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Morphology and function of the perforation (keyhole) in Pygopidae (Terebratulida, Brachiopoda)

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Abstract – For examination of their internal features, 14 specimens of *Pygope* and *Antinomia* from the Bakony Mts. were sectioned longitudinally and transversely. The perforation of the dorsal valve continues in a long tube which joins a short collar of the ventral valve. In slightly opened shells a narrow gap appears between the collar and the tube. The posterior part of the gap is near the rim of the ventral collar. In the new model of the feeding mechanism of pygopides this feature involves that the exhalant jet passed directly over the ventral entrance of the tube. The propulsion of the exhalant jet might generate a low-pressure regime in the tube. An advantage of this process is increasing circulation through the mantle cavities of the lateral lobes, by the sucking effect of the low-pressure regime. The pygopide might lift itself from the mud by contracting the adjustor muscles of its pedicle. The underlying unconsolidated mud is stirred up and the fine grained organic-rich material may be sucked into the low-pressure area of the tube. Then this suspended matter might be ejected off the tube and the food might be recycled by the inhalant currents. With 14 figures and one table.

Key words – Bakony Mts., feeding, food recycling, internal morphology, pygopides

INTRODUCTION

Brachiopods have been adapted to various marine bottom habitats during the last more than 500 million years of the history of life, and developed many curious shell morphologies from alate to coarsely spinose, or flatly cemented to conically rooted (Ager 1965, 1967; Rudwick 1970). One of the most perplexing morphological invention in brachiopod history, a broad medial hole perforating through both valves, appeared at 160 million years ago among the Pygopidae. In contrast to the many specialized brachiopod morphologies which recurred several times in the course of the Phanerozic, this phenomenon was never recorded before the Late Jurassic and after the Early Cretaceous.

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The hollow (or keyhole) is in fact the surface entrance of a narrow tube piercing the valves. The infillings of these tubes were recognized and sketchily illustrated even by the early authors (Suess 1852; Zittel 1870). Nevertheless, the cause and reason of the central perforation and the tube of the pygopides was puzzling for the palaeontologists and induced quite irrational ideas (e.g. by Dacqué 1921, namely that the animal put its own pedicle through its own body).

The growing knowledge on the ecology of present-day brachiopods revealed that, during the ciliary suspension feeding, the lophophore of the bilateral animal generated two lateral inhalant flows and a jet-like antero-medial exhalant stream (Rudwick 1962). Soon it was also pointed out that the sulcate shell morphology of brachiopods and its extreme development i.e. the perforation tube of the pygopides had significance in optimizing the feeding process of those brachiopods (Rudwick 1965, 1970; Vogel 1966). These recognitions and models were refined by Michalík (1996) and Colás & García Joral (2011).

The comprehensive examinations of the present study improve the knowledge on the internal morphology of the perforation tube of the pygopides and throw new light to the function of this curious structure.

MATERIAL AND METHODS

In the framework of a comprehensive project the present author had the possibility to study a large brachiopod material from the Upper Jurassic to Lower Cretaceous formations of the Bakony Mountains (Hungary); the results were published in separate volumes (Vörös 2022a, 2022b). The brachiopod fauna (1816 specimens, 32 species) was predominated by Pygopidae (1272 specimens). The abundance of perforate genera *Antinomia* (435 specimens) and *Pygope* (223 specimens) allowed destroying some specimens aiming at the detailed investigation of their internal features including the morphology of their perforation tubes. For the latter purpose, 14 specimens were cut or broken along the plane of symmetry of the specimens (Table 1), additionally serial transverse and longitudinal sections were prepared (Fig. 1). The investigated specimens are deposited in the collection of the Department of Palaeontology and Geology of the Hungarian Natural History Museum (HNHM), Budapest under the inventory numbers prefixed by “PAL”, or “INV”.

In the process of serial grinding, the brachiopod was embedded, with a definite (transverse or longitudinal) orientation, into plaster. The block of plaster (with the oriented brachiopod in it) was mounted on a steel plate of the Cutrock-Croft parallel grinding instrument. This device keeps the orientation and grinds in very narrow intervals. In the practice, usually 0.1 mm grinding intervals were used. The brachiopods were sectioned across the visible parts of the perforation tube. In each phase, the actual cross section was examined; if some significant change appeared, the cross section was documented by colour photograph (by Canon EOS 700D camera). In the figures, the distances between the particular sections are given in millimetres.

External observations were made on the details of the ventral entrance of the perforation tubes of several *Antinomia* specimens and the details were documented by close-up photographs.

Table 1. List of Pygopidae specimens examined for the perforation tubes.

