigned to paleogeographic zones of the Tethys realm.

DATA BASE

The following data are listed for each locality:
— name, geographic location,
— age,
— rock (lithostratigraphic unit),
— presence of perforate pygopids (referred to by specific name only),
— associated fauna,
— tectonic unit (down to the nappe level, where possible),
— paleogeographic zone,
— discussion.

Localities are grouped by paleogeographic regions (Subalpine, etc.). Their code is used on Text-figs. 1 and 2.

Subalpine region (SE France) = S

Most of the region extending between the Western Alps and the Cévennes is occupied by the Vocontian Trough (Fosse vocontienne). Rich, *diphyoides*-containing fauna inhabited the interior and the slopes of the basin. MIDDLEMISS (1973) recognized the Tethyan character of the fauna. The Jura-type, shallow marine faunas inhabit the surrounding plateaux (SANDY 1986).

S.1. Berrias (Ardeche) (D'ORBIGNY 1847–1851; PICTET 1867). Vocontian Trough. Neocomian compact limestone: many *diphyoides*.
S.2. Barreme (D'ORBIGNY 1847–1851). Vocontian Trough. Neocomian: *diphyoides.*
S.3. Cheiron (D'ORBIGNY 1847–1851) Southern margin of the Vocontian Trough. Neocomian: *diphyoides*.

Helvetic zone = H

A northern extension of the Vocontian Trough, containing similar deep marine formations, extends to

the north as far as Geneva. Here we assign it to the Helvetic zone of the Alps, although it occupies a somewhat more external position. Tithonian faunas contain *Pygope janitor.*

H.1. Porte-de-France (near Grenoble in the Dauphiné Alps) (PICTET 1867). Black limestone bed and grey beds: *janitor* (4 figured specimens).
H.2. Lémenc (near Chambéry) (PICTET 1868): *janitor.*
H.3. Talloires (Annecy SE) (EBRAY 1872, *fide* NEUMAYR 1873): *janitor* (determined by PICTET).

Faunas of the Helvetic zone s.str. occur between Lake Geneva and Vorarlberg. Tithonian strata contain *Pygope janitor.*

H.4. Riondonnaire (near Châtel-Saint-Denis, Montreux N) (PICTET 1867; FAVRE 1880). Fribourg Alps. White, marly, Tithonian limestone: *janitor.*
H.5. Bakerboden (Justisthal, Thun Lake NE) (PICTET 1867): *diphyoides.*
H.6. Dat (Fribourg Alps) (FAVRE 1880). White, marly, Tithonian limestone: *janitor.*
H.7. Prayouds (Fribourg Alps) (FAVRE 1880). White, marly, Tithonian limestone: *janitor.*
H.8. Brienz (GERBER 1930). Light, Tithonian limestone: *janitor.* Valanginian marl: *janitor.*
H.9. Au (Bregenzer Wald), Säntis Nappe (MYLIUS 1911). Upper Jurassic "Auerkalk" (Au Limestone), Stramberg horizon with *Calpionella alpina.* Listed: *diphya.* Light grey, Valanginian marly shale: *diphyoides.*

Subbriançonnais = Sb

Northern slope of the Briançonnais ridge.

Sb.1. Grandvillard (Fribourg Alps), Klippendecke = nappe des Préalpes médianes (Médianes plastiques) (FAVRE 1880): *catulloi* or *diphya.*

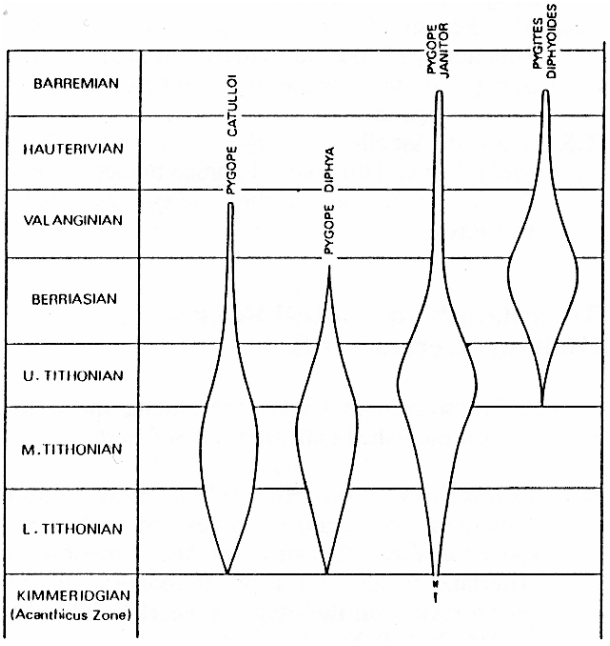
Northern Calcareous Alps = N

Three localities have been selected from a large number (TRAUTH 1948); the rest also contains *Pygope diphya.*

