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On the morphology, morphogenesis and systematics
of *Thigmophrya* Ch. Lw. (*Ciliata*, *Thigmotrichida*) with
a description of *T. saxicavae* sp. n.

Thigmophrya Ch. Lw. (*Ciliata*, *Thigmotrichida*), dens morfologi,
morfogenese og systematiske stilling, med en beskrivelse af *T. saxicavae*
sp. n.

The genus *Thigmophrya*, a group of ciliates inhabiting the mantle cavity of marine bivalves, was described by Chatton et Lwoff 1923. In this and subsequent papers (1926, 1949) these authors classified *Thigmophrya* as a thigmotrich ciliate because of the posteriorly situated mouth and the resemblance to the species of *Conchophthiridae*. They believed *Thigmophrya* to be a primitive genus from which other thigmotrich ciliates had evolved since *Thigmophrya* possesses a dense ciliation and reduction of the somatic ciliation is a general trend within some thigmotrich families (*Hemispeiridae*, *Ancistrocomidae*). Raabe 1936, to whom we owe the best description of the genus, studied *T. macomae* Ch. Lw. from the Baltic Sea. He too considered *Thigmophrya* as a thigmotrich genus and placed the genera *Myxophyllum* Raabe and *Conchophyllum* Raabe in the family *Thigmophryidae* Ch. Lw.

Neither Chatton et Lwoff nor Raabe could demonstrate the presence of adoral rows (i.e. an undulating membrane and an adoral zone of membranelles) in *Thigmophrya*. These rows are characteristic as well of all other thigmotrichs possessing a mouth as of their ancestors: the hymenostome ciliates, and their descendants: the spirotrich and the peritrich ciliates (Fauré-Fremiet 1950, Corliss 1956). It was therefore found desirable to restudy the morphology and morphogenesis of *Thigmophrya* in order to clarify the systematic position held by this genus.

Since it is now generally agreed that the thigmotrich ciliates are descendants of the hymenostome ciliates and that the mouth parts of the two groups are homologous (Fauré-Fremiet 1950, Corliss 1956, Raabe 1963), it is found desirable to describe the mouth of thigmotrichs in terms indicating the corresponding organelles in hymenostome ciliates. Therefore the right adoral row, which is called "row number 1" and "la cinétie stomatogène" by Chatton et Lwoff 1936, 1949, and Raabe 1959, 1963, will be called the undulating membrane (UM). The left adoral row, called "la cinétie A + B" by these authors, will be called the adoral zone of membranelles (AZM). In the following "row number 1" means the first somatic row to the right of the UM.

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Materials and methods

The study was carried out at the Zoological Station of Kristineberg situated on the Gullmarfjord at the west coast of Sweden. The lamellibranch *Saxicava arctica* (L.) was found to harbour a hitherto undescribed *Thigmophrya* sp. The ciliates were studied both living and after fixation and staining. The nuclei were studied after fixation in Carnoy's fluid and staining in pyronin-methylgreen. The infraciliature was studied by the silver method of Chatton and Lwoff (Corliss 1953) and by a modification of this method described by Chatton 1940.

Thigmophrya saxicavae sp. n.

The species resembles, like other *Thigmophrya* species, *Paramecium caudatum* in the form of the body, the greatest width being in the posterior third of the body. The length was found to be 142μ ($126-160\mu$) and the width 37μ ($28-47\mu$). There are 50-60 somatic kineties arranged in a left and a right system. On the ventral side the two systems meet near the anterior end and behind the mouth. They form an anterior and a posterior suture of kineties. The anterior suture continues along the anterior rim to the dorsal side. The anterior part of the kineties of the left system is developed as a thigmotactic field; in accordance with this the anterior left side is slightly concave. The somatic rows are nearly parallel to the body axis, in contrast to *T. macomae*, where there is some torsion of the rows.

The mouth (Fig. 1 C) is situated on the ventral side about $\frac{1}{4}$ of the body length from the posterior end. As characteristic for *Thigmophrya*, it is situated in a vestibulum. It opens to the outside in a slit which is directed obliquely to the right. The vestibulum consists of a triangular pocket. The last kineties of the left system, about 7, go into the vestibulum, the walls of which they cover. The two first rows of the right system curve a little into the vestibulum. The pores of the contractile vacuole, usually 2-5, appear in the vestibulum between rows number 1 and 2.