Species	Locality	Age	Nature of treatment
Pygope diphya (Buch, 1834)	Szilas Ravine 41	Berriasian	Longitudinal broken surface
Pygope diphya (Buch, 1834)	Szilas Ravine 41	Berriasian	Longitudinal section
Pygope diphya (Buch, 1834)	Lókút 9	Upper Tithonian	Longitudinal section
Pygope diphya (Buch, 1834)	Lókút 10	Upper Tithonian	Longitudinal broken surface
Pygope diphya (Buch, 1834)	Lókút 13	Upper Tithonian	Longitudinal serial sections
Pygope diphya (Buch, 1834)	Szilas Ravine 70	Lower Tithonian	Longitudinal section
Antinomia catulloi (Pictet, 1867)	Hárskút 12/a 10	Berriasian	Longitudinal broken surface
Antinomia catulloi (Pictet, 1867)	Lókút 8	Upper Tithonian	Longitudinal section
Antinomia catulloi (Pictet, 1867)	Lókút 10	Upper Tithonian	Longitudinal serial sections
Antinomia catulloi (Pictet, 1867)	Lókút 15	Upper Tithonian	Longitudinal section
Antinomia catulloi (Pictet, 1867)	Lókút 18	Upper Tithonian	Longitudinal section
Antinomia catulloi (Pictet, 1867)	Lókút 24	Upper Tithonian	Longitudinal serial sections
Antinomia catulloi (Pictet, 1867)	Lókút 27	Lower Tithonian	Transverse serial sections
Antinomia catulloi (Pictet, 1867)	Lókút 46	Lower Tithonian	Longitudinal broken surface

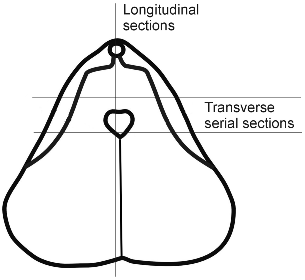

Figure 1. Positions of sections and serial sections through a pygopide shell (not to scale).

RESULTS

The new data and observations of the present study significantly improved the previous knowledge on the morphology of the perforation tube of the Pygopidae brachiopods.

The longitudinal sections and cuttings through the specimens of *Pygope diphya* (Buch, 1834) and *Antinomia catulloi* (Pictet, 1867) revealed that the dorsal entrance of the perforation continues in a funnel-shaped and anteriorly arched tube through the interior of the dorsal valve. This tube regularly narrows in ventral direction and its ventral termination is directed to, but does not reach the corresponding perforation of the ventral valve (Figs 2–3). The perforation of the ventral valve is narrower than that of the dorsal one; it continues in a short collar inwards, which joins the ventral termination of the dorsal tube (Figs 2–3). It was also visible that the ventral collar fit almost perfectly to the end of the dorsal tube if the valves of the specimen were closed. In slightly opened shells a narrow gap appears between the collar and the tube. The gap is not perpendicular to the tube; the posterior slit opens near the ventral surface of the ventral valve, while the anterior part of the slit is situated much more inward in the tube (Figs 2–3).

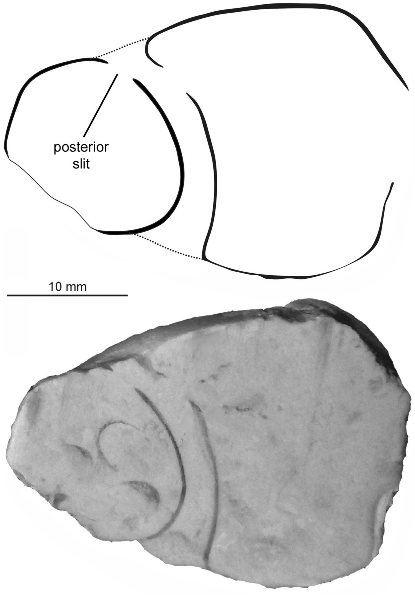

Figure 2. Polished longitudinal section (below) and interpreted drawing (above) through a specimen of *Pygope diphya* (Buch, 1834) showing the details of the perforation tube; Borzavár, Szilas Ravine 41; Cretaceous, Berriasian.

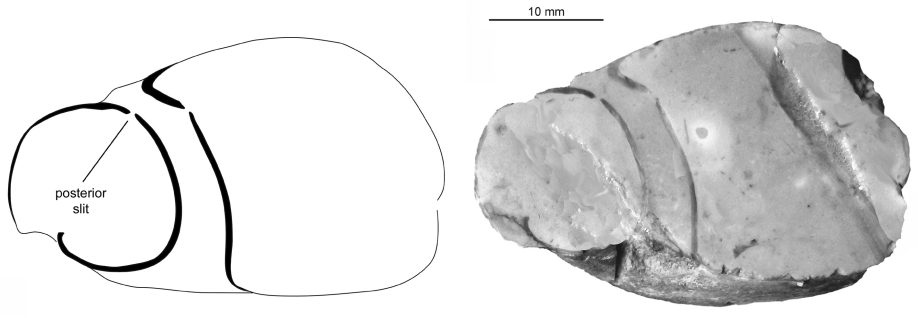

Figure 3. Polished longitudinal section (right) and interpreted drawing (left) through a specimen of *Antinomia catulloi* (Pictet, 1867) showing the details of the perforation tube; Lókút, Lókút Hill 15; Jurassic, upper Tithonian.

The longitudinal serial sections through a specimen of *Antinomia catulloi* (Pictet, 1867) endorsed the previous observations and provided further details on the connection between the dorsal tube and the ventral collar (Fig. 4).