N.1. Ruhpolding (ZITTEL 1870). Red marble with *Terebratula sima* (i.e. *diphya*).
N.2. Salzburg (SUESS 1867): "une trace de... marbres rouges a *Terebratula diphya*".
N.3. Gresten (STELZNER 1865). Neocomian limestone: *diphyoides* in Fleckenkalk (spotty limestone) (determined by SUESS).

Drauzug (Drau Range) = D

A single, poorly preserved specimen from the Jurassic sequence of the Northern Karavanka Mts.



Text-fig. 2—Stratigraphic range of the selected pygopid species (after DIENI and MIDDLEMISS 1981, modified).

D.1. Wildensteiner Wasserfall (Northern Karavanka Mts.) (SCHRÖDER 1988). Kimmeridgian-Tithonian, red limestone with aptychi: a poorly preserved steinkern, probably *catulloi* or *diphya.*

Trento plateau (Southern Alps) = T

A large-scale revision of Pygopidae has been carried out by DIENI and MIDDLEMISS (1981) on a collection of specimens from the Veneto Alps. This region is part of the terminal Jurassic Trento plateau, which has been reduced to the western margin of its former extension, sloping eastward towards the foot of the true neritic Friuli platform (WEISSERT 1981). Further papers show that the Pygopidae fauna occupied significantly larger part of the former Trento plateau.

Although the species composition of each locality of DIENI and MIDDLEMISS (1981) is not known, the total fauna is dominated by *catulloi* + *diphya* (106 specimens); the *janitor* + *diphya* group is represented by 1–1 "vagabond" specimens only. The number of specimens is not known at the rest of the localities.

T.1. Monte Baldo (BENECKE 1866). Diphyakalk, Schichten den *Ammonites acanthicus*: *diphya* (60 specimens).
T.2. Veneto Alps (DIENI and MIDDLEMISS 1981). Trento plateau and the western margin of the Belluno basin. Ammonitico rosso and Biancone: *catulloi* (74 specimens), *diphya* (32), *janitor* (1); Valanginian–Hauterivian marl: *diphyoides* (1).
T.3. Sette Communi (MUNIER 1891). Tithonian: *diphya;* Berriasian: *janitor.*

T.4. Alpi Feltrine (near Belluno) (DAL PIAZ 1907). Tithonian, red, nodular, cherty limestone: *diphya*. Upper Tithonian, white, marly, cherty limestone: *diphya* + *janitor*.

T.5. Quarti di Asnello (Rovero) (NICOLIS and PARONA 1886). Upper Tithonian "Titonico bianco": *janitor* (2), *diphya* from 4 localities and *catulloi* cited as a variety.

Transdanubian Central Range (Bakony, Gerecse) = B

The Transdanubian faunas are among the richest ones; the few published data are reviewed here .

B.1. Tardosbánya, Szél Hill (VIGH 1961). Lower Tithonian, red, compact limestone with yellow spots: *diphya*. So-called *diphya* limestone in "Hierlatz" facies with dwarf ammonoids: *janitor*. (For a review on the usage of 'Hierlatz limestone' see VÖRÖS 1991).

B.2. Hárskút, Közös-kúti Ravine (FÜLÖP 1964). Barremian, sandy marl: *diphyoides*. Valanginian Biancone: *diphyoides* and *dilatata* (considered *catulloi* by DIENI and MIDDLEMISS 1981).

B.3. Zirc, Istenes-malom (FÜLÖP 1964). Berriasian, light red to white limestone with tintinnids and rare crinoids: *dilatata* (considered *catulloi* by DIENI and MIDDLEMISS 1981).

B.4. Szentgál, Városlõd, and Herend (three localities of VADÁSZ 1911). Lower Tithonian, red or yellow, locally brecciated limestone: *diphya*; BÖCKH (1874): red limestone with *diphya*; ZITTEL (1870) lists a specimen of *catulloi*.

