"Variation of the tentacles in *Paludicella*": the unfinished work of the German bryozoologist and embryologist Fritz Braem

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1. Introduction

During a visit to the *Zoologische Staatssammlung München* (ZSM; Zoological State Collections Munich) in November 2015, Bernhard Ruthensteiner (section leader Evertebrata varia) handed over to one of us (JS) two envelopes with documents from two German

We dedicate our contribution to the memory of Michael Türkay (1948–2015), who had always been fond of science history research, and who once suggested a study on Fritz Braem, the least known member of the German *Valdivia* Deep Sea Expedition (1888/89).

In memoriam Michael Türkay (1948–2015), head of the Department of Invertebrate Zoology (presently Marine Zoology) at the Senckenberg Research Institute from 1989–2014.

bryozoologists that he donated to the archive of the Senckenberg Gesellschaft für Naturforschung (SGN; Senckenberg Society for Natural Sciences) in Frankfurt am Main, Germany. While one of the envelopes included drawings, film strips, letters and other documents by Dietrich Schneider (1919–2008), the other envelope contained drawings and a letter by Fritz Braem (1862–?). A handwritten note on the cover of the letter comprising the Braem material (Figure 1) confirmed that these documents were handed over by Braem *ca*. 1950 to Wulf Emmo Ankel (1897–1983) and in *ca*. 1960, Ankel passed along Braem's documents to Schneider. Schneider donated the material and his own material to the ZSM thereafter.

Dietrich Schneider worked on marine bryozoans (especially *Bugula* Oken, 1815 and phototropism in Bryozoa) during the 1950s to 1960s (e.g. Schneider 1959; Schneider & Kaissling 1964). Accordingly, Schneider's documents include correspondence letters with several leading bryozoologists of this period including Diethardt Jebram (1937–2004), Ehrhard Voigt (1905–2004) and Claus Nielsen (born 1938). The documents also confirm that Schneider attended the 1983 IBA Conference in Vienna, and visited Voigt in Hamburg. In our article, however, we shall focus on the contents of the second envelope, which is the legacy of Fritz Braem.

Fritz Braem was a bryozoologist and embryologist from Germany, who published for over 63 years on freshwater and brackish bryozoans. He is considered as being one of the pioneers in the study of the anatomy and the embryology of ctenostome and phylactolaemate bryozoans. Still, almost nothing is known about Fritz Braem. This may be due to the fact that Braem's works were not so well received by the scientific community when he was

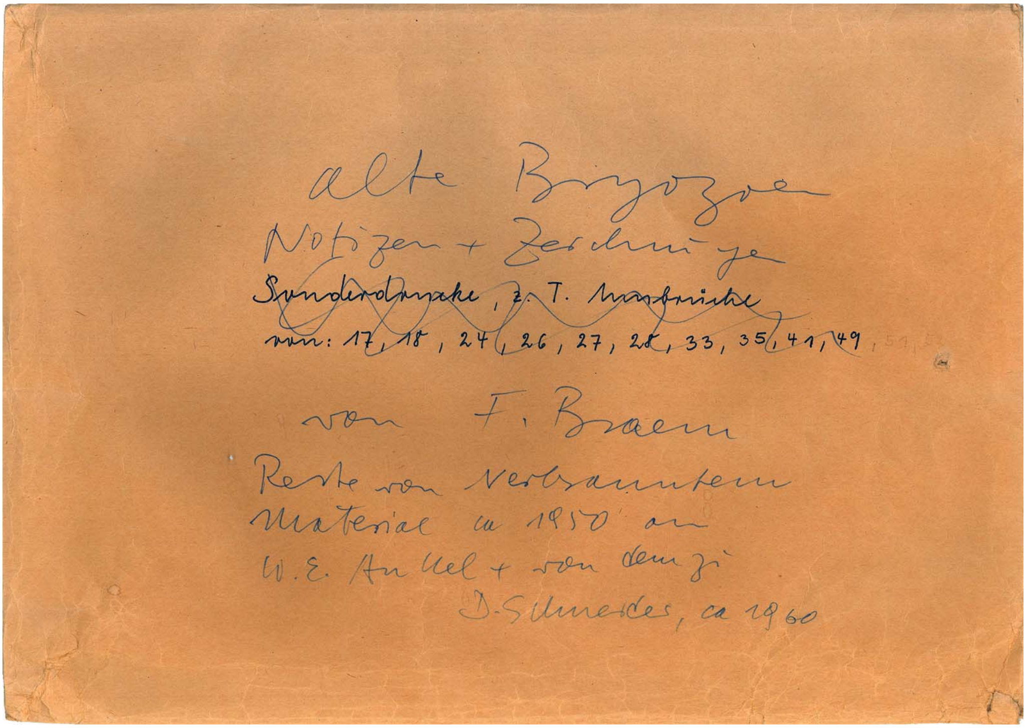


*Figure 1. Envelope containing the recovered documents of Fritz Braem. The handwriting on the cover of the envelope reads „*alte Bryozoen Notizen *(sic)* + Zeichnungen von F. Braem. Reste von verbranntem Material ca. 1950 an W.E. Ankel + von dem zu D. Schneider, ca. 1960 *("old bryozoan notes + drawings by F. Braem. Remains of burnt material ca. 1950 [handed] to W.E. Ankel + then [handed] to D. Schneider, ca. 1960)".*

still alive and he had many scientific disputes with other bryozoologists including Charles Benedict Davenport (1866–1944), Karl Kraepelin (1848–1915) and Asajiro Oka (1866–1944). Despite the want of appreciation by the scientific community and despite having abandoned a science career in 1899, Braem continued his studies on freshwater and brackish bryozoans and continued publishing his results. The recovered material shows that Braem had at least one unfinished project, most of the material and results of which, however, were burnt during World War II.

The recovered material includes a handwritten letter by Fritz Braem, in which he describes, what he remembers from a long-term study on the variation of the tentacles of *Paludicella articulata* (Ehrenberg, 1831). The study included of about 14,000 tentacle measurements on *P. articulata* from rivers and creeks near Berlin, Breslau and Königsberg. Braem observed a large variation in the number of tentacles (5 to 20 tentacles per zooid)[1] and an increase in the number of tentacles in *Paludicella* from the same locality over the year with a peak in October to November. He also found a positive relationship between the length of the tentacles and the amount of tentacles per zooid. A translation of the full letter is provided in Section 4.

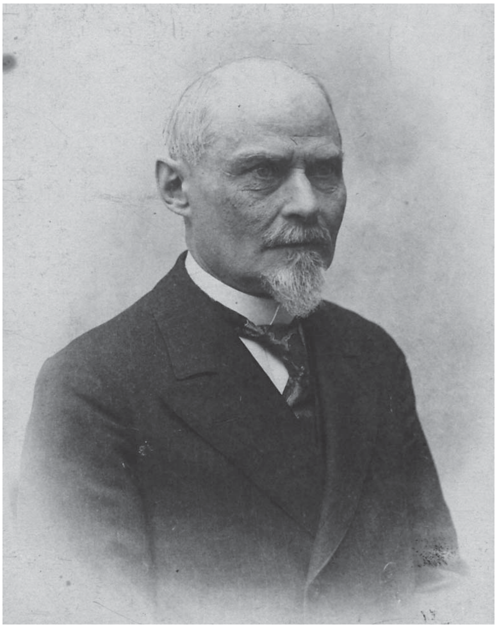


Figure 2. Fritz Braem (1862–?) in 1921. Photograph courtesy of the Staatsblibliothek zu Berlin (State Library of Berlin).

The documents, both of Fritz Braem and of Dietrich Schneider, are now stored in the archive of the SGN (V 176 Nr. 6626 at the Institut für Stadtgeschichte Frankfurt am Main; repository of the archive of the SGN) as suggested by Bernhard Ruthensteiner. The drawings were scanned and are available, as well as PDFs of Fritz Braem's publications, from the authors of this article.

2. Biography of Fritz Braem

Not much is known about the life of Fritz Braem (Figure 2). Most information of his early life is available from the curriculum vitae in his Ph.D. thesis (Braem 1890a), while some insight into his later life was recorded in the yearbooks of the German librarians (*Jahrbuch der Deutschen Bibliothekare*), where Braem is listed from 1902 to 1931. Virtually nothing was found on the private life of Braem. Thus, it remains unclear, whether he ever married and whether he had children, brothers or sisters.

Fritz Braem was born on 1 November 1862 to Minna Braem, née Schmidt, and Heinrich Braem on the estate of his parents in Prilacken, 20 km NW of Königsberg, Prussia (now Kaliningrad, Russian Federation). He attended the Altstädtisches Gymnasium in Königsberg from 1871 and graduated in 1881. The same year, he started to study philology (study of languages) at the Albertus-University of Königsberg, a decision that he regretted later on.[2] In early 1885, he shifted his attention towards the study of natural sciences.

Carl Chun (1852–1914), Professor of Zoology at the Albertus-University of Königsberg at that time, advised Braem to focus his studies on freshwater bryozoans, which Braem started in the summer of 1886.[3] In June 1888, he graduated from the University of Königsberg after passing a state examination and continued his studies as a Ph.D. student of Chun. Braem completed his Ph.D. thesis on the systematics and biogenesis of Prussian freshwater bryozoans on 16 July 1890. He continued to work for Chun as a research fellow and followed him to the Schlesische Friedrich-Wilhelms University in Breslau (now Wroclaw, Poland) in April 1891. He gained a further qualification (habilitation) in June 1893 working on swifts (Braem 1893a) for zoology and comparative anatomy and continued working at the University of Breslau as an associate professor (*Privatdozent*). Fritz Braem belonged to the scientific staff of the first German deep-sea cruise, the *Valdivia* expedition from July 1898 to April 1899 (Figure 3) that was organized by Chun. The scientific career of Braem ended directly after the return of the SS *Valdivia*. The reasons for this turning point in Braem's life have not been made public. We assume that it was not Braem's free choice taking into account his continued scientific ambitions. Braem stayed in correspondence with Chun, but they never saw each other again.[4] Chun edited one of Braem's later publications (Braem 1908a) and Braem contributed with an article to a 'Festschrift' on the occasion of Chun's 60th birthday (Braem 1913).