In the vestibulum there is a triangular naked area between the rows number 1 and *n*. This area is situated on the right wall of the vestibulum. On silver impregnated specimens, lying on their right side, two rows of disorderly arranged kinetosomes are seen in the naked area. The rows run parallel to row number 1. Due to their position in a naked peristomal field between the right and the left systems of kineties and due to their behaviour during fission (see below), they are believed to be homologous with the adoral rows of other thigmotrich ciliates.

There is one ovoid macronucleus and one spheric micronucleus. Raabe 1939, mentions the occurrence of "Chromatinkörnchen" which are spheric bodies found in the macronucleus. Staining with pyronin-methylgreen shows that these spheres are big RNA-containing nucleoli imbedded in a matrix of much smaller DNA-containing granules (Fig. 1 B).

Conjugating pairs were found not infrequently. The conjugating individuals were attached to each other as shown on Fig. 1 D.

Thigmophrya saxicavae was found to infect nearly all big specimens of *Saxicava arctica* from dense populations in the Gullmarfjord.

Diagnosis of *Thigmophrya saxicavae* sp. n.

Length $142\ \mu$ ($126\text{--}160\ \mu$) and width $37\ \mu$ ($28\text{--}47\ \mu$). 50–60 somatic kineties running parallel to the body axis. About 7 somatic kineties go into the vestibulum, the opening of which is obliquely oriented. Living in the mantle cavity of *Saxicava arctica* (L.) in the Gullmarfjord (west coast of Sweden). Type slides are deposited in the International Collection of Ciliate Types, University of Illinois, Urbana, Illinois, U.S.A.

