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# The parental care in cheilostome bryozoans: a historical review

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1. Ovicells, oviposition and placental brooding
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3. Internal brood chambers and intracoelomic brooding
4. External brooding sacs
5. Acknowledgements

Cheilostome bryozoans possess a range of methods for embryonic incubation. Embryos are brooded in the external membranous sacs, skeletal (calcified) chambers and internal brooding sacs formed by non-calcified zooidal walls, or develop intracoelomically in viviparous species. In some instances extraembryonic nutrition has been evolved.

Most cheilostomes keep their young in the skeletal chambers called ovicells. Presence or absence of the ovicells as well as their morphology is considered to be important characters in the taxonomy of Cheilostomata. There are several morphological types of ovicells, and most common are hyperstomial ones that often look like hemispherical bubbles or helmets on the colony surface. Basically, the hyperstomial ovicell consists of a two-walled calcified fold (ooecium) with a coelomic cavity inside, a non-calcified distal wall of the maternal autozoid (that produces eggs), and the brooding cavity between them (Figure 1). The outer ooecial wall is called ectooecium; that surrounding the brooding cavity, entoecium. The ovicell opening is closed either by the operculum of the zooidal aperture, or by an evagination of the maternal cystid wall called an ooecial (inner) vesicle or ooecial plug. The ooecial vesicle can contract by the special muscle bands, opening the ovicell entrance. Depending on the type of formation, the ooecial coelomic cavity communicates either with the coelom of the daughter or maternal zoid through communication pore(s).<sup>1-6</sup> If the ooecium originates from the daughter zoid, the pore is normally plugged by non-specialized epithelial cells, and direct communication between the coelomic cavities mentioned becomes impossible. For this reason the ooecial fold is