Figure 3. The participants of the Valdivia *expedition (1898–1899), which was organised by Carl Chun (white circle). Braem (black circle) belonged to the scientific staff of the deep-sea expedition. Photograph courtesy of the Senckenberg archive (Institut für Stadtgeschichte Frankfurt am Main; V 176 Nr. 3219).*

Braem seems to have returned to his hometown Königsberg in 1899 and begun a traineeship at the University Library of Königsberg in 1901. He then started to work as a volunteer at the University Library of Berlin on 15 April 1902 and shortly afterwards at the *Deutsches Bureau der Internationalen Bibliographie der Naturwissenschaften* ("German Bureau for the International Bibliography of Natural Sciences"). Braem received the title Professor on 15 March 1912. He returned from the Bureau to the University Library of Berlin in December 1915, but started to work as an assistant at the State Library of Berlin in November 1916. Braem finally was appointed as *Bibliotheksrat* ('senior librarian officer') in July 1918 and worked at the State Library until he retired on 31 March 1928.

Braem lived in Uhlandstrasse 88 in Berlin-Wilmersdorf, this address being attested for the last time in the address register of Berlin for the year 1943. He died after July 1950, but it was not possible to find any other evidence, neither in the genealogy records of FamilySearch, the world's largest genealogy organization, nor in the register of deaths for Berlin-Wilmersdorf housed in the state archive of Berlin. The last signs of his life are actually the newly discovered letter dated June and July 1950 and his last publication of a manuscript completed much earlier in August 1943 (Braem 1951). Braem handed over his unpublished drawings, a letter and the manuscript for his last publication to Wulf Emmo Ankel, who edited this publication for *Zoologica* in late 1950.

3. Fritz Braem's publications on bryozoans

Braem made 25 scientific contributions to bryozoology that were published over a range of 63 years. His publications can be subdivided into three phases. The first publications appeared during his early scientific career, when he belonged to the scientific staff of Carl Chun at the Universities of Königsberg and Breslau. This phase includes twelve works on bryozoans from 1888 to 1897. His first publications (Braem 1888a, b, 1889a, b) are preliminary results of his Ph.D. thesis. In these publications he referred several times to the first part of Karl Kraepelin's work on German freshwater bryozoans (Kraepelin 1887). It is interesting that Braem accused Kraepelin of having included findings that Braem had communicated to him in his work[5], and he attacked and corrected Kraepelin in his preliminary results several times, making his point also in his later publications. It must be considered very risky by Braem, since he was a student at that time and Kraepelin a professor. Braem finished his Ph.D. thesis on the systematics of freshwater bryozoans in Prussia in 1890 (Braem 1890a), and published a more comprehensive monograph dealing with the anatomy, germination, embryology, sexual reproduction, statoblast formation (Figure 4) and funiculus formation of phylactolaemates and the ctenostome *Paludicella ehrenbergii* van Beneden, 1848 [= *P. articulata* Ehrenberg, 1831] (Braem 1890b). Braem continued thereafter to study the germ layers of freshwater bryozoans (Braem 1892, 1895) and worked on the sexual reproduction of the ctenostome *P. ehrenbergii* [= *P. articulata*] (Braem 1897) and the phylactolaemate *Plumatella fungosa* (Pallas, 1768) (Braem 1896). In a short note, Braem confirmed the finding of

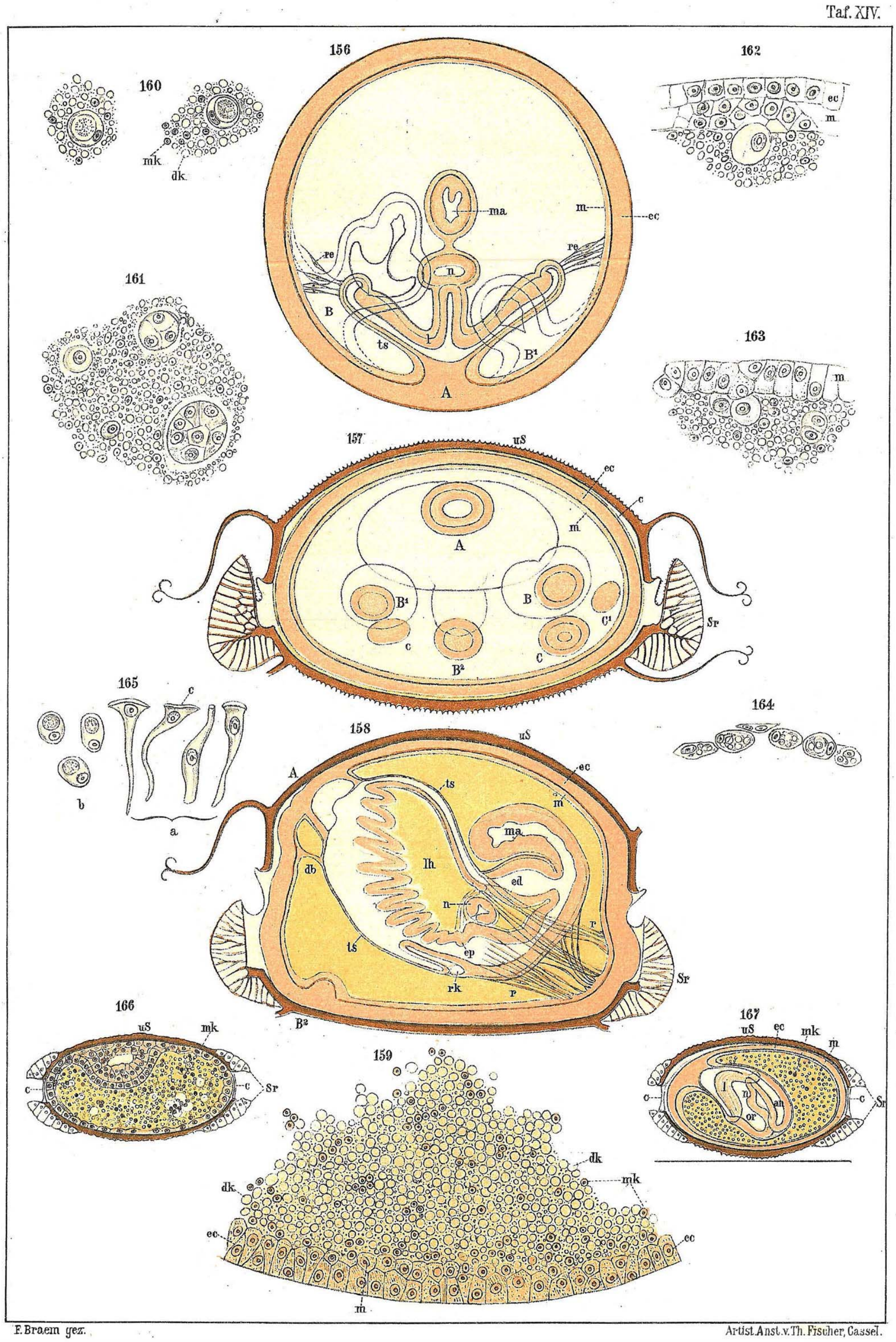


Figure 4. Braem's colour plate (1890b, pl. XIV) showing the germination of statoblasts in Cristatella mucedo *Cuvier, 1798.*

Cristatella mucedo Cuvier, 1798 in Kamchatka, the statoblasts of which were collected by the Polish zoologist Benedykt Dybowski (1833–1930), and he also reported a parasite found in *Cristatella* from Prussia (Braem 1893b). After Kraepelin published the second part of his work on German freshwater bryozoans (Kraepelin 1892) and criticized many of Braem's previous findings, Braem responded by accusing Kraepelin of claiming credits for the work of others and making false statements due to the lack of scientific results (Braem 1893c).[6]

Braem stopped publishing on bryozoans a couple of years prior to the start of the *Valdivia* expedition, but he returned to his studies while working at the German Bureau for the International Bibliography of Natural Sciences in the 1900s. Between 1908 and 1914, he published ten additional studies on bryozoans. In 1908 alone, four publications appeared in which he studied the sexual reproduction of *Fredericella sultana* (Blumenbach, 1779) (Braem 1908a), the spermatozoa of freshwater phylactolaemates (Braem 1908c) and ctenostomes (Braem 1908b) and the ovum of *P. fungosa* (Braem 1908d). Braem later received material from the Issyk-Kul in Kyrgyzstan collected by the Russian zoologist Dmitry D. Pedashenko (1868–1927) and described the fauna consisting of one phylactolaemate and one ctenostome bryozoan and studied the parasites found in the former (Braem 1911a). He continued his work by comparing the larvae of cheilostome bryozoans and pterobranchs (Braem 1911c) and studying the variation in the statoblasts of *Pectinatella magnifica* (Leidy, 1851) (Braem 1911b, 1912), and the germination of statoblasts in *C. mucedo* and *P. magnifica* (Braem 1913). Braem's last work from the second phase of publications was on the budding in *Paludicella* (Braem 1914b).

Braem stopped publishing on bryozoans in 1914, the reason being probably that Braem changed his position twice and was promoted to a senior librarian officer at the State Library of Berlin in 1918. It may be safe to speculate that Braem did not have enough time and opportunities anymore to maintain his scientific research especially during WWI. However, subsequently he continued his research on bryozoans in his own free time and using his own resources, since most of the fieldwork for his final contribution (Braem 1951) was done in 1921–1929. During the 1930s, he mainly worked on the variations of the tentacles of *Paludicella*, the results of which are summarized in his letter (Section 4 below), but in the late 1930s to early 1940s, Braem would complete another four publications. Braem corresponded with Sidney Harmer (1862–1950) in 1926[7] and started a revision of material from the *Siboga* expedition of *Victorella sibogae* Harmer, 1915, which was the only species assigned to *Victorella* Saville Kent, 1870 from a marine environment. He found that the species belonged to a yet undescribed genus and family (Braem 1939). In Braem (1940a), he revised material of *Pottsiella erecta* (Potts, 1884) from Pennsylvania and erected a new family for this ctenostome bryozoan. In another publication, he compared the intestines of cheilostome and ctenostome gymnolaemate bryozoans (Braem 1940b). Braem's last manuscript was written by August 1943, but would not be published until 1951. Braem (1951) described the brackish bryozoan fauna of the River Ryck near Greifswald and the results of a long-term study started in 1911 and completed in 1941.