B.5. Tata, Kálvária Hill (FÜLÖP 1976). Berriasian: *Pygope sima* (=*diphya*?); VIGH (1981): Upper Tithonian: *P. discissa tenuis* (=*catulloi*), *P. vomer*.

B.6. Agostyán (VIGH 1961). Dark red, argillaceous crinoidal limestone: *diphya*.

Klippen and olistoliths of the Carpathian flysch belt = F

The three localities listed below are insufficient for establishing a comprehensive paleogeographic picture; localities of the same age, but not containing Pygopidae should be considered in a further study.

F.1. Štramberk. Olistolith(s) in the Silesian nappe. The classical uppermost Tithonian–Valanginian Nesselsdorf Limestone (new name: Koprivnica Formation): *diphyoides* (248 specimens) (NEKVASILOVÁ 1980). REMES (1899) *janitor* (1). Further references: SUESS (1858, under the name *diphya*), NEKVASILOVÁ (1969), HOUSA (1975).

The Štramberk klippe bears a Helvetian-type – or rather a Vocontian-type – fauna with the almost exclusive occurrence of *diphyoides*. Other klippen in practically the same tectonic zone (e.g. Ernstbrunn, Mikulov) do not contain any pygopids and the rest of the fauna shows less Alpine characters. Probably the Štramberk sequence has been deposited farther away from the European shelf than the rest of the klippen in the same tectonic unit. The similar idea of TOLLMANN (*fide* HOUŠA 1975) was corroborated by the paleogeographic reconstruction based on microfauna and carbonate microfacies (ELIÁŠ and ELIÁŠOVÁ 1984). The Štramberk klippe was part of the hypothetical Baška cordillera, separated by a flysch basin from the European continental margin bearing the Ernstbrunn zone.

F.2. Bachowice (KSI¥¯KIEWICZ 1956). Paleozoic to Cretaceous olistoliths in a Lower Tertiary volcano-sedimentary matrix. The Bachowice tectonic scale is the outermost unit of the Subsilesian nappe. Associated ammonite fauna is of Mediterranean character; there are other molluscs in the Tithonian white, fine-crystalline limestone with sponge spicules: 1 complete *diphya* and several fragments (*diphya* or *catulloi*).

The Jurassic fauna at Bachowice displays a uniquely Mediterranean character (KSI¥¯KIEWICZ 1956) within the Carpathian belt. Unfortunately, no comparisons with the Bakony faunas have been made. The following reasons can be considered for the exotic position of the Mediterranean fauna very near to the NW European Kraków localities:

– There was an ocean N of the Pieniny Zone and of the Baška cordillera in the Jurassic, deeper than that, hosting a more Mediterranean fauna;

– the olistoliths derived from an uppermost Gemeric-type nappe of the Western Carpathians (similar to the Ultra-Styrian nappe of TOLLMANN 1987);

– during the lateral displacement of the Pieniny Klippen Belt (KÁZMÉR and KOVÁCS 1989) minor crustal fragments bearing Mediterranean faunas have been emplaced N of the Pieniny units;

– olistoliths derived from an unknown Mediterranean unit (e.g. the Pieniny Exotic Cordillera = Andrusov Ridge, BIRKENMAJER 1988) suffered long transport by turbidity currents along the flysch trough.

F.3. Svidovetz (south of Körösmezõ = Yasinya (HAUER and RICHTHOFEN 1859). Klippen in the front of the Porkuletz nappe system. Large boulders of white limestone embedded in basalt: frequent *diphya*. According to PICTET (*in* SUESS 1867, footnote), it is probably *janitor*.

At Svidovetz we can recognize the presence of pygopids only. It may be a Štramberk- or Bachowice-type olistolith or klippe, or member of another, yet unknown facies unit.

Inner West Carpathians
High Tatric unit = HT

HT.1. Osobita (Western Tatra) (KOTANSKI and RADWANSKI 1959). Tithonian crinoid-brachiopod limestone occurring nowhere else in the Tatra ("Tithonian Hierlatz"). The figured *diphya*-looking specimens are considered as *janitor* by JARRE (1962) and BARCZYK (1972). DIENI and MIDDLEMISS (1981) suggest a possible Berriasian age for the locality.

Krížna nappe = K

Only scattered data are available from lists of faunas.

K. 1. Èierna Lehota (Strážov Mountains) (MAHE¼ 1982). Upper Dogger–Berriasian red limestone: *diphya*; Tithonian pink–grey micritic limestone: *catulloi* (determined by PEVNÝ).