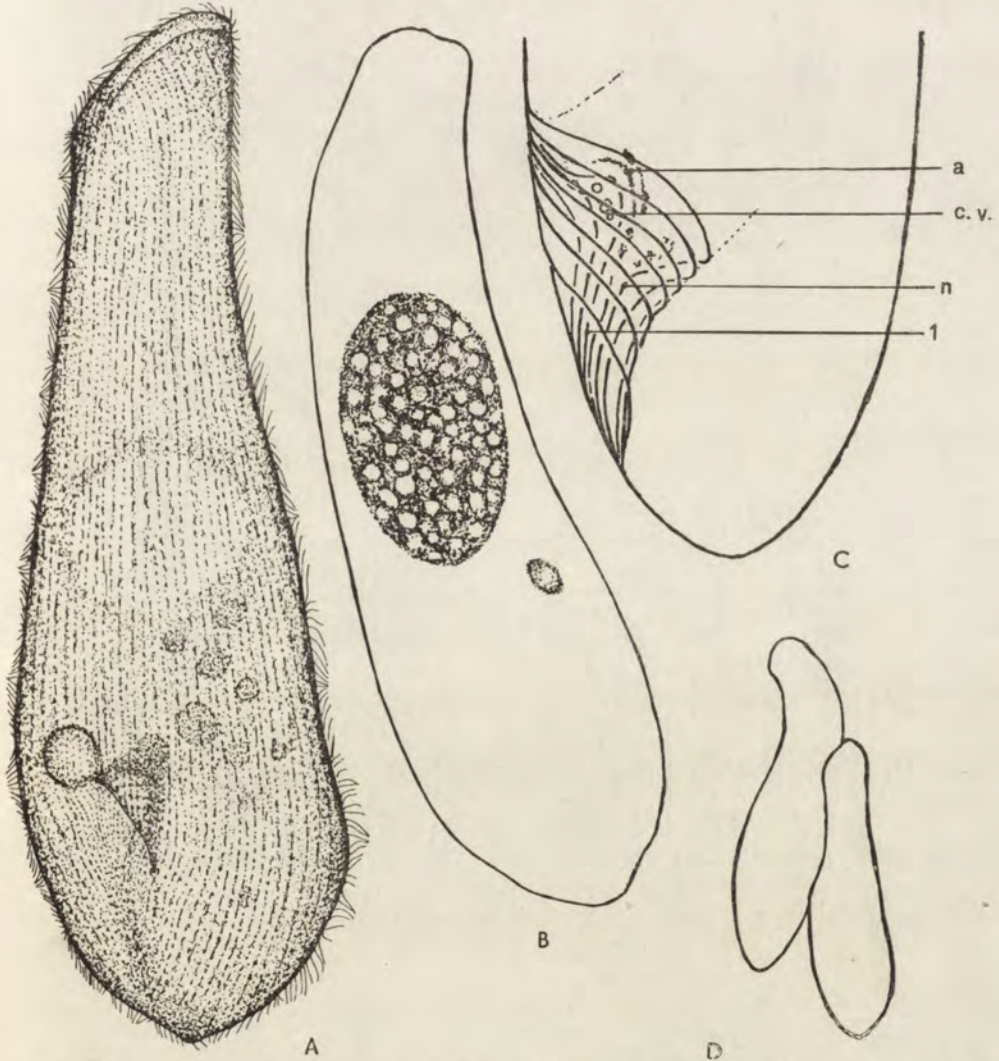


Fig. 1. *Thigmophrya saxicavae* sp. n. A. The living animal seen from the ventral side. B. Individual stained with pyronin-methylgreen. C. The mouth; schematic drawing after silver impregnated specimen seen from the left side. D. Outline of a conjugating pair; a — the adoral rows, c. v. — contractile vacuole pores, 1 and n — extreme somatic rows

The morphogenesis during division

The morphogenesis, especially the stomatogenesis, of thigmotrich ciliates has been studied in detail in two cases. Chatton et Lwoff 1936, studied

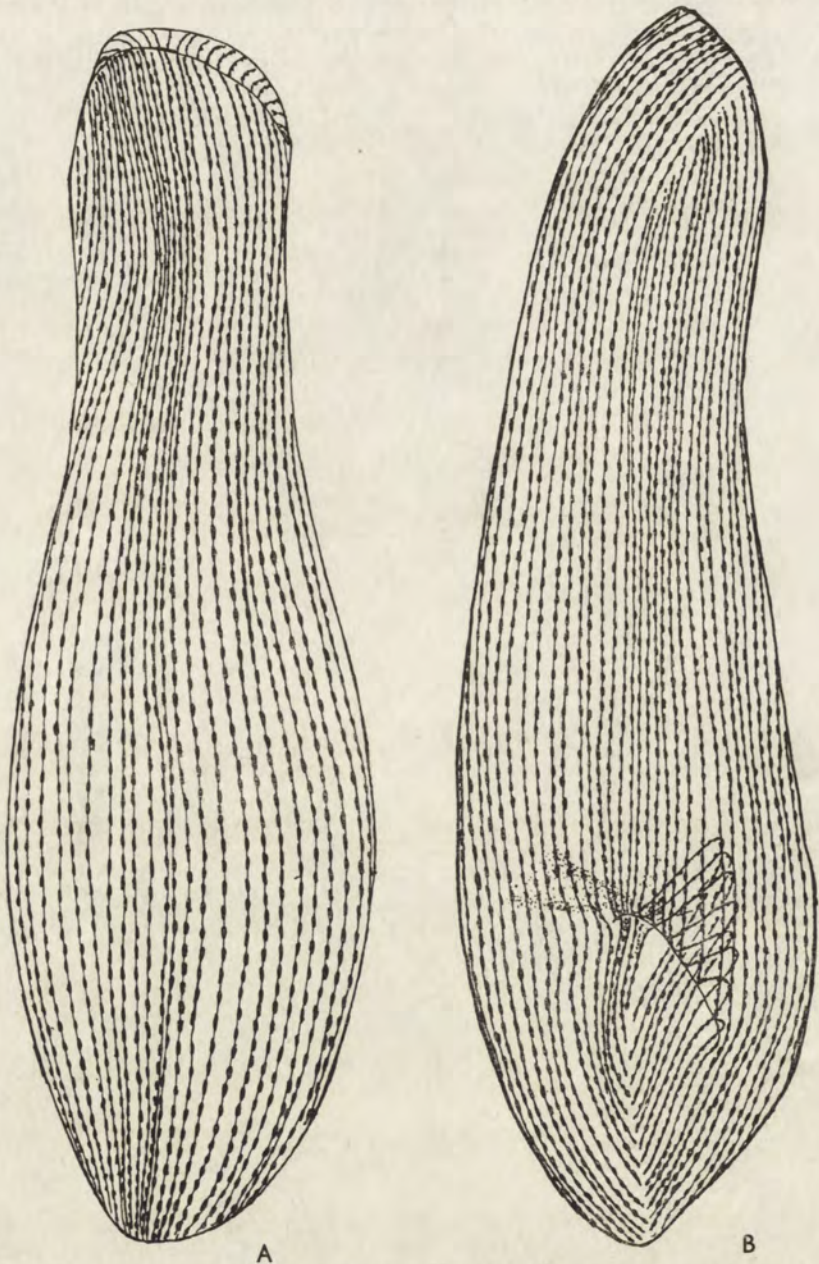


Fig. 2. *T. saxicavae* sp. n.; silver impregnated individuals seen from the dorsal left and the ventral side