4. Variation of the tentacles in *Paludicella*

A translation of Braem's letter (Figures 5–9) reads as follows:

Among my burnt [during WWII] materials, there were also charts with approximately 14,000 (fourteen thousand) absolutely definite tentacle counts of *Paludicella*. The animals were mostly derived from the area around Königsberg in Prussia, Breslau and Berlin, most of them from the Woltersdorfer Fließ near Berlin. Origin, date, and when appropriate the kind of individual (whether dietallae, intercalary or regenerative bud or individual larvae) were noted down for all. Extreme cases (of significantly high or low numbers) were documented by a series of sections.

The amount of variation in *Paludicella* is extremely high, it reaches from five to 20 tentacles. Five tentacles build an exception as they were found only once. I do not recall whether it was a dietalla, intercalary or regenerative bud. The animal was developed normally in all parts. Six tentacles did not occur which might also be a coincidence. From seven to 20 tentacles, the series was complete and all numbers were represented, while seven, eight and 20 tentacles were of smaller numbers; maybe below ten. Eight tentacles were not more frequent than seven, but were even short of seven which is most likely coincidence; in any case this shows that (*Pal*. bares no closer relation to the eight tentacle forms [crossed out]) number eight in *Pal*. in no way dominates, which could be expected since this number is the predominant one in relatives of *Pal*. and also the case in *Victorella*. Nine tentacles are already significantly more frequent and frequency increases now with growing numbers until it reaches its peak with 16 or 17 tentacles. In one case of animals that were collected in June 1929 at the Lauther Mühlenfließ near Königsberg (under the Chausseebridge), the count (more than one hundred individuals) even showed 18 as the most frequent number. After a slow rise to the peak, frequency decreases rapidly: 19 tentacles are considerably rarer than 18, and 20, the highest number that I have encountered, is a very infrequent case.

The result of the average value of numbers of tentacles determined for the Woltersdorf specimens for the respective months was a slow increase in the course of the year so that they were highest in October and November. I cannot say for sure what this resulted from.

[Crossed out section] *The length of tentacles increases (by a multiple* [crossed out]) *according to their number. On average ten tentacles are longer than nine tentacles, eleven longer than ten and so on. In general, this is the case, but of course there are single cases of deviation. The shortest tentacles were not those of the animal with five t.* [tentacles]*, but of one with a number of seven t., the longest not those of one with 20, (but with 18 t.* [crossed out]*, I (also do not think with 19 t., but one with 18 or 17 t.)* [replaced here] *since the lengths also vary when the number of tentacles is identical, thus reaching into areas of higher or lower numbers of tentacles.*

The length of tent. increases significantly according to their number. On average ten are longer than nine, eleven longer than ten and so on. In general this is the case but of course there are single cases of deviation since the lengths also vary when the number of tentacles is identical, thus reaching into areas of higher or lower numbers of tentacles. I remember for instance that the shortest of all tentacles were not those of an animal with five, but with seven t., the longest not those of one with 20, I also do not think with 19 t., but one with 18 or 17 t. I cannot give exact measures. The longest tentacles remain below 1 mm, the shortest may have measured 1/10 or fewer.

The increase of length according to the number of tentacles stands in opposition to the behaviour of the phylactolamates' statoblasts' spines, whose size decreases with growing number. This is due to that as essential organs the tentacles stand in approximately determined relation to the size of the whole body, which in *Pal.* varies to the same amount as the size and number of the tent. In comparison to the biggest, the smallest individuals of *Pal.* are true midgets, and could neither produce nor operate such an immense tentacle apparatus as the former could. In the statoblasts that are of approximately the same size, the number of cells available for the formation of spines is equivalent, and where many spines evolve, their size inevitably needs to be smaller than where only few of them are present.

This is what I kept from the charts. They are raw material that was awaiting subtler attention, which I could not give them.

June 1950

The following data on the tentacles of ancestrulae that evolved from larvae between the years 1935–37 is not based on memories, but on notes that were saved. The colonies covered with eggs were placed into glasses of water stuffed with microscope slides and collodium lamellae at which the hatched larvae could find the opportunity to settle. In order to examine the growth, the microscope slides etc. were removed and investigated under the microscope in flat small bowls. The entire material originated from the old Havel at Birkenwerder.

In the following collocation, the number of ancestrulae observed with their number of tentacles is indicated below the year dates.

	1935	**1936**	**1937**	**1935–37**
mother colonies	from July and Aug.	f. June a. July	f. July a. Aug.	f. June–Aug.
9 tent.		1	1	2
10 –	5	17	4	26
11 –	20	48	11	29
12 –	1	8	2	11
	26	74	18	118

One can observe that in all three years with 60 % of all cases eleven tentacles were most frequent, followed by ten tent., then 12 and finally nine. This may also be the case for other years of which the records are lost, however, I remember also having found 13 tent. Within the 118 pieces, one finding I made in October 1935 at a time I had presumed the sexual development as long completed, is not being measured. Up to then the latest date, I had found *Paludicella* become sexually mature was August 30, 1935. Due to sickness during September that year, I could not visit the site. When I came back there on 3 October, I stumbled upon a stick covered with eggs. This also remained the latest date in the following years for me to discover such. At home, 13 larvae from these eggs developed into young small colonies with protrudable ancestrulae, [with] eight a. nine tent., [in] each one colony, ten tent. [in] nine [colonies] a. eleven tent. [in] two colonies. Here, in contrast to the summer animals, the scale of tentacles went down one level, twelve tent. are entirely missing and eight add, while ten tent., instead of eleven tent. in summer, presents the dominant number. This can only be an effect of the lower temperatures in my rooms that ranged between 16 and 18°C back then. The feeding can only be a factor after protrusibility[8] since the larva up to then lives on the yolk accumulated inside and the degenerating larval organs of which remnants can often be even found in the rectum even when protrusibility has been reached. The longer duration of development of these autumnal individuals can also be led back to the influence of temperature. The 118 summer specimens needed at least four, mostly five, and sometimes six days from settlement to protrusibility of the primary polypide. The same took the 13 autumn specimens once seven, mostly eight, once nine a. once eleven days. When in one incident after 19 days no protrusibility had occurred. I conserved the animal and determined the number of tentacles by section (nine tent.).

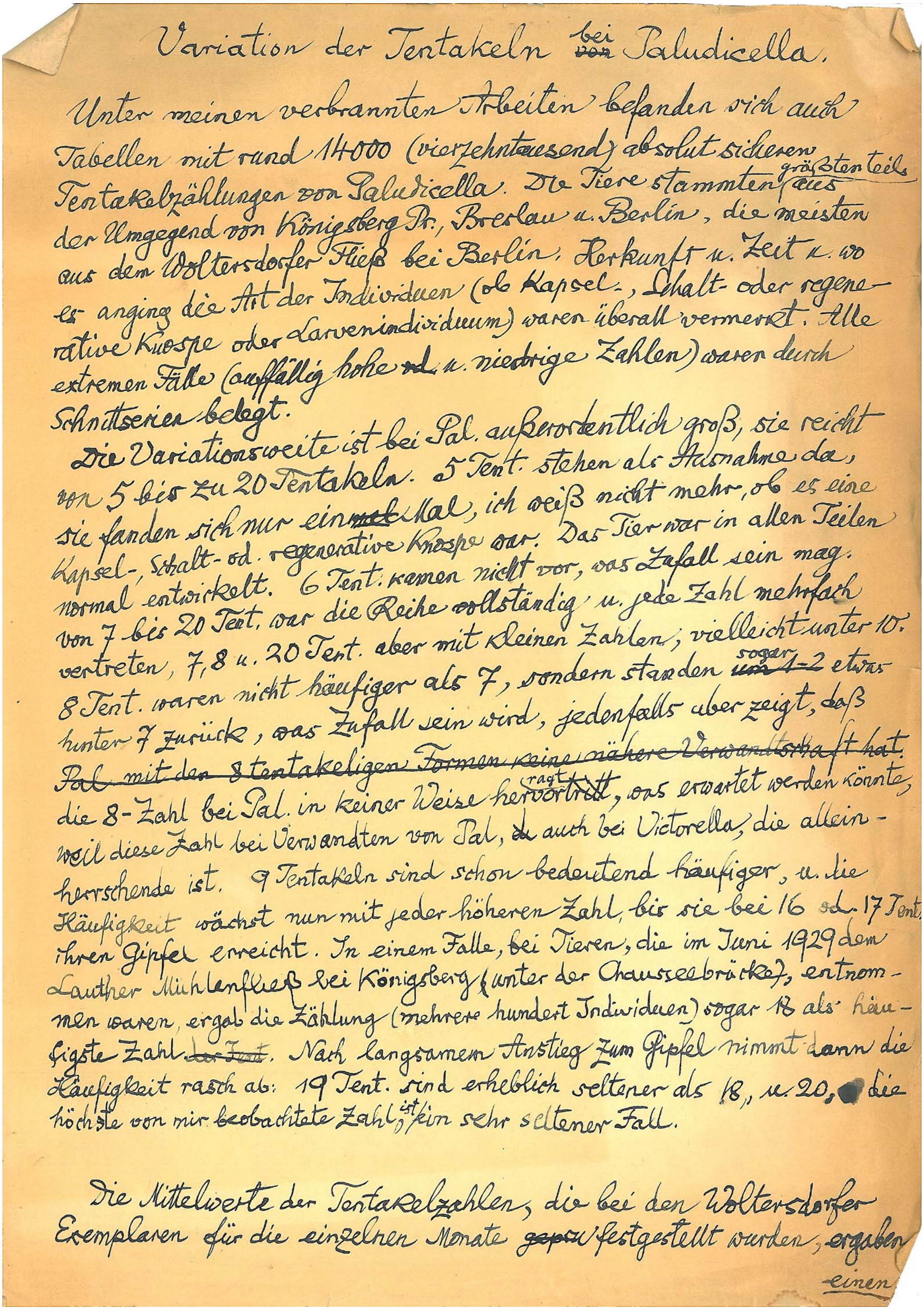
Measuring the tentacles of the primary animals shortly after first becoming protrusible showed the following results: nine tent. 0.1 mm, 10 t. 0.12–0.17 mm, 11 t. 0.13–0.22 mm, 12 t. 0.16–0.23 mm.