Pieniny Klippen Belt = P

The richest pygopid fauna occurs here besides the Subalpine–Helvetic faunas. The classical descriptions need revision; an earlier attempt (BARCZYK 1972) was further revised by DIENI and MIDDLEMISS (1981). A first glance suggests that the fauna is dominated by *diphya* with minor amount of *janitor.*

P.1. Vršatec (SIBLÍK 1979). Czorsztyn nappe, Tithonian, light, argillaceous limestone: *diphya* (21 specimens); Berriasian, red crinoid limestone: *diphyoides* (3). DIENI and MIDDLEMISS (1981) doubt the latter determination, because even the author (SIBLÍK 1979) recognized the large, central perforation.

P.2. Dohnany (near Trenèín). Collection of the Department of Paleontology, Eötvös University: *catulloi* (3) under the name *diphya* and juvenile *janitor*? (2)

P.3. Zázrivá (Orava). HAŠKO and POLÁK 1979). Orava succession, Tithonian limestone with calpionellids: *diphya* (in a list only).

P.4. RogoŸnik (ZITTEL 1870): *diphya.* NEUMAYR (1871): white, brecciated limestone *diphya* + *sima.* ZEJSZNER (1846): 7 species; a number of specimens of *diphya* accepted by DIENI and MIDDLEMISS (1981). PUSCH (1837): *diphya.* BIRKENMAJER (1963): Czorsztyn succession, Tithonian red RogoŸnik lumachella: *diphya*, white RogoŸnik lumachella: *diphya* + *sima.*

P.5. Záskalie (Babierzowskie Ska³ki) (NEUMAYR 1871). The most important and richest locality in the Pieniny Klippen Belt. Red limestone with ammonoids: *diphya*. BIRKENMAJER (1963): Tithonian, red RogoŸnik lumachella: *diphya* + *sima*.

P.6. Czorsztyn (BIRKENMAJER 1963). Red calpionellid limestone: *diphya* + *sima.* BARCZYK (1972) Tithonian brachiopodal and crinoidal limestone: *diphya* (37), *catulloi* (9), *janitor* (28) (several of the latter ones seems to be *catulloi*). DIENI and MIDDLEMISS (1981) rejected the identification of several specimens of *diphya*, without further comments.

P.7. Biała Woda (BIRKENMAJER 1963). Tithonian brachiopodal-crinoidal limestone: *diphya* + *sima.*

P.8. Falsztyn (BIRKENMAJER 1963). Tithonian brachiopodal limestone: *diphya* + *sima.*

P.9. Maruszyna (NEUMAYR 1873). Brick-red limestone: *diphya.*

P.10. Jarabina (Spiš klippen) (NEUMAYR 1871). Pink limestone with ammonoids: *diphya*.

P.11. Kyjov (Sariš klippen) (HAUER and RICHTHOFEN 1859; NEUMAYR 1871). Whitish grey limestone with rich fauna: *diphya* + *sima.* Green, red, grey crinoid breccia (RogoŸnik breccia): *sima.* NEUMAYR (1873): *janitor.*

P.12. Plavec (Sariš klippen) ((HAUER and RICHTHOFEN 1859). Red and white limestone, similar to the RogoŸnik Klippenkalk: *diphya.* NEUMAYR (1873): *janitor.*

P.13. Pereèin (Transcarpathian Ukraine) (KRUGLOV 1971). Tithonian, white, porcelaneous, chert-free Svaljava beds: *janitor.* Grey, siliceous or cherty, compact limestone: ex gr. *diphya.*

Mecsek = M

VADÁSZ (1935) lists *janitor*, *diphya*, and *dilatata* from the Lower Tithonian red, cherty limestone (without precise indication of locality).

Vardar Zone = V

The locality near Belgrade lies between the Carpathians and the Dinarides (DIMITRIJEVIÆ 1982), within the Vardar zone in a very broad sense.

V.1. Rakovica monastery (GOÈANIN 1938). Tithonian limestone (Stramberger Tithon): *janitor.*

Getic nappes = G

G.1. Anina (Reºiþa–Moldova Nouã zone of the Southern Carpathians). Bradet Limestone (NÃSTÃSEANU and SAVU 1968). ROTH (1891): yellow, fine-grained limestone: *T. janitor* (ROTH's note: "it should be noted, that no *Terebratula diphya* has been found in the quarry"). BUCUR and STRUSIEWICZ (1988): Upper Kimmeridgian–Lower Portlandian Bradet Limestone: *janitor* (first figured here but already mentioned by UHLIG (1881)).