The transverse serial sections through a specimen of *Antinomia catulloi* (Pictet, 1867) (Fig. 5) exposed that the tube is roughly triangular in cross section; it is formed by the linguiform extension of the deep dorsal sulcus, and the posterior endings of the fused lateral lobes of the dorsal valve. Near the dorsal entrance the cross-section is drop-shaped with arched posterior and pointed anterior walls. The ventral termination of the tube and the connected collar are formed by the convex medial fold of the ventral valve and the endings of the fused lateral lobes of the ventral valve; consequently it is somewhat chalice-shaped in cross section. The anterior shell wall of the ventral collar is markedly thickened (Fig. 5).

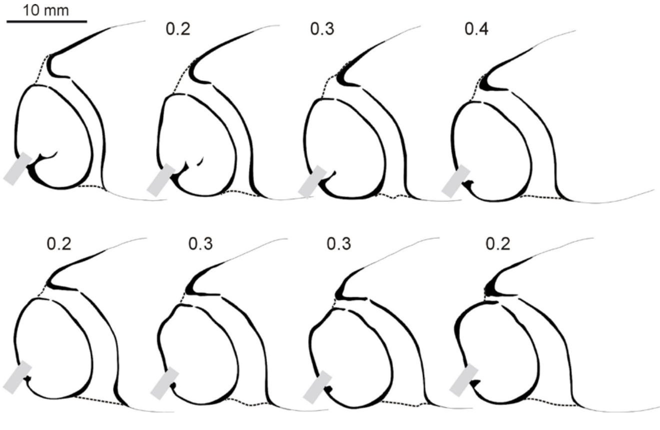

Figure 4. Drawings of longitudinal serial sections through a specimen of *Antinomia catulloi* (Pictet, 1867); Lókút, Lókút Hill 10; Jurassic, upper Tithonian. Numbers indicate the distances between the particular sections. Grey rectangles symbolize the former pedicle of the animal (not fossilized).

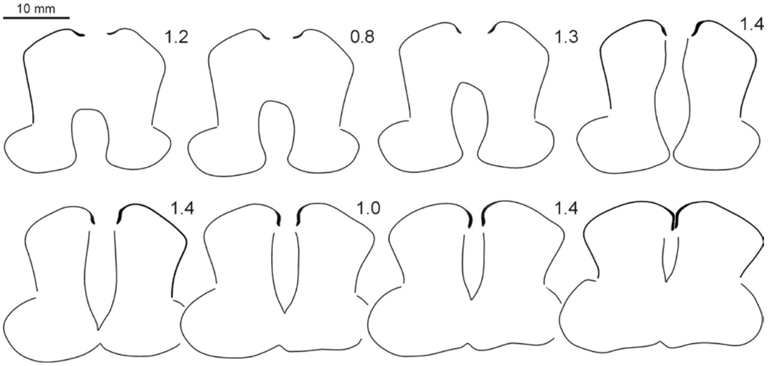

Figure 5. Drawings of transverse serial sections through a specimen of *Antinomia catulloi* (Pictet, 1867); Lókút, Lókút Hill 27; Jurassic, lower Tithonian. Numbers indicate the distances between the particular sections; ventral valve up.

By closer examination of the ventral entrance of some well-preserved *Antinomia* specimens it was seen that the medial fold of the ventral valve, bordered by marked depressions, showed a regular, posteriorly convex pattern of growth lines. During the late phase of the ontogeny the growth vector of the fold started to change from longitudinal (anterior) to inward (anterodorsal) direction (Figs 6–7). As a result, the line of contact with the ventral end of the linguiform extension (i.e. the posterior slit) was removed inward to the entrance of the ventral perforation. Certainly, this change involves some degree of resorption of the ventral end of the linguiform extension. This whole process was synchronous with the final phase of the fusion of the large anterior lobes of the shell, because at the penultimate phase of the fusion of the anterior lobes, the posterior slit was still in extreme ventral position (Fig. 8). This means that the animal organized the inward shift of the posterior slit in the time of the fusion of the lobes, i.e. in the final accomplishment of the tube.

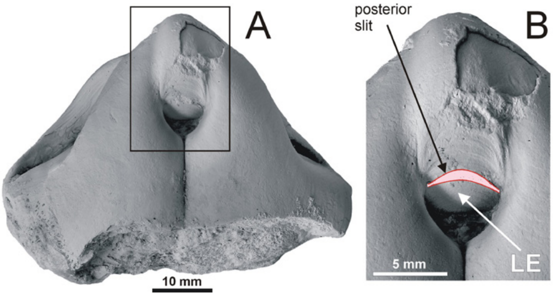

Figure 6. A = ventral view of *Antinomia picteti* Vörös, 2022; Hárskút, HK-12/11; Cretaceous, lower Valanginian; B = detail of A (marked by rectangle), showing the ventral entrance of the perforation; LE = ventral termination of the linguiform extension of the dorsal valve; the posterior slit is slightly open.

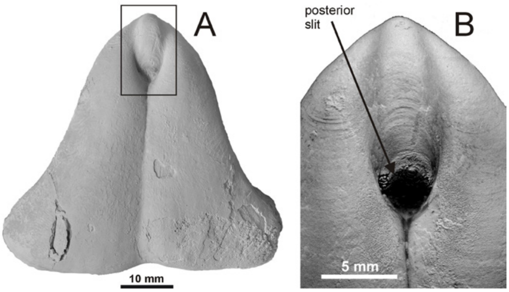

Figure 7. A = ventral view of *Antinomia catulloi* (Pictet, 1867); Hárskút, HK-12/20; Cretaceous, Berriasian; B = detail of A (marked by rectangle), showing the ventral entrance of the perforation; disarticulated ventral valve, therefore the termination of the linguiform extension of the dorsal valve is missing (filled with host rock).