The letter is accompanied by a short note (Figure 10).

Everything else, meaning the largest part, is burnt.

F. Braem

July 1950



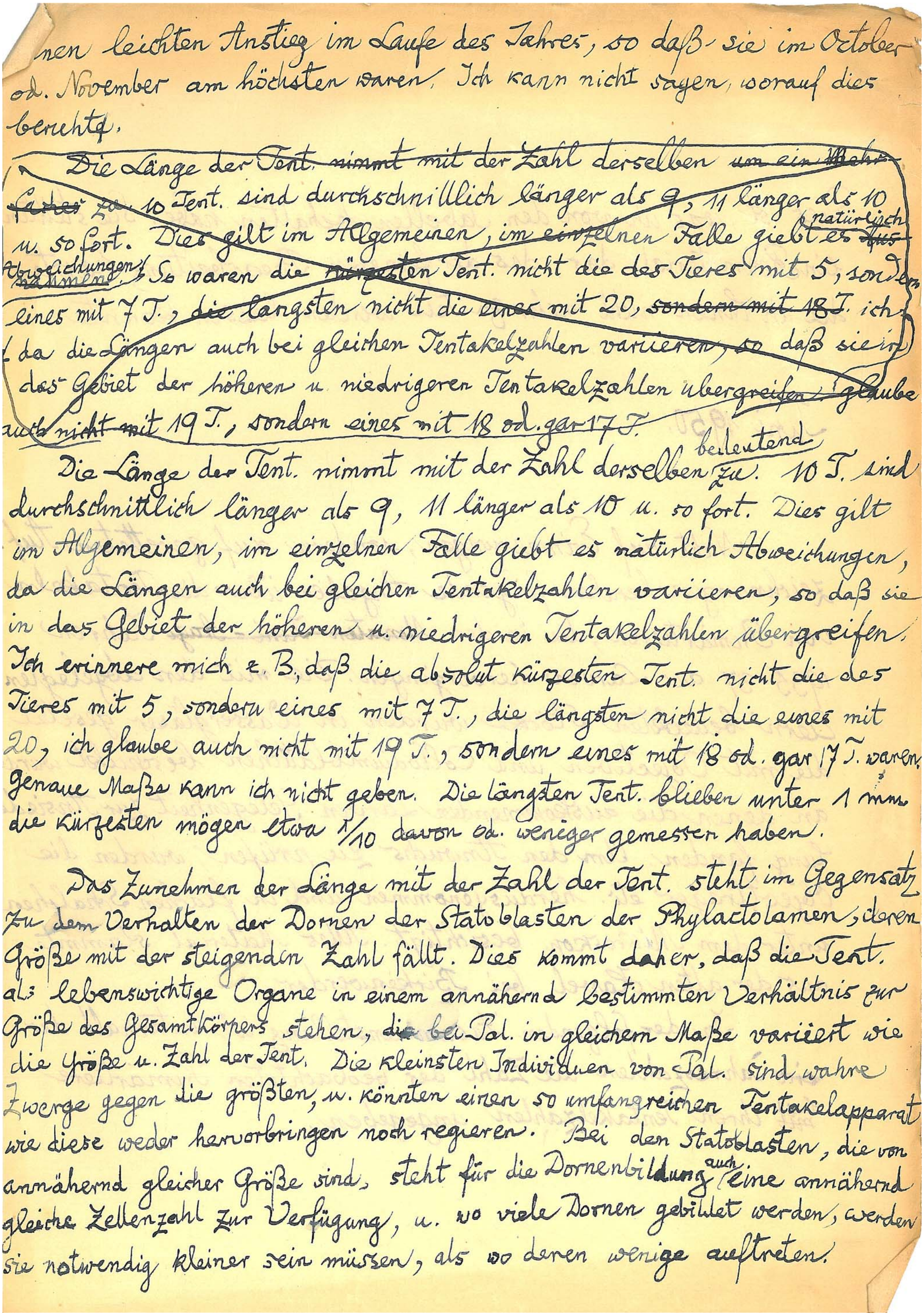
Variation der Tentakeln bei ~~von~~ Paludicella.

Unter meinen verbrannten Arbeiten befanden sich auch Tabellen mit rund 14000 (vierzehntausend) absolut sicheren Tentakelzählungen von Paludicella. Die Tiere stammten größtenteils aus der Umgegend von Königsberg Pr., Breslau u. Berlin, die meisten aus dem Woltersdorfer Fließ bei Berlin. Herkunft u. Zeit u. wo es anging die Art der Individuen (ob Kapsel-, Schalt- oder regenerative Knospe oder Larvenindividuum) waren überall vermerkt. Alle extremen Fälle (auffällig hohe ~~od.~~ u. niedrige Zahlen) waren durch Schnittserien belegt.

Die Variationsweite ist bei Pal. außerordentlich groß, sie reicht von 5 bis zu 20 Tentakeln. 5 Tent. stehen als Ausnahme da, sie fanden sich nur ein~~mal~~ Mal, ich weiß nicht mehr, ob es eine Kapsel-, Schalt- od. regenerative Knospe war. Das Tier war in allen Teilen normal entwickelt. 6 Tent. kamen nicht vor, was Zufall sein mag. Von 7 bis 20 Tent. war die Reihe vollständig u. jede Zahl mehrfach vertreten, 7, 8 u. 20 Tent. aber mit kleinen Zahlen, vielleicht unter 10. 8 Tent. waren nicht häufiger als 7, sondern standen sogar ~~um~~ 1-2 etwas hinter 7 zurück, was Zufall sein wird, jedenfalls aber zeigt, daß ~~Pal mit den 8 tentakeligen Formen keine nähere Verwandtschaft hat.~~ die 8-Zahl bei Pal. in keiner Weise ragt ~~hervortritt~~, was erwartet werden könnte, weil diese Zahl bei Verwandten von Pal, ~~da~~ auch bei Victorella, die allein-herrschende ist. 9 Tentakeln sind schon bedeutend häufiger, u. die Häufigkeit wächst nun mit jeder höheren Zahl, bis sie bei 16 od. 17 Tent. ihren Gipfel erreicht. In einem Falle, bei Tieren, die im Juni 1929 dem Lauther Mühlenfließ bei Königsberg (unter der Chausseebrücke), entnommen waren, ergab die Zählung (mehrere hundert Individuen) sogar 18 als häufigste Zahl ~~der Tent.~~. Nach langsamem Anstieg zum Gipfel nimmt dann die Häufigkeit rasch ab: 19 Tent. sind erheblich seltener als 18, u. 20, die höchste von mir beobachtete Zahl, ist ein sehr seltener Fall.

Die Mittelwerte der Tentakelzahlen, die bei den Woltersdorfer Exemplaren für die einzelnen Monate ~~gegen~~ festgestellt wurden, ergaben einen

Figure 5. First page of Braem's letter on the variation of the tentacles in Paludicella articulata. *(Institut für Stadtgeschichte Frankfurt am Main; V 176 Nr. 6626)*



nen leichten Anstieg im Laufe des Jahres, so daß sie im October od. November am höchsten waren. Ich kann nicht sagen, worauf dies beruhte.

~~Die Länge der Tent. nimmt mit der Zahl derselben um ein Mehrfaches zu. 10 Tent. sind durchschnittlich länger als 9, 11 länger als 10 u. so fort. Dies gilt im Allgemeinen, im einzelnen Falle giebt es natürlich Ausnahmen Abweichungen. So waren die kürzesten Tent. nicht die des Tieres mit 5, sondern eines mit 7 T., die längsten nicht die eines mit 20, sondern mit 18 T. ich da die Längen auch bei gleichen Tentakelzahlen variieren, so daß sie in das Gebiet der höheren u. niedrigeren Tentakelzahlen übergreifen. glaube auch nicht mit 19 T., sondern eines mit 18 od. gar 17 T.~~

Die Länge der Tent. nimmt mit der Zahl derselben bedeutend zu. 10 T. sind durchschnittlich länger als 9, 11 länger als 10 u. so fort. Dies gilt im Allgemeinen, im einzelnen Falle giebt es natürlich Abweichungen, da die Längen auch bei gleichen Tentakelzahlen variieren, so daß sie in das Gebiet der höheren u. niedrigeren Tentakelzahlen übergreifen. Ich erinnere mich z. B., daß die absolut kürzesten Tent. nicht die des Tieres mit 5, sondern eines mit 7 T., die längsten nicht die eines mit 20, ich glaube auch nicht mit 19 T., sondern eines mit 18 od. gar 17 T. waren. Genaue Maße kann ich nicht geben. Die längsten Tent. blieben unter 1 mm, die kürzesten mögen etwa 1/10 davon od. weniger gemessen haben.

Das Zunehmen der Länge mit der Zahl der Tent. steht im Gegensatz zu dem Verhalten der Dornen der Statoblasten der Phylactolamen, deren Größe mit der steigenden Zahl fällt. Dies kommt daher, daß die Tent. als lebenswichtige Organe in einem annähernd bestimmten Verhältnis zur Größe des Gesamtkörpers stehen, die bei Pal. in gleichem Maße variiert wie die Größe u. Zahl der Tent. Die kleinsten Individuen von Pal. sind wahre Zwerge gegen die größten, u. könnten einen so umfangreichen Tentakelapparat wie diese weder hervorbringen noch regieren. Bei den Statoblasten, die von annähernd gleicher Größe sind, steht für die Dornenbildung auch eine annähernd gleiche Zellenzahl zur Verfügung, u. wo viele Dornen gebildet werden, werden sie notwendig kleiner sein müssen, als wo deren wenige auftreten.

Figure 6. Second page of Braem's letter on the variation of the tentacles in P. articulata.