Ceahlău nappes = C

C.1. Doftana Valley (AVRAM 1976): *diphya* (according to DIENI and MIDDLEMISS 1981: *janitor*). From Tithonian limestone blocks embedded in Barremian conglomerates in the upper part of the Sinaia Flysch. The Upper Hauterivian–Barremian breccia-conglomerate unit is part of the innermost, Bratocea digitation of the Ceahlău nappe (SĂNDULESCU et al. 1981).

C.2. Gîlma Ialomiþei (Bucegi Mts.) (PATRULIUS 1969). Kimmeridgian–Lower Tithonian klippe in Barremian flysch *(*Bratocea digitation); red, brecciated, limestone with microoncoids: *janitor*.

C.3. Bucegi Mts. (JEKELIUS 1916). Light, nodular limestone: *janitor* (2).

C.4. Leaota–Bucegi Mts. (PATRULIUS et al. 1968). Hauterivian, marl;, glauconitic limestone: *diphyoides*. The locality belongs either to the autochthonous sedimentary cover of the Leaota massif or the the Ceahlău nappe.

Eastern Carpathians
Transylvanian nappes = Ts

Ts. 1. Gyilkos-kõ (Baia Bãlan). (NEUMAYR 1873). Acanthicum beds: *janitor* or *diphya*. More than 100 specimens from the upper part of green, sandy limestone. HÉBERT (1877): at least 1 *janitor* in the material.

Balkan Mountains

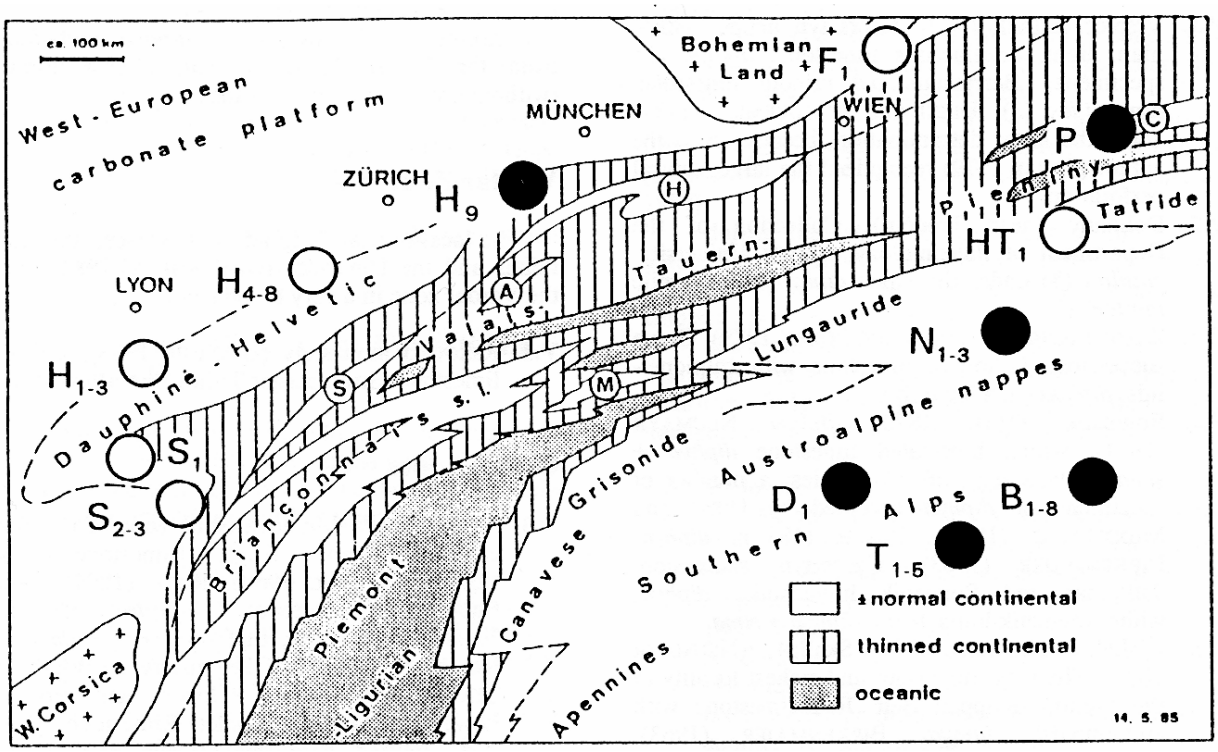
The locality at Belotinci (in the Central Moesian basin) has been part of the European continental margin. The other three localities cannot be assigned to any well-determined tectonic unit now. Although the 1:500,000 Geological Map of Bulgaria and DERCOURT and RICOU (1987) clearly indicates the occurrence of lateral displacements and nappes; SAPUNOV et al. (1988) does not take these into account when plotting the otherwise very detailed paleogeographic map series of the Bulgarian Jurassic.