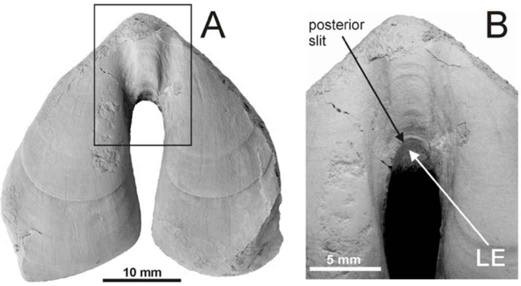

Figure 8. A = ventral view of *Antinomia contracta* Vörös, 2022; Lókút, Lókút Hill 47; Jurassic, lower Tithonian; B = detail of A (marked by rectangle), showing the ventral entrance of the perforation; LE: ventral termination of the linguiform extension of the dorsal valve; the posterior slit is closed.

DISCUSSION

The growing knowledge on the feeding mechanisms of present-day brachiopods revealed that the mantle cavity of the bilateral animal was always divided by the lophophore into inhalant and exhalant chambers with separate apertures, with two lateral inhalant flows and a jet-like antero-medial exhalant stream (Rudwick 1962; McCammon 1969; Steele-Petrović 1976; Williams et al. 1997; Peck et al. 1997). For brachiopods, as ciliary suspension feeders, it is crucial to prevent the mixing of the inhalant and the food depleted exhalant flows, particularly in habitats with limited food supply. In a great compendium on the adaptation of Mesozoic brachiopods to different environments Ager (1965, pp. 161–165) signalled the pygopides as markers of "deeper and/or calmer sea-floors", with the notion that in very quiet waters the separation of inhalant and exhalant currents was vital where the waste material was not readily swept away.

The homeland of pygopides, the Mediterranean faunal province perfectly corresponds to the above statements. In Late Jurassic and earliest Cretaceous times the pygopides thrived on the Mediterranean microcontinent system in the western part of the Tethys Ocean (Vörös 1993, 2005). This submarine plateau ("thalassobathyal" sensu Zezina 1997) was isolated from the surrounding continental areas by wide deep-sea basins, which hindered the influx of the land-derived organic matter to this palaeoenvironment. The Mediterranean province was characterized by slow deposition of pelagic calcareous muddy sediments with very restricted amount of organic particles (Hallam 1975; Vörös 2005). In this region, just as in the present-day pelagic environments, the source of the sedimentary material and the food supply was the result of the primary productivity in the surface zone of the ocean, from where the minute particles sunk down to the sea-floor. The calcareous ooze came from the micro- and nannoplankton (shells of foraminifers and coccoliths) and their decayed tissues yielded the limited amount of organic matter as nutrients (Hüneke & Heinrich 2011). The pygopides of the Mediterranean province, among other bottom-dweller animals, had to adapt to this special nutrient-deficient environment.

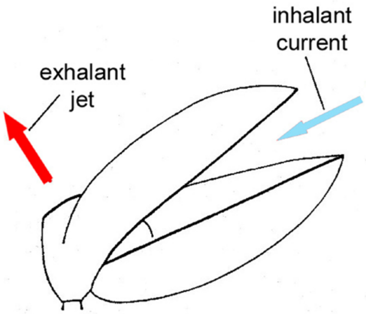

Figure 9. The system and divergence between the inhalant and exhalant currents in pygopides in Rudwick's model (modified from Rudwick 1970).

It is obviously advantageous if the direction of the exhalant current which is depleted in organic particles, deviates from the inhalant flow in order to avoid the mixing and recycling the exhausted water. This divergence is achieved by the modification of the anterior margin of the brachiopod shells as it is exemplified by the sulcate morphotypes prevalently occurring in deep sea environments with limited food supply (Cooper 1972; Zezina 1997). The advantage of the sulcate morphology in utilization of food was proved by the models of the feeding currents generated by the ciliary action of the lophophore as reconstructed by Rudwick (1965, 1970) and Vogel (1966). These models were further discussed and enhanced by Michalík (1996) and Colás & García Joral (2011) but apparently without exhaustive information on the internal structure of the pygopide shell, particularly the tube. For the palaeobiological interpretation of the pygopide perforation, the fundamental feature, highlighted by the above authors, was the angle of deviation between the inhalant and exhalant currents. Rudwick (1970) and Colás & García Joral (2011) estimated this deviation as exceeding 90° (Fig. 9), whereas in the reconstruction by Michalík (1996) the divergence seems to approach even 180° as suggested by the extreme posteroventral position of the posterior gap in the umbonal chamber

(Fig. 10). A remarkable improvement of Michalík's model was the recognition of the anterior gap (or slit) within the tube, although positioned too much dorsally in the reconstruction. In fact, the formation of the tube, i.e. the fusion of the lateral lobes further enhanced the feeding process: instead of two lateral inhalant currents, the intake became possible along the whole enlarged anterior margin in the adult perforate pygopide.