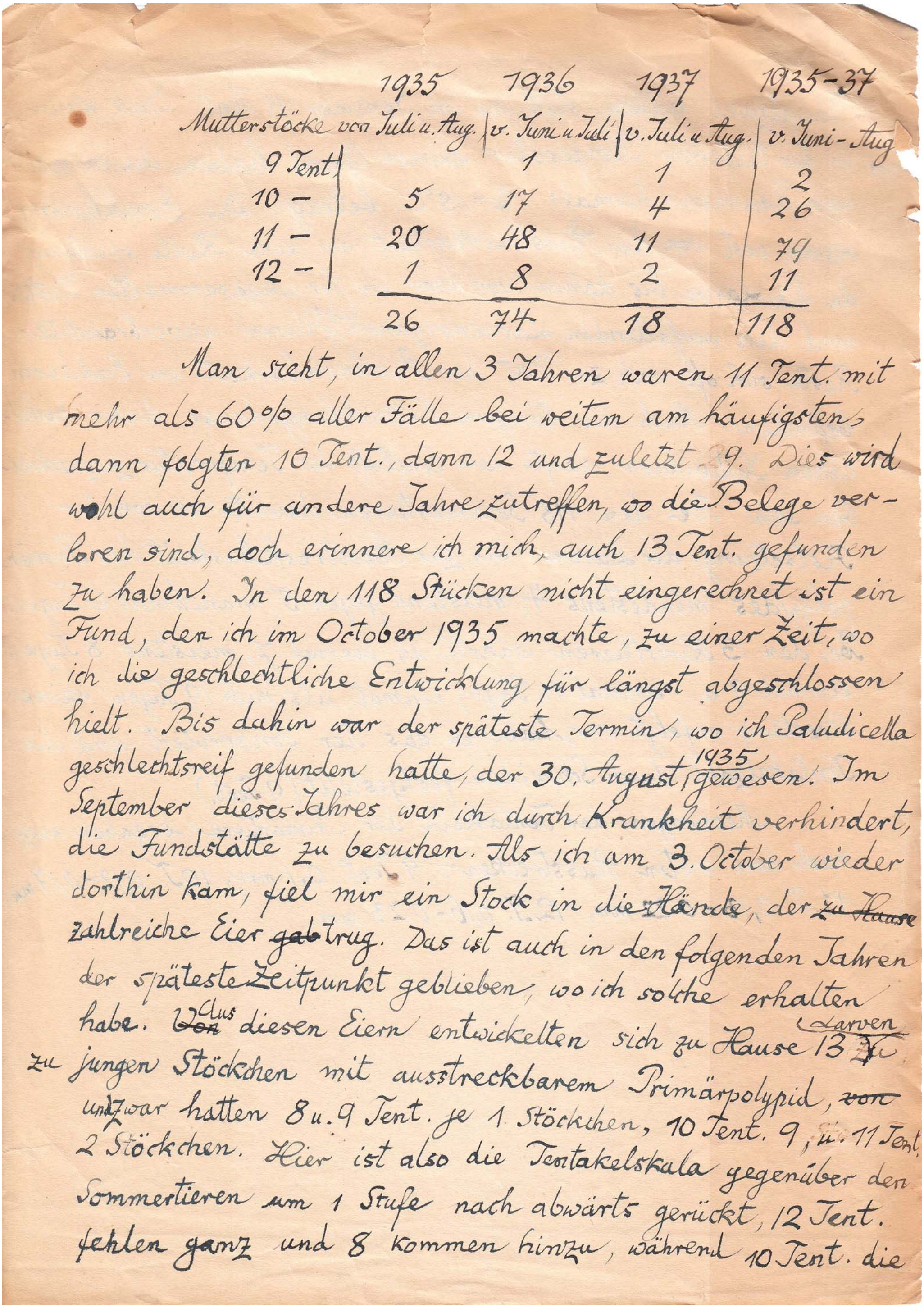
Dies ist, was ich von den Tabellen behalten habe. Sie stellten ein Rohmaterial dar, das der feineren Bearbeitung harrte, die ich ihnen nicht mehr zu Teil werden lassen konnte.

Juni 1950.

Nicht auf Erinnerungen, sondern auf geretteten Aufzeichnungen beruhen folgende Angaben über die Tentakeln von Primärtieren, die in den ~~Monaten Juni - Aug.~~ Jahren 1935-37 aus Larven hervorgingen. Die mit den abgelegten Eiern bedeckten Stöcke wurden in Wassergläser gesetzt, die mit Objectiven und Collodiumblättchen beschickt wurden, an denen die auskommenden Larven Gelegenheit zur Ansiedelung fanden. Um den Anwuchs zu prüfen, wurden die Objectträger etc. herausgenommen und in flachen Schälchen unter dem Microskop besichtigt. Alles Material stammte aus der alten Havel bei Birkenwerder.

In der folgenden Zusammenstellung ist unterhalb der ~~ein~~ Jahreszahlen die Zahl der beobachteten Primärtiere ~~mit~~ bei ihren Tentakelzahlen angegeben.

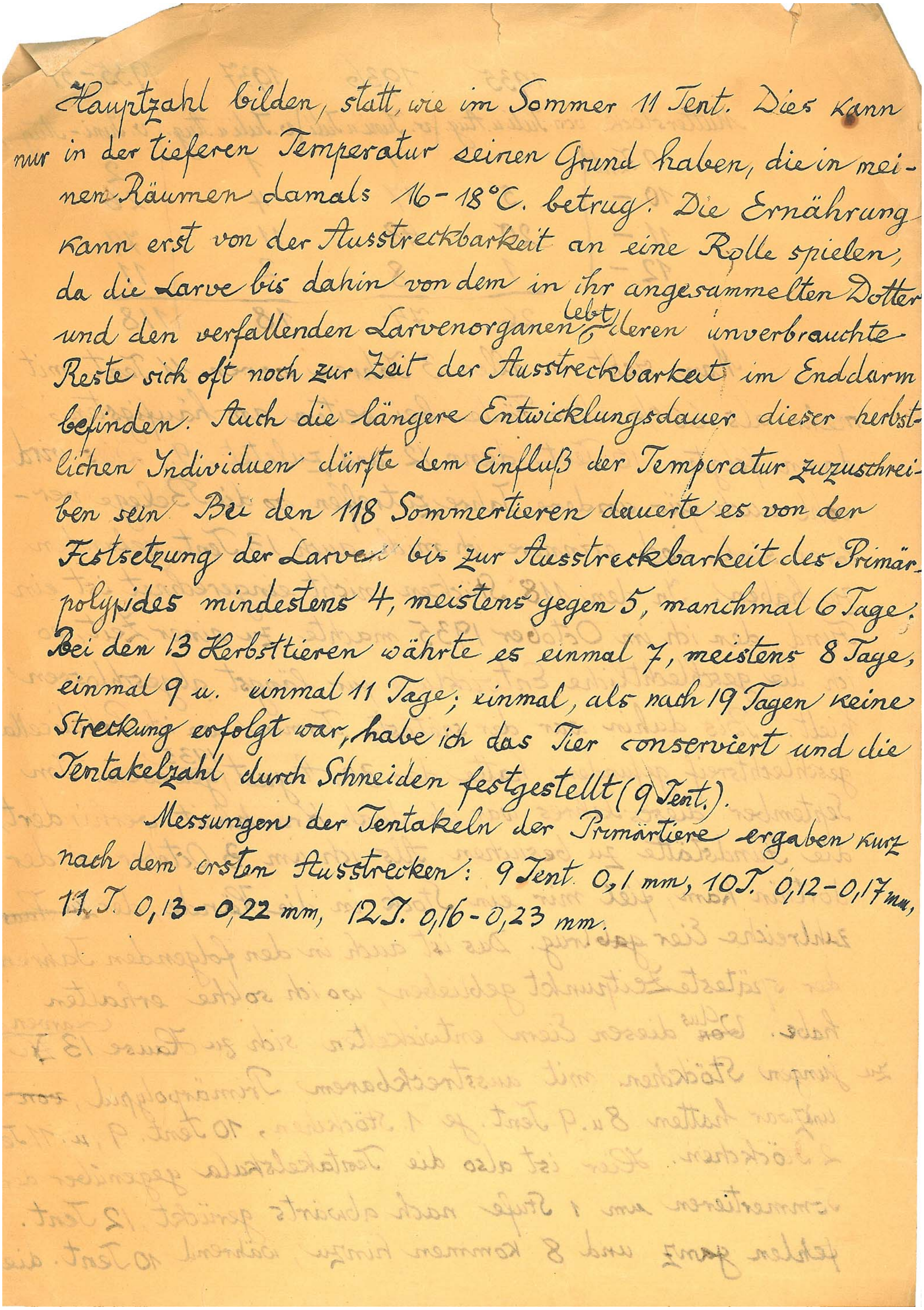
Figure 7. Third page of Braem's letter on the variation of the tentacles in P. articulata.



	1935	1936	1937	1935–37
Mutterstöcke	von Juli u. Aug.	v. Juni u. Juli	v. Juli u. Aug.	v. Juni–Aug.
9 Tent.		1	1	2
10 –	5	17	4	26
11 –	20	48	11	79
12 –	1	8	2	11
	26	74	18	118

Man sieht, in allen 3 Jahren waren 11 Tent. mit mehr als 60% aller Fälle bei weitem am häufigsten, dann folgten 10 Tent., dann 12 und zuletzt 9. Dies wird wohl auch für andere Jahre zutreffen, wo die Belege verloren sind, doch erinnere ich mich, auch 13 Tent. gefunden zu haben. In den 118 Stücken nicht eingerechnet ist ein Fund, den ich im October 1935 machte, zu einer Zeit, wo ich die geschlechtliche Entwicklung für längst abgeschlossen hielt. Bis dahin war der späteste Termin, wo ich Paludicella geschlechtsreif gefunden hatte, der 30. August (1935) gewesen. Im September dieses Jahres war ich durch Krankheit verhindert, die Fundstätte zu besuchen. Als ich am 3. October wieder dorthin kam, fiel mir ein Stock in die Hände, der ~~zu Hause~~ zahlreiche Eier ~~gab~~ trug. Das ist auch in den folgenden Jahren der späteste Zeitpunkt geblieben, wo ich solche erhalten habe. ~~Von~~ Aus diesen Eiern entwickelten sich zu Hause 13 Larven zu jungen Stöckchen mit ausstreckbarem Primärpolypid, ~~von~~ und zwar hatten 8 u. 9 Tent. je 1 Stöckchen, 10 Tent. 9, u. 11 Tent. 2 Stöckchen. Hier ist also die Tentakelskala gegenüber den Sommertieren um 1 Stufe nach abwärts gerückt, 12 Tent. fehlen ganz und 8 kommen hinzu, während 10 Tent. die

Figure 8. Fourth page of Braem's letter on the variation of the tentacles in P. articulata.