the stomatogenesis of *Proboveria* Ch. Lw. and Raabe 1963, studied the stomatogenesis of *Conchophthirus* St. The findings of Chatton et Lwoff are in short the following. During division the UM is divided in two parts, one to the proter and one to the opisthe. The level of cleavage goes through the UM. AZM goes unchanged to the proter. To the left of the UM a number of membranelles appear in both the proter and in the opisthe. In the proter they disappear again and the old AZM is retained. In the opisthe three of the new membranelles form the new AZM of the opisthe while the rest disappears.

The fundamental findings of Raabe agree essentially with those of Chatton et Lwoff. In *Conchophthirus*, however, he found that the level of cleavage is behind the mouth. In both cases a pattern of membranelles resembling the tetrahymenal type are formed and some of the membranelles disappear again in a later phase of fission.

During the study of *T. saxicavae*, a great number of dividing individuals were found. However, some phases of division, especially the earliest, are lacking in the material. A possible explanation may be that some of these phases are of very short duration (c.f. Raabe 1963).

The first sign of division in *Thigmophrya* is the disappearance of the contractile vacuole pores and the straightening of the vestibulum and its somatic kineties.

In the earliest phases of division, which were studied, two mouth anlagen were already seen situated near each other behind the middle of the animal (Fig. 3 A). In the anlage of the proter the kinetosomes are more or less arranged in two rows, while the anlage of the opisthe only consists of one row of scattered kinetosomes. Between the rows number 1 and n the two anlagen are connected by a band of scattered kinetosomes. The somatic rows curve around the two anlagen. It is believed that the level of cleavage is established through or behind the old mouth since in the earliest phases of division, the opisthe is always smaller than the proter. The new contractile vacuole pores, which are formed during an early phase of the fission, appear between the rows 1 and 2 at the level of the mouth anlage. The number of kinetosomes in the mouth anlage increases. In the proter the right row becomes very distinct, and the left part becomes a dense cluster of kinetosomes (Fig. 3—4). It was difficult to observe the right row in the opisthe. Also here a dense cluster of kinetosomes appears.

Thereafter the formation of the vestibulum begins, first in the opisthe, later in the proter. The sinking starts at the mouth anlage and proceeds towards the left until about seven somatic rows are drawn into the vestibulum (Fig. 4). The stomatogenesis is completed by the disappearance of kinetosomes in the anlagen, especially in the left part, until only the two insignificant adoral rows visible in the vegetative individuals are left.

If in *Thigmophrya* the right adoral row is considered identical with the UM and the left one is considered identical with the AZM, the stomatogenesis of this genus resembles the stomatogenesis described previously for other thigmotrich genera. The main difference is that in *Thigmophrya* the AZM is not seen to be split into several membranelles in any phase of division.

The stomatogenesis of the previously studied genera as well as that of *Thigmophrya* are autonomous, i.e. the new mouth parts are formed by the old mouth. In all cases the old UM seems to be retained in both the proter