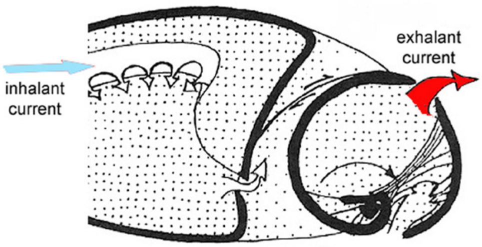

Figure 10. The system and divergence between the inhalant and exhalant currents in pygopides in Michalík's model (modified from Michalík 1996); note the presence of the anterior gap within the perforation tube.

The new theoretical model of the feeding current system of perforate pygopides is shown in Fig. 11. Here the animal is depicted with slightly opened shell in life position, resting on its dorsal side and fastened by its pedicle to the bottom. The principal geometry of the reconstruction was developed on the basis of the examinations and observations presented in this study. Particularly the longitudinal sections (Figs 2–4) unanimously demonstrated that, in contrary to Michalík's model, the anterior and posterior gaps (or slits) were situated near the ventral entrance of the tube. The opening of the posterior gap of the umbonal chamber approximately faced with the opposing rim of the tube. This involves that the exhalant jet has to pass directly over the ventral entrance of the tube.

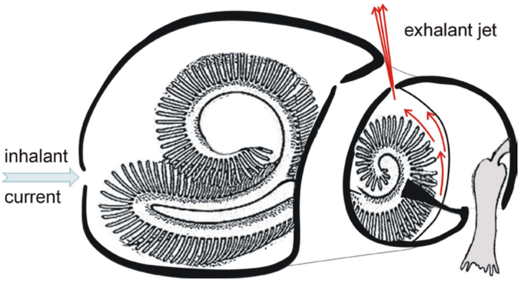

Figure 11. Longitudinal cross section showing the new theoretical model of the feeding current system of perforate pygopides. The animal, with slightly opened shell, is in life position resting on its dorsal side and fastened by its pedicle to the bottom. Note that the posterior slit is near the ventral entrance of the tube and the exhalant jet only just passes over the rim of the tube.

The propulsion of the exhalant jet above the entrance of a tube recalls the author's mind to the every-day spray devices working on the basis of Bernoulli's principle. For the sake of accuracy, the definition of the principle states that: "An increase in the speed of a fluid occurs simultaneously with a decrease in pressure" (https://en.wikipedia.org/wiki/Bernoulli's_principle). Perhaps we may go further and cite also the related Venturi effect: "When flowing through a constricted area of a pipe, a fluid's velocity increases and its static pressure decreases" (https://en.wikipedia.org/wiki/Venturi_effect). It is true that the posterior slit of the umbonal chamber is not a pipe, still we may suppose that the propulsion of the exhalant jet generated a low-pressure regime in the tube (Fig. 12).

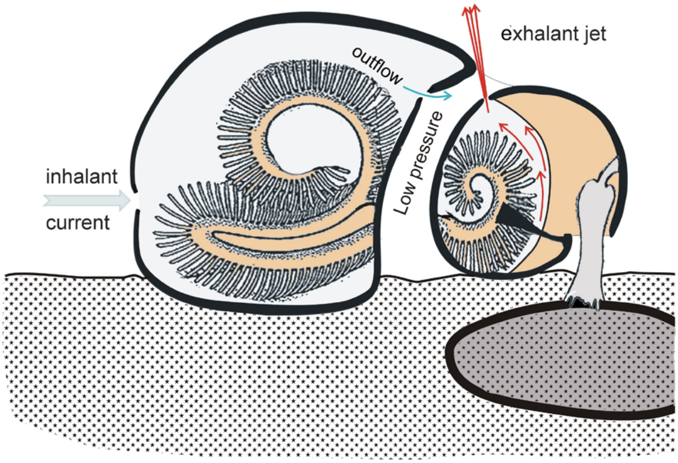

Figure 12. Longitudinal cross section showing the upgraded theoretical model of the feeding current system of perforate pygopides. With the application of Bernoulli's principle and the Venturi effect, it is supposed that the propulsion of the exhalant jet generated a low-pressure regime in the tube. This may trigger an outflow through the anterior slit of the tube, generated by the sucking effect of the low-pressure regime, with the benefit of the increase the slow circulation through the large mantle cavities of the lateral lobes.

Considering that, as it was demonstrated above (Figs 6–8), the anterior transfer of the posterior slit to the entrance of the tube proceeded in the latest phase of the ontogeny i.e. in the time of the final accomplishment of the tube, a causal relationship between the two processes cannot be excluded. Without being entangled with teleology, we may further speculate on the potential benefits of a low-pressure regime in the tube of a pygopide animal. One obvious advantage would be the increase of the speed of the slow circulation through the large anterior mantle cavities, which was certainly useful in collecting the organic particles by the ciliary arms. This may be achieved by the outflow through the anterior slit of the tube, generated by the sucking effect of the low-pressure regime.