Hauptzahl bilden, statt, wie im Sommer 11 Tent. Dies kann nur in der tieferen Temperatur seinen Grund haben, die in meinen Räumen damals 16–18°C. betrug. Die Ernährung kann erst von der Ausstreckbarkeit an eine Rolle spielen, da die Larve bis dahin von dem in ihr angesammelten Dotter und den verfallenden Larvenorganen lebt, deren unverbrauchte Reste sich oft noch zur Zeit der Ausstreckbarkeit im Enddarm befinden. Auch die längere Entwicklungsdauer dieser herbstlichen Individuen dürfte dem Einfluß der Temperatur zuzuschreiben sein. Bei den 118 Sommertieren dauerte es von der Festsetzung der Larven bis zur Ausstreckbarkeit des Primärpolypides mindestens 4, meistens gegen 5, manchmal 6 Tage; Bei den 13 Herbsttieren währte es einmal 7, meistens 8 Tage, einmal 9 u. einmal 11 Tage; einmal, als nach 19 Tagen keine Streckung erfolgt war, habe ich das Tier conserviert und die Tentakelzahl durch Schneiden festgestellt (9 Tent.).

Messungen der Tentakeln der Primärtiere ergaben kurz nach dem ersten Ausstrecken: 9 Tent. 0,1 mm, 10 T. 0,12–0,17 mm, 11 T. 0,13–0,22 mm, 12 T. 0,16–0,23 mm.

Figure 9. Fifth page of Braem's letter on the variation of the tentacles in P. articulata.

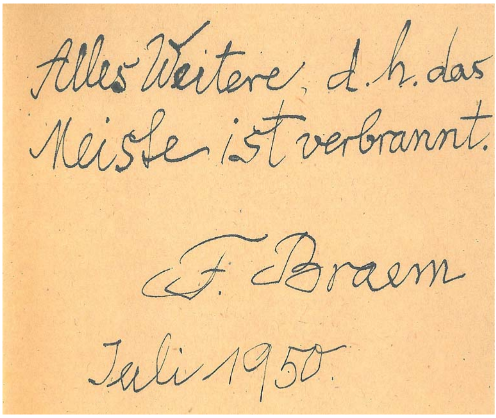


Figure 10. Note accompanying the recovered material of Fritz Braem.

5. New taxa erected by Fritz Braem

Fritz Braem was no taxonomist but an anatomist. Nevertheless, in his later publications, he suggested some new taxa, the first of which was a freshwater ctenostome that he found in bryozoan material from the Issyk-Kul (Braem 1911a). Overall, Braem erected six new bryozoan taxa, all of which are ctenostomes (Table 1). Among these are two new species, three new genera and one new family; *Bulbella* Braem, 1951 (type species *B. abscondita* Braem, 1951), Pottsiellidae (type genus *Pottsiella* Kraepelin, 1887), *Sundanella* Braem, 1939 (type species *Victorella sibogae* Harmer, 1915), *Tanganella* Braem, 1951 (type species *Paludicella muelleri* Kraepelin, 1887) and *Victorella continentalis* Braem, 1911a.

In his revision of *Victorella sibogae* Harmer, 1915, Braem (1939) found that the species is quite distinctive from any *Victorella* species and created the new, monospecific genus *Sundanella*. He also found that the species was so distinctive from any other ctenostome that he proposed a new family for it. Although the proposed family included only one genus, which would be the stem for the family-group name, he did not clearly use the name

Table 1. Bryozoan taxa erected by Fritz Braem. All taxa are Ctenostomata.

Taxon	**First description**	**Occurrence**	**Habitat**
Bulbella	Braem, 1951	Ryck, Germany	Brackish
Bulbella abscondita	Braem, 1951	Ryck, Germany	Brackish
Pottsiellidae	Braem, 1940a	Tacony Creek, USA	Freshwater
Sundanella	Braem, 1939	Java Sea, Indonesia	Marine
Tanganella	Braem, 1951	Ryck, Germany	Brackish
Victorella continentalis	Braem, 1911a	Issyk-Kul, Kyrgyzstan	Freshwater

to refer to the new family.[9] This is a violation of Article 11.7 of the *International Code of Zoological Nomenclature* (ICZN 1999) and the family name Sundanellidae is attributed to Jebram (1973), who was the first to use it as a scientific name.[10] The name Pottsiellidae was also proposed in Jebram (1986), Braem (1940a) not being cited by Jebram (1986). Since the use of Pottsiellidae in Braem (1940a) is in accordance with the *International Code of Zoological Nomenclature*, the family name proposed in Jebram (1986) is a homonym and the oldest available name, i.e. Pottsiellidae Braem, 1940a, has to be considered the valid name for the taxon (ICZN 1999, Article 23.1).

6. Braem's drawings

The recovered documents contain approximately 350 sheets with drawings and explanatory notes of Fritz Braem. The drawings are usually made on the reverse sides of advertisements, wedding invitations and others. Part of the drawings were also produced on papers from the *Valdivia* expedition. From the dates indicated on some of the reverse sides, we can say that Braem conducted his studies in the 1920s to 1930s. Braem's drawings are very diverse and very detailed. Most show different aspects in the embryonic development of *Paludicella articulata* (Ehrenberg, 1831). However, there are also some drawings of other freshwater and marine ctenostomes including *Amathia pustulosa* (Ellis & Solander, 1786), *Buskia socialis* Hincks, 1887 and *Pottsiella erecta* (Potts, 1884) that show different aspects in the morphology of these species.

Out of the material, we selected to depict three drawings, all of which show new information that have not been previously published to our knowledge. Figure 11 shows the early cleavage in *P. articulata* including also polar bodies, which are extremely difficult to observe and mitotic spindles. Braem also has tracked the fate of early blastomeres, which is a remarkable achievement. In Figure 12, the early embryonic development, the gastrulation, of *P. articulata* is depicted and in Figure 13, Braem showed a fully developed larva of this species. Its embryonic development and the full larva itself are shown in more detail than previously available. Note that no scale is provided, nor are all the drawings prepared by Braem to the same scale.

7. Braem's work on bryozoan anatomy and reproductive biology

Several of Braem's achievements are still unsurpassed today. Our knowledge on the embryonic development of Phylactolaemata largely results from his works (Braem 1890b, 1897, 1908a). There were several contributions to this field from other authors (e.g. Reinhard 1881, Kraepelin 1892, Marcus 1934, Mukai 1982), but none are as detailed and beautifully illustrated as those of Braem. Studying particularly the early embryonic development is extremely difficult since early brooding sacs resemble asexually produced buds and thus are difficult to discriminate. Likewise, Braem was one of the first to recognize the placental nourishment of the embryos in this group (summarized in Ostrovsky *et al.* 2016) as well as the first to describe and illustrate larval metamorphosis

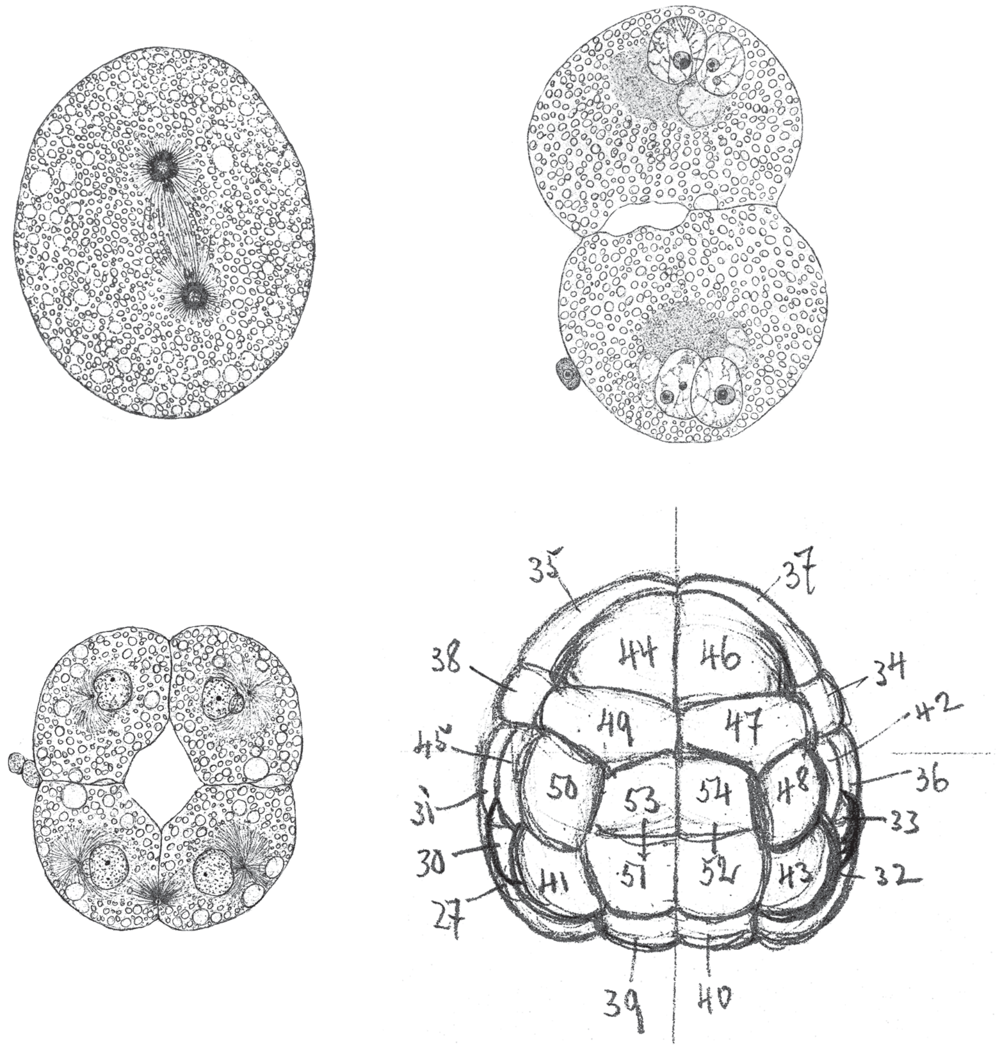


Figure 11. Early cleavage in Paludicella articulata *(Ehrenberg, 1831), showing polar bodies, mitotic spindles, and tracking the ancestry of blastomeres.*

in Phylactolaemata.