Bl.1. Belotinci, Nechinska Bara. TCHOUMATCHENCO (1978): *janitor* (6). Pre-Balkan? The locality is part of the Upper Jurassic–Lower Cretaceous basin of Central Moesia (SAPUNOV et al. 1988).

Bl.2. Gorna Luka near Vratsa (AGER 1975). Aphanitic, organogenic, nodular limestone at the Jurassic/ Cretaceous boundary: *diphyoides*. Vratsa horst (SAPUNOV et al. 1988).

Bl.3. Isker gorge (Stara Planina) (ZLATARSKI 1908). Callovian–Barremian carbonate group of the West Balkan. aphanitic, compact, organogenic limestone: *diphya.* Unnamed basin between the Vratsa and Dragoman horsts SAPUNOV et al. 1988).

Bl.4. Javorets (Gabrovo, Pre-Balkan) (ZLATARSKI 1908): *diphya*. Valanginian–Hauterivian Kamèija Formation of Berriasian–Hauterivian Hanevci Group (according to the 1:500,000 Geological Map of Bulgaria).



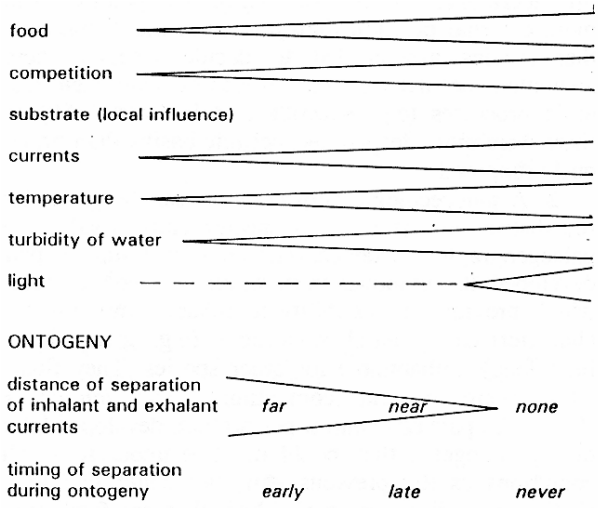
Text-fig. 3—Localities of the *janitor* + *diphyoides* group (central perforation) (open circles), and the *catulloi* + *diphya* group (umbonal perforation) (solid circles) in a palinspastic sketch of the terminal Jurassic Tethys (base map after LEMOINE and TRÜMPY 1987).

REMARKS ON PALEOECOLOGY

Members of Pygopidae were well adapted to deep marine conditions, where moderate current activity supplied little food to the animals (VOGEL 1966). Probably they lived on seamount slopes and in the surrounding basins (GRAHAM 1983). However, some localities yielded pygopid fauna together with shallow marine fossils (e.g. Štramberk). Here the latter ones were probably redeposited into the deep marine environment favoured by the Pygopidae.

AGER (1971) suggested that agitation of water or its absence – shown by the type of the sediment – may have been a more important factor in the distribution of Pygopidae than the depth of the sea.