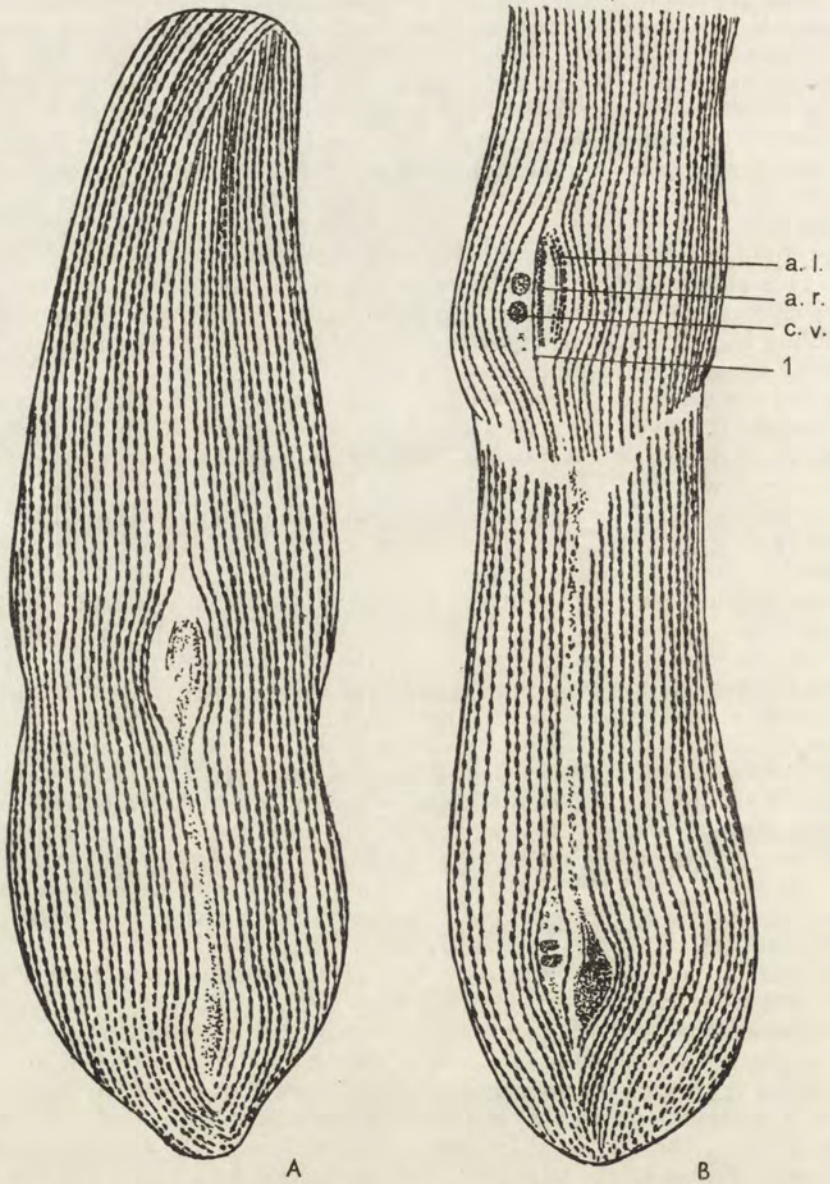


Fig. 3. *T. saxicavae* sp. n.; the first phases of division; a. l. — anlagen of the AZM, a. r. — anlagen of the UM, c. v. — contractile vacuole pores
1 — the first somatic row

and the opisthe, and the old AZM seems to be retained in the proter. Common to all three genera is also the increasing of the number of the kinetosomes of the AZM during division and the subsequent disappearance of some of the kinetosomes.