Statoblasts are phylactolaemate specific dormant buds that are mainly used for overwintering and dispersal. The germination of these dormant stages is triggered by different environmental cues (e.g. Brown 1933, Oda 1959, Mukai 1982). Braem (1890b) was the first to experimentally test different factors, such as temperature on the germination of statoblasts. Likewise, he was one of few investigators studying the germination process on a histological level (Braem 1890b, 1913). In fact, his observations giving details on the organization of the early epithelium, formation of the internal bud and organogenesis during the germination process provide the original data on these matters. There are

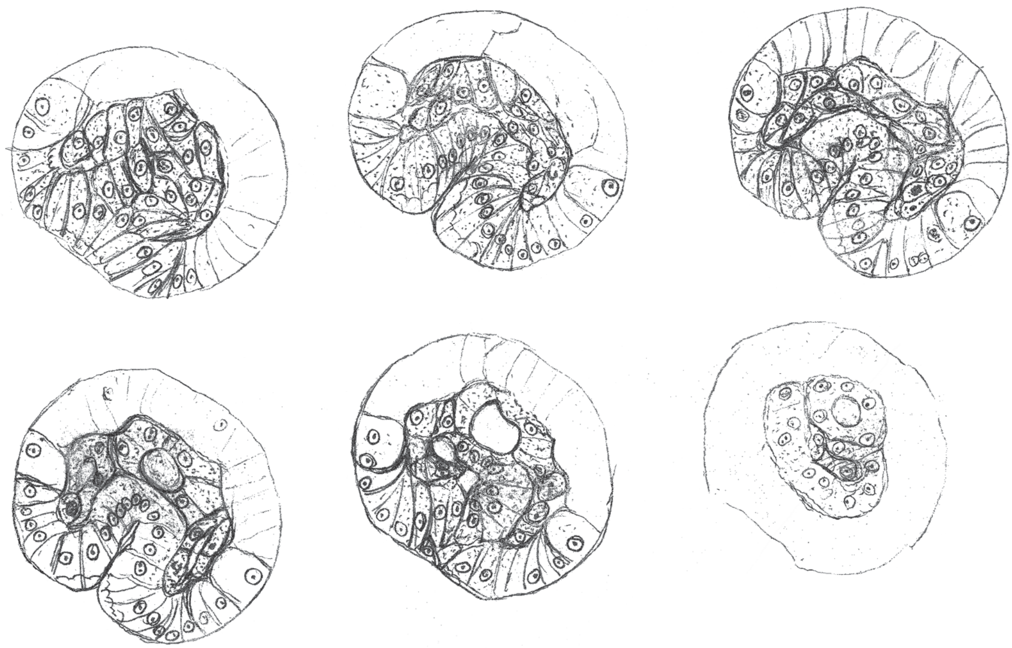


Figure 12. Early embryonic development in Paludicella articulata *(Ehrenberg, 1831) showing gastrulation.*

Figure 13. Fully developed larva of Paludicella articulata *(Ehrenberg, 1831).*

several difficulties beset with such a study: first, early germination stages develop with the statoblast valves closed and when the latter open, the polypide bud is already quite advanced (see also Handschuh *et al.* 2008). Thus, the analysis of these early stages is quite time consuming and needs a large amount of material. Second, histological preparation of the closed statoblasts requires a lot of technical skill. This comprises of mechanical cutting of the statoblast to ensure proper infiltration of chemical media including embedding media, as well as sectioning hard substances, such as statoblast valves, in the relatively soft paraffin. This shows that Braem was a very patient and accurate morphologist, which is reflected in the precision of his descriptions as well as his accurate drawings – particularly in his early period when he was still an active scientist. Interestingly his works, after his scientific career was over, were never as beautiful as in his early years – presumably due to lack of time.

Braem's second most important contribution in bryozoology was the study of primarily victorellid ctenostomes. His work from 1951 is still the largest and most thorough investigation on victorellid morphology. This does not just include the morphology of adults, but also developmental aspects like budding as well as sexual development. His observations on brooding were the first in victorellid ctenostomes and only a few other researchers have investigated this group in this respect (Smith *et al*. 2003, Vieira *et al*. 2014). As mentioned above, he described some new victorellid species and was the first to describe their larval structure and metamorphosis (in *Bulbella abscondita* and *Tanganella muelleri*). In this context, Braem was the first to recognize soft-body morphological features, such as the cardiac sphincter for species discrimination. Based on his work on ctenostomes, a particular interesting feature which Braem published on in 1940 was the cross-striation of the pharynx in gymnolaemaetes which represent myoepithelial muscle fibres (Braem 1940b, Mukai *et al*. 1997). As he mentioned himself, he was not the first to describe this feature, but he comparatively discussed its importance for the suction feeding in non-phylactolaemates. It is noteworthy that he also studied sectioned material of cyclostome bryozoans (*Crisia eburnea*) (Braem 1940b). Additionally, Fritz Braem was the first to describe and illustrate the presence of the placental nourishment in Ctenostomata when describing the embryonic growth and development in *Sundanella sibogae* (Braem 1939). It is clear from reading this paper that Braem did not understand the process.

In regard to the lost manuscript mentioned above, it should also be mentioned that Braem was the first, and has been the only one, to observe embryos and larvae of *Paludicella articulata*, probably the sole genus of the ctenostome superfamily Paludicelloidea (Braem 1896, unpublished observations from above). While gonads had been previously observed (Allman 1856, Kraepelin 1887), it is even more surprising that nobody has been able to observe larvae – or even gonads – subsequently in this species, despite its cosmopolitan distribution and high abundance. Consequently, Braem's contributions also are the only ones for the Paludicelloidea.

Conclusively, Fritz Braem was one of the most accurate bryozoan anatomists ever and a very careful observer and descriptor. His scientific legacy comprises his significant research output that provides the most reliable information and forms the foundation of our knowledge on phylactolaemate and ctenostome internal morphology, as well as embryology. His data is still actively used nowadays and, thus, this great researcher is not forgotten.

8. The *Valdivia* bryozoans

The *Valdivia* expedition was the first German expedition to explore the deep sea and it was organized by Carl Chun. The focus of the *Valdivia* expedition was the Indian Ocean, since the British *Challenger* expedition (1872–1876) had only passed through the southern Indian Ocean. A steam ship, the SS *Valdivia*, was selected in early 1898 for the expedition and was rebuilt in order to meet the criteria of a deep-sea research vessel. The expedition that was named after the vessel started in Hamburg on 31 July 1898 and took altogether nine months (Figure 14). The *Valdivia* explored the eastern Atlantic Ocean from the Faroe Islands to the Bouvet Island, and then passed through the Southern Ocean during the winter. The SS *Valdivia* sailed via the Kerguelen into the Indian Ocean. The expedition officially ended on 5 April 1899, when the vessel reached Aden. The SS *Valdivia* returned via the Red Sea, the Suez Canal, the Mediterranean Sea and the

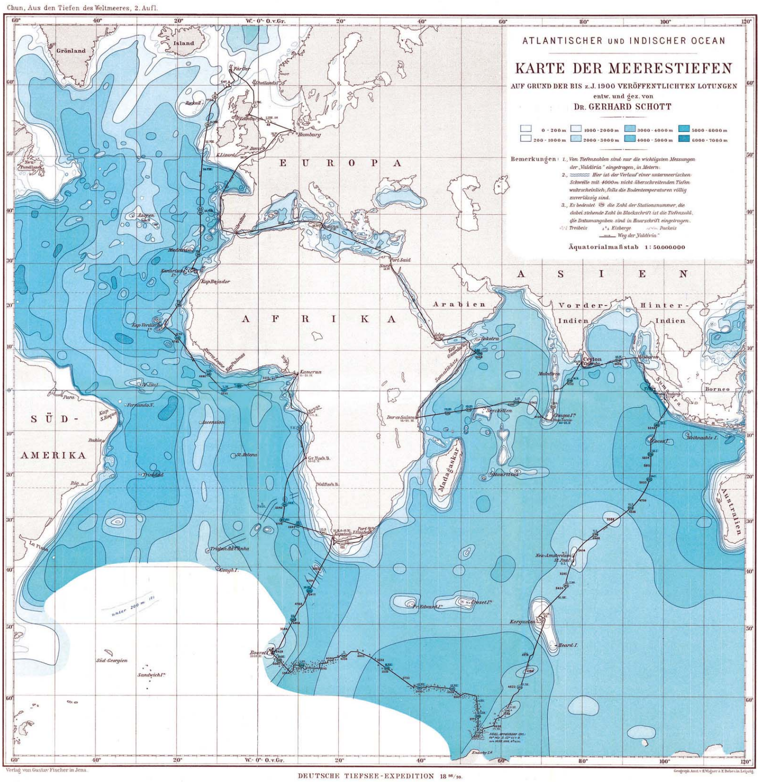


Figure 14. The Valdivia *expedition started in Hamburg and led first to the Faroe Islands. From there, the* Valdivia *crossed the northeastern Atlantic Ocean and navigated along the African coast into the Southern Ocean. The* Valdivia *then crossed the Indian Ocean and returned via the Red Sea and the Mediterranean Sea into the northeastern Atlantic Ocean and back to Hamburg. Photograph from Chun (1905).*