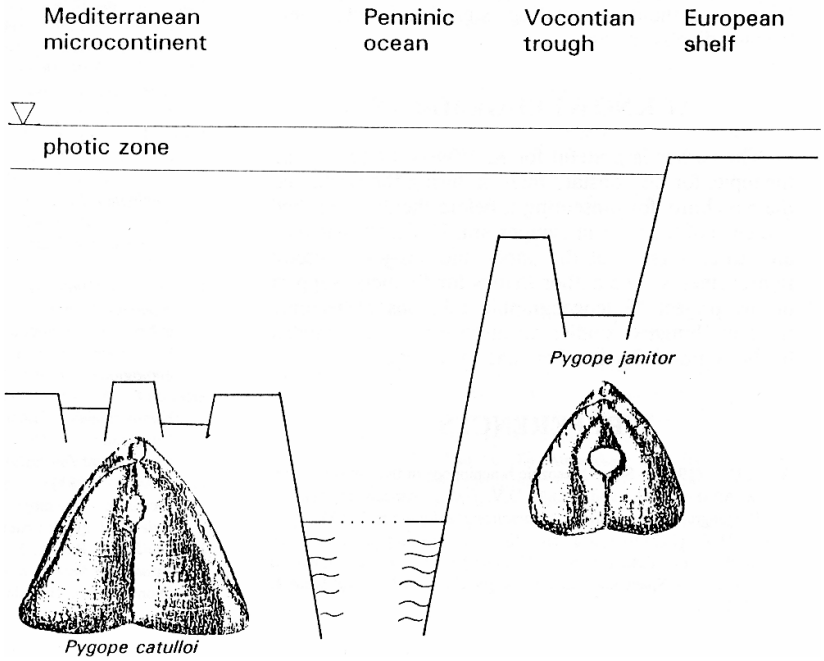
MIŠÍK (1974) considered the West Carpathian localities (e.g. Osobitá, RogoŸnik) as neritic, although he admitted that they occur in calpionellid limestone indicating significantly greater depths (Èierná Lehota). To solve the contradiction he suggests that the latter may have been a relatively shallow region within the pelagic environment where the calpionellids lived.



Text-fig. 4—Top: postulated trends of ecological factors affecting pygopid distribution in a SE–NW profile between Apulia (the Mediterranean microcontinent) and Europe. Bottom: the degree of separation of inhalant and exhalant currents in brachiopods, measured by the distance of perforation from the umbo.

DISCUSSION AND CONCLUSIONS

1. The *diphya* + *catulloi* group, bearing a small, umbonal perforation occur on the southern, Apulian margin of the Tethys (Mediterranean microcontinent: Trento plateau, Northern Calcareous Alps, Bakony) (Text-fig. 3). The *janitor* + *diphyoides* pair with large, central perforation lived on the northern margin of Tethys (Vocontian trough, Helvetic zone). A few exceptions (southern species in the northern Subbriançonnais zone and in the Helvetic of Vorarlberg, a few northern "vagabond" specimens on the Trento plateau) do not interfere with the overall picture (VÖRÖS in SANDY 1988). The barrier between the northern and southern provinces was the Penninic ocean, too wide for crossing by short-lived brachiopod larvae.



Text-fig. 5—A hypothetical SE–NW cross-section from the southern to the northern margin of Tethys (not to scale). Pygopids with umbonal perforations probably lived in deeper water (supplying less food) than those with central perforations

This general rule becomes less clear in the Carpathians. The *diphya*-bearing fauna of Bachowice is in a more external position than the *diphyoides*-bearing Štramberk one; *diphya* of the Pieniny Klippen Belt is in more external position than *janitor* of the Tatra. Further studies are needed to decide whether these anomalous occurrences were caused by subsequent tectonic processes (e.g. KÁZMÉR and KOVÁCS 1989) or there were more deep-water, oceanic basins than previously supposed.

2. A paleoecologic consideration can be given for the distribution of the two species pairs besides the paleogeographic evidence. The *catulloi* + *diphya* pair developed the umbonal perforation at a young stage, which provided a possibility to inhabit environments characterized by harsh conditions (e.g. great depth, little food), unhabitable for other species. They flourished there without competitors. The *janitor* + *diphyoides* pair had central perforation, developed later during ontogeny; they could not live under so harsh conditions as the previous pair, but could live in a shallower environment probably with more food, successfully competing with other brachiopods and other animals. However, here the *catulloi* + *diphya* pair, successful in deep water, could not take up competition (Text-fig. 4).

If these complex environmental differences are oversimplified to difference in water depth, one can say that the recognition of paleogeographic differences by VÖRÖS (*in* SANDY 1988) implies that the southern, Apulian margin (on the Mediterranean microcontinent) provided deeper water habitats for pygopids than the northern margin (Text-fig. 5).

Applying this speculation for the Carpathian region, there the seemingly anomalous distribution of Pygopidae can be explained by environmental and depth differences without postulating significant subsequent tectonic displacements.

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