In a more hypothetic model, the generated low-pressure regime is combined with possible movements of the whole shell of the pygopide animal by using its stiff pedicle, firmly attached to a hard object in the sea-floor (Fig. 13). In most of its life the animal is resting on and slightly sinking in the soft muddy surface of the sea-floor. For short moments, it is capable to lift itself from the mud by contracting the adjustor muscles of its pedicle. By this action the underlying unconsolidated mud is stirred or whipped up and the fine grained and partly organic-rich material may be sucked into the low-pressure area of the tube. Moreover, at least a fraction of this suspended matter may be ejected off the tube, helped by the exhalant jet. Simultaneously, the expelled cloud of suspension may be swept away by the slow but steady currents of the surrounding sea water. In fortunate case the currents may sweep the suspended matter with organic particles near to the anterior margin of the shell, where the inhalant current may bring the extra food particles to the mantle cavity of the animal.

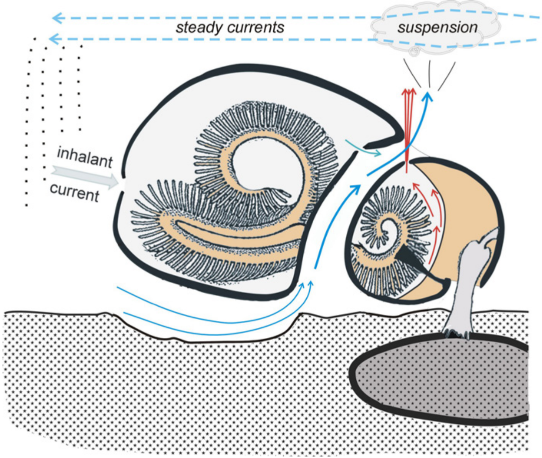

Figure 13. Longitudinal cross section showing the hypothetically advanced theoretical model of the feeding current system of perforate pygopides. The animal lifted itself from the mud by contracting the adjustor muscles of its pedicle. The underlying unconsolidated mud is stirred up and the fine grained organic-rich material sucked into the low-pressure area of the tube. This suspended matter may be ejected off the tube and the expelled suspension may be swept away by the slow currents of the sea water. The suspended matter with organic particles may reach the anterior margin of the shell, where the inhalant current may bring the extra food particles to the mantle cavity of the animal. This may give an ancient example of recycling of food in environments of restricted supply.

But if the pygopide lifted its shell, it would also be able to rotate the whole body by the contractions of the adjustor muscles, on the analogy of some living brachiopods (Richardson 1981). By this rotation around the pedicle as a pivot, the animal might settle its shell to adjacent surfaces of the muddy sea-floor and might exploit the sparse organic particles previously deposited on that site. This movement might be repeated from time to time in the life of the pygopide animal (Fig. 14).

Provided that this model worked in fact, this process would be considered a nice ancient example of recycling of food in environments of restricted supply.

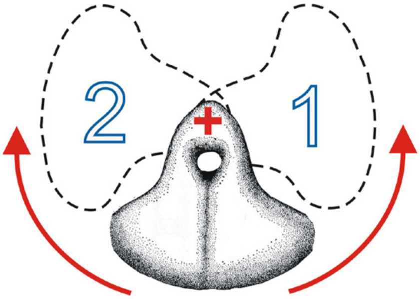

Figure 14. The pygopide might rotate its lifted shell by the actions of the adjustor muscles around the pedicle as a pivot, and might settle to adjacent surfaces of the muddy sea-floor. Thus it might exploit the sparse organic particles previously deposited on that site. This movement might be repeated from time to time in the life of the pygopide.

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REFERENCES

Ager D. V. 1965: The adaptation of Mesozoic brachiopods to different environments. – *Palaeogeography, Palaeoclimatology, Palaeoecology* **1**: 143–172. https://doi.org/10.1016/0031-0182(65)90011-8

Ager D. V. 1967: Brachiopod palaeoecology. – *Earth Science Reviews* **3**: 157–179. https://doi.org/10.1016/0012-8252(67)90375-3

Colás J. & García Joral F. 2011: Morphology and environment in the Jurassic Nucleatidae (Brachiopoda) from Western Tethys. – *Lethaia* **45**: 178–190. https://doi.org/10.1111/j.1502-3931.2011.00270.x

Cooper G. A. 1972: Homeomorphy in Recent deep-sea brachiopods. – *Smithsonian Contributions to Paleobiology* **11**: 1–25. https://doi.org/10.5479/si.00810266.11.1

Dacqué E. 1921: *Vergleichende biologische Formenkunde der fossilen niederen Tiere.* – Borntraeger, Berlin, 777 pp.

Hallam A. 1975: *Jurassic environments.* – Cambridge University Press, Cambridge, ix +284 pp.

Hüneke H. & Henrich R. 2011: Pelagic Sedimentation in Modern and Ancient Oceans. – In: Hüneke H. & Mulder T. (eds): *Developments in Sedimentology* **63:** pp. 215–351. https://doi.org/10.1016/B978-0-444-53000-4.00004-4

McCammon H. M. 1969: The food of articulate brachiopods. – *Journal of Paleontology* **43**: 976-985.

Michalík J. 1996: Functional morphology – paleoecology of pygopid brachiopods from the Western Carpathian Mesozoic. – In: Copper P. & Jisuo Jin (eds.): *Proceedings of the Third International Brachiopod Congress, Sudbury, Ontario, Canada, 2–5 September 1995.* Balkema, Rotterdam, pp. 175–178.