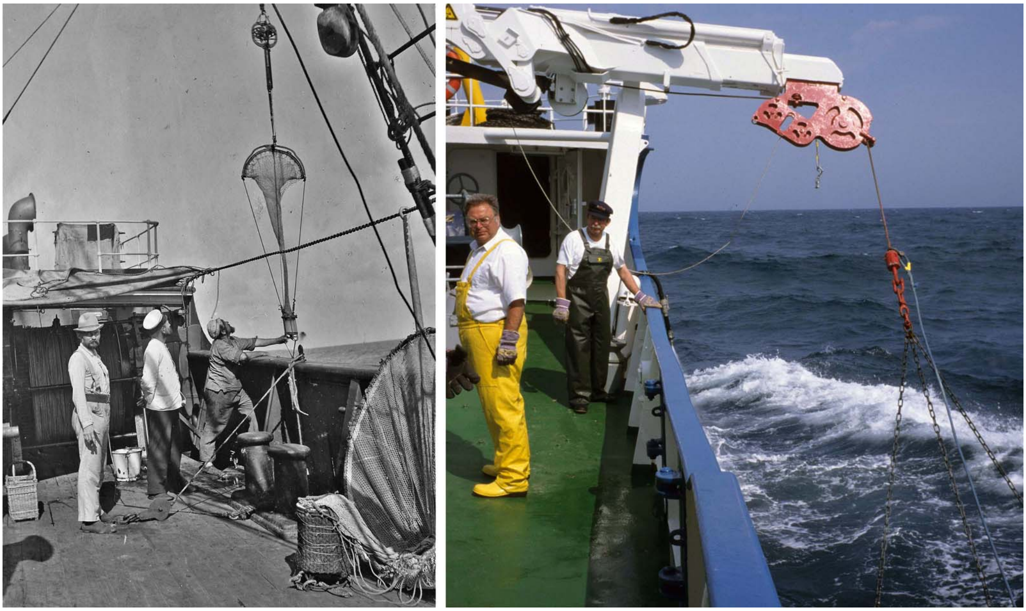


Figure 15. Then and now: Fritz Braem (1862–?) on deck of SS Valdivia *in 1898/9 (left) and Michael Türkay (1948–2015) on deck of FK* Senckenberg *in 1999 (right). Photographs courtesy of the Senckenberg archive (Institut für Stadtgeschichte Frankfurt am Main; V 176 Nr. 3219) and Dieter Fiege.*

northeastern Atlantic Ocean to Hamburg, where the vessel arrived on 1 May 1899.

The expedition was a huge scientific success. The Bouvet Island was rediscovered and its geographical position was fixed. Furthermore, it was verified that the whole water column is populated by organisms, while many researchers at that time believed that only the surface water and the sea floor would be populated. The scientific results of the *Valdivia* expedition were published in 24 volumes between 1902 and 1940. A huge focus was taxonomical work. However, bryozoans are among the least concerned phyla, despite bryozoans having been reported to be very numerous among the collected material.[11] In the first editions of the scientific results, Braem (Figure 15) was listed by Chun to work on the bryozoan material, but he never accomplished this task and Braem also had no other contributions to the scientific results of the *Valdivia* expedition. Carl Apstein (1862–1950), another participant of the *Valdivia* expedition, who edited the last volumes of the scientific results, passed over the *Valdivia* bryozoans to Wilhelm Hasenbank, who conducted a Ph.D. thesis on the material in the early 1930s. However, the Ph.D. thesis remained unfinished and it is unknown what happened to Hasenbank. Still, a part of Hasenbank's work was published in the scientific results (Hasenbank 1932). In this work, Hasenbank described and illustrated 45 species of anascan cheilostomes that were collected in the Atlantic, the Southern and the Indian Oceans. Among these are 14 new (sub) species and two new genera (Table 2). All the bryozoan material of the *Valdivia* expedition, including also Hasenbank's type material, is now lodged at the *Museum für Naturkunde* in Berlin and still awaits proper revision.

Table 2. New cheilostome bryozoan taxa proposed in Hasenbank (1932) for material from the Valdivia expedition. Some of the species have been referred to other genera by subsequent authors. However, since no proper revision of the material occurred, the original classification is used in this list.

Taxon	**Station(s)**	**Locality**	**Bathymetry**
Bugula apsteini	210	SW of Great Nicobar Island, India	752 m
Bugula hessei	211	SW of Katchal Island, India	805 m
Bugula leontodon cornuta	250	SE of Kaambooni, Somalia	1668 m
Cabereopsis			
Cabereopsis elongata	211	SW of Katchal Island, India	805 m
Carbasea macropora	96	S of Cape Agulhas, South Africa	80 m
Eupaxia			
Eupaxia incarnata	250	SE of Kaambooni, Somalia	1668 m
Flustra albida	211	SW of Katchal Island, India	805 m
Flustra gracilenta	28	NW of Cape Bojador, W. Sahara	146 m
Gemellaria loricata aurita	3, 6, 7	NE of Scotland, United Kingdom	79 m
Levinsenella tecta	211	SW of Katchal Island, India	805 m
Menipea klugei nom. nov.	127	SE of Bouvet Island, Norway	567 m
Menipea obtusa	131	SE of Bouvet Island, Norway	457 m
Menipea undulata	250	SE of Kaambooni, Somalia	1668 m
Scruparia spiralis	100	St Francis Bay, South Africa	50 m
Spiralaria denticulata brevimandibulata	100	St Francis Bay, South Africa	50 m

9 Acknowledgements

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Notes

1 To our knowledge such a low number of tentacles for *Paludicella ariculata* has never been reported by anyone else. One of us (TS), who studied *P. articulata* from March till September in Austria never noticed any large tentacle variation, the average number of tentacles being 15–16. However, during these studies, gonads could not be observed and possibly the low tentacle numbers reported by Braem might be from ancestrulae.

2 Braem (Braem 1890b, p. 134) wrote "*Als ich vor 5 $^{1}/_{2}$ Jahren einen Irrweg verliess und voll heisser Liebe, aber voll Zweifel an meiner Kraft, an das allgewaltige Werk der Natur trat, war er* [Carl Chun] *es, dessen entgegenkommende Güte meine Schritte gefördert und auf ihrer Bahn gefestigt hat*." ("When I left a wrong track five and a half years ago and came full of hot love, but full of doubt in my power to the all-powerful work of nature, he [Carl Chun] was it, who, with his amiable goodness, promoted my steps and strengthened them in their track.").

3 Braem (1888b, p. 503f) wrote "*Im Sommer 1886 begann ich auf Anregung meines verehrten Lehrers, Herrn Prof. Carl Chun, unsern heimischen Süßwasserbryozoen ein einstellendes Studium zuzuwenden,* [...]" ("In summer 1886, I started a thorough study of our native freshwater bryozoans at the suggestion of my revered teacher, Mr Prof. Carl Chun, [...]").

4 In an obituary for Carl Chun, Braem (1914a) stated: "*Nach der Expedition, also während des größten Teiles der Leipziger Zeit, habe ich nur noch brieflich mit ihm verkehrt*." ("After the expedition, thus for most of the Leipzig Period, I only communicated by letter with him.")

5 Braem (1888b, p. 504) wrote "*Da nun mittlerweile die Ergebnisse meiner Bemühungen in der jüngst erschienenen Arbeit von Herrn Prof. Kraepelin der Hauptsache nach bereits mitgetheilt sind, so beschränke ich mich hier auf die Angabe der Funde, über*

welche an jener Stelle noch nicht berichtet werden konnte." ("Now that the results of my efforts have mainly been communicated in the recently published work of Mr Prof Kraepelin, I restrict myself here to report the findings that have not been mentioned there."). In Braem (1890b, p. 5), he added: "*Neuerdings ist in Folge meiner Mittheilungen an Prof. Kraepelin in Hamburg der grösste Theil meiner Funde bekannt geworden, und ich selbst habe in einem im Zoolog. Anzeiger v. J. 1888 Nr. 288 veröffentlichten Bericht das noch Fehlende nachgetragen*." ("Lately, as a result of my messages to Prof. Kraepelin in Hamburg, most of my findings have become known, and I myself have added the remainder in a published report to the Zoolog. Anzeiger anno 1888 nr. 288.").

6 Braem (1893c, p. 14) concludes: "*Die Polemik Kraepelins zu charakterisiren, ihren Werth, ihre Tragweite zu ermessen, das war der Zweck dieser Zeilen. Die Polemik Kraepelins in ihrer wissenschaftlichen Hinfälligkeit zu beleuchten, das war ich der Sache, das war ich denjenigen schuldig, die meiner Arbeit die Wege geebnet haben. Ich selbst sehe dem Urtheil der Zukunft mit vieler Ruhe entgegen.* [...] *Und eben dies bürgt dafür, dass der Kampf ums Dasein, der in der Wissenschaft so gut wie im praktischen Leben gekämpft wird, doch wohl am Ende ein Kampf um die Wahrheit bleibt*." ("To characterize the polemics of Kraepelin, their value, to balance their consequences, this was the purpose of these lines. Illuminating Kraepelin's polemics in their scientific weakness, this I owed to the subject, this I owed those who paved the way for my work. I myself look with much tranquillity forward to the future judgement. [...] And it is this, what guarantees that the struggle for existence, which is fought in science as good as in the daily life, remains a struggle for the truth after all.").

7 Braem (1939, p. 267).

8 Zooids are able to protrude their lophophore.

9 Braem (1939, p. 278) wrote "*Ich sehe in* Victorella Sibogae *Harmer nicht nur den Vertreter einer neuen Gattung, sondern auch den einer neuen Familie, die in die Nähe der Cylindroeciiden zu stellen sein dürfte. Für die Gattung schlage ich den Namen Sundanella vor*." ("I see in *Victorella Sibogae* Harmer not only the representative of a new genus, but also of a new family, which might be closely related to the Cylindroeciidae. For the genus, I suggest the name *Sundanella*.").

10 Jebram (1973, p. 39).

11 Hasenbank (1932, 319).

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