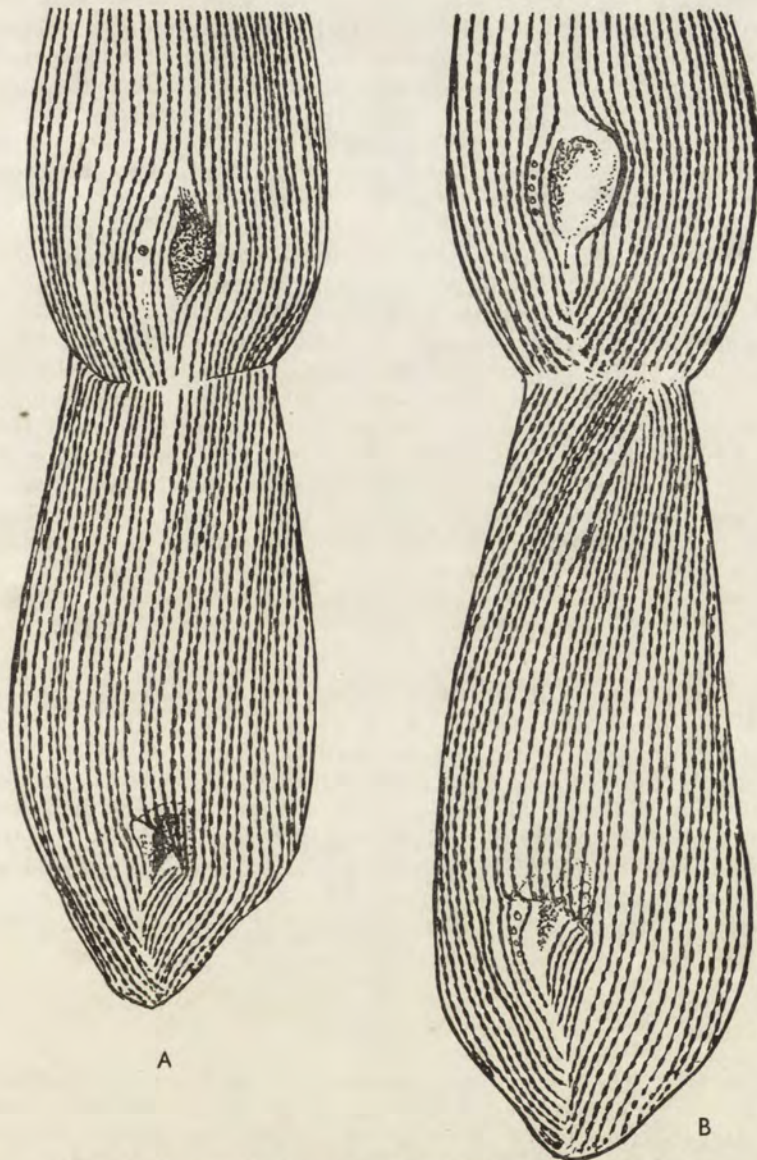


Fig. 4. *T. saxicavae* sp. n.; the later phases of division

The systematic position of *Thigmophrya*

On the basis of the morphological features of *Thigmophrya* previously described (Chatton et Lwoff 1923, Raabe 1936) combined with the present finding of adoral rows and the mode of fission, *Thigmophrya* must be classified as a thigmotrich ciliate. Together with *Myxophyllum* and *Conchophyllum* it forms a family, *Thigmophryidae*, within the order *Thigmotri-*

chida. It is found very unprobable that the *Thigmophryidae* is a primitive family, since the reduced adoral rows and the vestibulum are specialized characters, and the family could not possibly be ancestor of *Hemispeiridae* the members of which have well developed undulating membranes and adoral membranelles.

Looking for the ancestors of *Thigmophryidae* among other thigmotrich groups, the *Conchophthiridae* is found to be the most likely. This group contains, like *Thigmophryidae*, densely ciliated ciliates with reduced adoral rows and a tendency to form a vestibulum. The vestibulum of the genus *Conchophthirus*, however, differs from that of *Thigmophrya*. In the former genus the kineties of the right system go into the vestibulum, in *Thigmophrya* the kineties from the left system do.

Thigmophryidae and *Conchophthiridae* form a group of thigmotrich ciliates, creeping around on the epithelia of their hosts, feeding on particles from the substratum. They are thus flexible forms covered with a dense ciliation and with reduced oral ciliature. Another type of adaptation is seen in *Hemispeiridae*. These ciliates tend to be sessile filter feeders feeding on suspended material. They have strongly developed thigmotactic ciliature and adoral rows, especially an UM, while the somatic ciliature tends to be reduced. These two types are in two fundamentally different ways equally well specialized to the commensalic life in molluscs.

Summary

This paper is concerned with the systematics of the genus *Thigmophrya* Ch. Lw. A new species *T. saxicavae* sp. n. living in the mantle cavity of *Saxicava arctica* (L.) is described. The presence of adoral rows (UM and AZM) in the vestibulum of *Thigmophrya* is demonstrated. The morphogenesis during fission has been studied; it has many points of resemblance with that of *Conchophthirus* St. (Raabe 1963) and that of *Proboveria* Ch. Lw. (Chatton et Lwoff 1936), but the AZM was in no case seen to be split into separate membranelles at any phase of fission. The systematics of *Thigmophryidae* is discussed, it is found to be a specialized family probably closely related to *Conchophthiridae*.

RESUME

Dette arbejde drejer sig om den systematiske stilling slægten *Thigmophrya* Ch. Lw. En ny art *T. saxicavae*, som lever i gællehulen af *Saxicava arctica* (L.), bliver beskrevet. Tilstedeværelsen af adoral rækker (en undulerende membran og en adoral membranelzone) påvises i vestibulum. Morfogenesen under delingen er undersøgt: den har mange lighedspunkter med morfogenesen, som den er blevet beskrevet hos *Conchophthirus* St. (Raabe 1963) og hos *Proboveria* Ch. Lw. (Chatton og Lwoff 1936), men den adoral membranelzone bliver ikke delt op i flere membraneler på noget delingsstadium. *Thigmophryidae*'s systematiske stilling diskuteres, formodentlig er den en specialiseret familie, nært beslægtet med *Conchophthiridae*.

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