Peck L. S., Rhodes M. C., Curry G. B. & Ansell A. D. 1997: Physiology. – In: Kaesler, R. L. (ed.): *Treatise on Invertebrate Palaeontology. Part H, Brachiopoda (Revised), Volume 1, Introduction.* – Geological Society of America and University of Kansas, Boulder, Colorado and Lawrence, Kansas, pp. H213–H242.

Richardson J. R. 1981: Brachiopods and pedicles. – *Paleobiology* 7(1): 87–95. https://doi.org/10.1017/S0094837300003808

Rudwick M. J. S. 1962: Filter-feeding mechanisms in some brachiopods from New Zealand. – *Journal of the Linnean Society, London, Zoology* **44**: 592–615. https://doi.org/10.1111/j.1096-3642.1962.tb01626.x

Rudwick M. J. S. 1965: Ecology and paleoecology. – In: Moore, R. C. (ed.): *Treatise on Invertebrate Paleontology, Part H, Brachiopoda*, Geological Society of America, Kansas, pp. H199–H214.

Rudwick M. J. S. 1970: *Living and fossil brachiopods.* – Hutchinson University Library, London, 199 pp.

Steele-Petrović H. M. 1976: Brachiopod food and feeding processes. – *Palaeontology* **19**(3): 417–436.

Suess E. 1852: Über Terebratula diphya. – *Sitzungsberichte der mathematisch-naturwissenschaftlichen Classe der kaiserlichen Akademie der Wissenschaften* **8**: 553–566.

Vogel M. 1966: Eine funktionsmorphologische Studie an der Brachiopodengattung Pygope (Malm bis Unterkreide). – *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **125**: 423–442.

Vörös A. 1993: Jurassic microplate movements and brachiopod migrations in the western part of the Tethys. – *Palaeogeography, Palaeoclimatology, Palaeoecology* **100**: 125–145. https://doi.org/10.1016/0031-0182(93)90037-J

Vörös A. 2005: The smooth brachiopods of the Mediterranean Jurassic: refugees or invaders? – *Palaeogeography, Palaeoclimatology, Palaeoecology* **223**: 222–242. https://doi.org/10.1016/j.palaeo.2005.04.006

Vörös A. 2022a: *The Late Jurassic and Early Cretaceous (Kimmeridgian to Barremian) brachiopods of the Bakony Mountains (Hungary).* – Hungarian Geological Society, Budapest, 156 pp.

Vörös A. 2022b: Late Jurassic to Early Cretaceous (Kimmeridgian–Barremian) brachiopods of the Bakony Mountains (Transdanubian Range, Hungary). – In: Főzy I. (ed.): *Fauna, biostratigraphy, facies and paleotectonic evolution of the Late Jurassic–Early Cretaceous formations in the Bakony Mountains (Transdanubian Range, Hungary).* – Institute of Geosciences, University of Szeged, GeoLitera Publishing House, Szeged, pp. 397–431.

Williams A, James M. A., Emig C. C., Mackay, S & Rhodes M. C. 1997: Anatomy. – In: Kaesler R. L. (ed.): *Treatise on Invertebrate Palaeontology. Part H, Brachiopoda (Revised), Volume 1, Introduction.* – Geological Society of America and University of Kansas, Boulder, Colorado and Lawrence, Kansas, pp. H7–H188. https://doi.org/10.17161/dt.v0i0.5553

Zezina O. N. 1997: Biogeography of the bathyal zone. – *Advances in Marine Biology* **32**: 389– 426. https://doi.org/10.1016/S0065-2881(08)60020-6

Zittel K. A. 1870: Die Fauna der aeltern cephalopodenfuehrenden Tithonbildungen. – *Palaeontographica, Supplement* **1–3**: 1–192.

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A Pygopefélék perforációjának morfológiája és funkciója (Terebratulida, Brachiopoda)

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Összefoglalás – Belső szerkezetük vizsgálata céljából 14 bakonyi *Pygope* és *Antinomia* példány hosszanti és haránt csiszolata készült el. A háti teknő perforációja egy hosszú csőben folytatódik, ami a hasi teknő rövid tölcséréhez illeszkedik. A kissé nyitott teknők esetében a cső és a tölcsér között szűk hézag jelenik meg. A hézag hátulsó nyílása közel esik a ventrális tölcsér pereméhez. A Pygopefélék táplálkozási rendszerének új modelljében ez a vonás azt jelenti, hogy a kilövellő áramlat közvetlenül a cső hasi nyílása fölött halad el. Az erős kilövellés nyomáscsökkenést idézhet elő a csőben. Ez a jelenség előnyös lehet a köpenyüreg áramlási rendszerének felgyorsításában, ami a csőben uralkodó csökkent nyomás szívóhatásából adódik. Az állat ki tudja emelni a testét az iszapból a nyélmozgató izmai segítségével. Ez által a még laza iszap felkavarodik és az apró szervesanyag-szemcsékkel együtt beszippantódhat a csökkent nyomású csőbe. Ezután a lebegtetett tápanyag szemcsék a bemenő áramlat útján újrahasznosulhatnak. 14 ábrával és egy táblázattal.

Kulcsszavak – Bakony-hegység, táplálkozás, táplálék újrahasznosítás, belső morfológia, Pygopefélék

ÁBRA- ÉS TÁBLAMAGYARÁZATOK

1. tábla. A perforációs csövekhez vizsgált Pygopefélék példányainak listája.

1. ábra. Pygopefélék teknőjén keresztül készített metszetek és sorozat-csiszolatok helyzete (nem méretarányos).

2. ábra. Csiszolt hosszanti metszet (alul) és értelmezett rajz (felül) egy *Pygope diphya* (Buch, 1834) példányon keresztül, a perforációs cső részleteinek bemutatására; Borzavár, Szilas-árok 41; kréta, berriasi.

3. ábra. Csiszolt hosszanti metszet (jobbra) és értelmezett rajz (balra) egy *Antinomia catulloi* (Pictet, 1867) példányon keresztül, a perforációs cső részleteinek bemutatására; Lókút, Lókúti-domb 15; jura, felső tithon.

4. ábra. Egy *Antinomia catulloi* (Pictet, 1867) példányon keresztül készült hosszanti sorozatcsiszolatok rajzai; Lókút, Lókúti-domb 10; jura, felső tithon. A számok az egyes csiszolatok közötti távolságokat mutatják; a szürke téglalapok az egykori (nem fosszilizálódott) nyél helyét jelzik.

5. ábra. Egy *Antinomia catulloi* (Pictet, 1867) példányon keresztül készült haránt irányú sorozatcsiszolatok rajzai; Lókút, Lókúti-domb 27; jura, alsó tithon. A számok az egyes csiszolatok közötti távolságokat mutatják; a hasi teknő van felül.

6. ábra. A = Egy *Antinomia picteti* Vörös, 2022 példány hasi nézete; Hárskút, HK-12/11; kréta, alsó valangini; B = Az előző kép (téglalappal jelölt) részlete a perforáció hasi nyílását mutatja; LE = a háti teknő nyelvalakú nyúlványának hasi elvégződése; a hátulsó hézag nyitott.

7. ábra. Egy *Antinomia catulloi* (Pictet, 1867) példány hasi nézete; Hárskút, HK-12/20; kréta, berriasi; B = Az előző kép (téglalappal jelölt) részlete a perforáció hasi nyílását mutatja; izolált hasi teknő, ezért háti teknő nyelv alakú nyúlványa hiányzik (a nyílást kőzetanyag tölti ki).

8. ábra. Egy *Antinomia contracta* Vörös, 2022 példány hasi nézete; Lókút, Lókúti-domb 47; jura, alsó tithon; B = Az előző kép (téglalappal jelölt) részlete a perforáció hasi nyílását mutatja; LE = a háti teknő nyelv alakú nyúlványának hasi elvégződése; a hátulsó hézag zárt.

9. ábra. A Pygopefélék bemenő és kimenő áramlásainak rendszere és irányeltérése Rudwick modellje szerint (Rudwick 1970 nyomán módosítva).

10. ábra. A Pygopefélék bemenő és kimenő áramlásainak rendszere és irányeltérése Michalík modellje szerint (Michalík 1996 nyomán módosítva); lényeges a mellső hézag feltüntetése a perforációs csövön belül.

11. ábra. Hosszanti keresztmetszet a perforált Pygopefélékben a lophophora által gerjesztett táplálkozási áramlási rendszer új elméleti modelljének bemutatására. Az állat élethelyzetben, kissé kinyitott teknőkkel a háti oldalán fekszik, és nyelével a tengeraljzathoz rögzül. A hátulsó hézag a cső hasi nyílásához közel van és a kilövellő áramlás éppen a cső pereme mellett halad el.

12. ábra. Hosszanti keresztmetszet a perforált Pygopefélékben a lophophora által gerjesztett táplálkozási áramlási rendszer továbbfejlesztett elméleti modelljének bemutatására. A Bernoulli-szabály és a Venturi-hatás alkalmazásával feltételezhető, hogy a kilövellő áramlás nyomáscsökkenést idéz elő a csőben. Ez a nyomáscsökkenés másodlagos kiáramlást válthat ki a cső mellső hézagján keresztül, ami megnövelheti a köpenyüregen belüli áramlás sebességét.

13. ábra. Hosszanti keresztmetszet a perforált Pygopefélékben a lophophora által gerjesztett táplálkozási áramlási rendszer feltételesen továbbfejlesztett elméleti modelljének bemutatására. A nyélizmai segítségével az állat kiemeli teknőit az iszapból. A még laza iszap felkavarodik és a finomszemcsés, szervesanyag-tartalmú zagyot az alacsony nyomású cső felszippanthatja. A lebegtetett szemcsék a kilövellő víz által kijutnak a csőből, és a környező tengeráramlás tovább sodorja őket a teknők mellső pereméhez, ahol a bemenő áramlás segítségével a tápanyag szemcsék bejutnak a köpenyüregbe. Ez a tápanyag újrahasznosításának egykori példája lehet.

14. ábra. A Pygopefélék a nyélizmok segítségével felemelt teknőiket el is fordíthatták a rögzített nyél körül, és egy szomszédos helyen újra letehették a tengerfenék iszapjának felszínére. Így az itt korábban lerakódott gyér szerves anyagot újra feldolgozhatták. Ezt a mozgást az állat az élete során többször megismételhette.