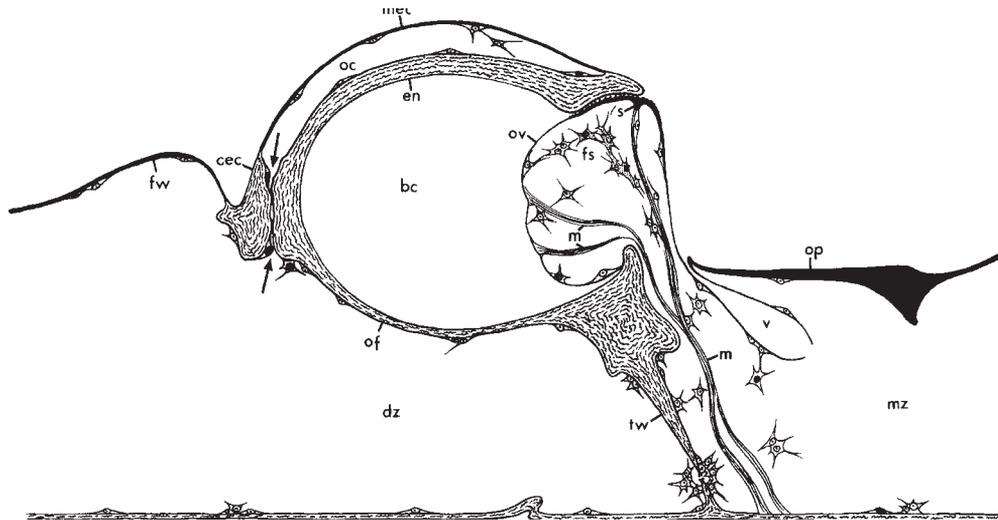


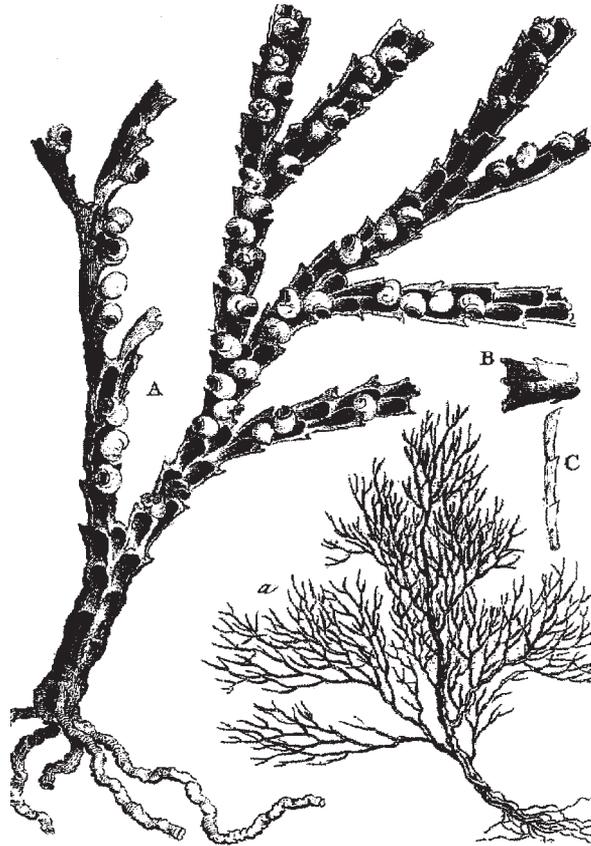
Figure 1. Ovicell structure in *Callopora dumerilii* (longitudinal section of calcified specimen). Abbreviations: bc – brooding cavity, cec – calcified part of ectooecium, dz – daughter (distal) autozoid, en - entoecium, fm – frontal membranous wall of the daughter zooid, fs – funicular strands, m – musculature of the oocelial vesicle, mec – membranous part of ectooecium, mz – maternal (proximal) autozoid, oc – oocelial coelomic cavity, of – ovicell floor, op - operculum, ov – oocelial vesicle, s – sclerit, tw – transversal wall, v – vestibulum. Communication canal and its pores shown by arrows (from Ostrovsky and Schäfer, 2003).

conventionally considered to be a special polymorph, a kenozooid, and the ovicells evolution is thought to be a manifestation of the most interesting and important colonial phenomenon, that of zooidal polymorphism.<sup>7-10</sup>

## 1. Ovicells, oviposition and placental brooding

The first author who described ovicells in cheilostomes was John Ellis.<sup>11-12</sup> In his famous book *Essay towards a natural history of the corallines...* he noted and figured ovicells in several species of the genera *Bugula*, *Bicellariella* and, probably, *Flustra*, and called them ‘Balls’, ‘testaceous Spherules’, or ‘testaceous Figures’.<sup>13</sup> Describing ovicells in one of the ‘Corallines Celluleuses’ (*Bugula neritina* (Linnaeus, 1758) according to Levinsen<sup>14</sup>), Ellis suggested that they could be ‘Niduses or Matrices of certain testaceous Animals, like small snails or Neritae’,<sup>15</sup> from the eggs of which the colony originates. This remarkable opinion was further expressed in the drawing of *B. neritina*, where the ovicells were pictured as spirorbid polychaetes, foraminiferans and gastropods with a spiral shell (Figure 2).<sup>16</sup> It could be that Ellis possibly saw in some cases actual spirorbids and foraminiferans attached to the bryozoan colonies, and confused them with brood chambers. Furthermore, he suggested that the similar relationship existed between some bryozoans and bivalves.<sup>17</sup>

Figure 2. Drawing of *Bugula neritina* with ovicells and adhered shells of polychaetes-spirorbids (from Ellis, 1755, Plate XIX, figure A).



Peter Simon Pallas expressed the view that ‘bullas’ (ovicells) are ovaria in encrusting bryozoans,<sup>18</sup> and this opinion was retained for a century. Concerning ovicells in erect *Bugula neritina* and *B. avicularia* (Linnaeus, 1758) (both identified therein as *Cellularia*), this author suggested that they and avicularia are organs of similar nature, and could be somehow related with ovicells in encrusting ‘*Eschara*’. Pallas speculated that both ovicells and avicularia could serve for fertilization, and sometimes called them ‘Nectariums’.<sup>19</sup>

In his later work, Ellis agreed with the opinion of Pallas, and admitted that the ‘pearl-like studs (bullulae supra cellulas)’ in *Flustra*<sup>20</sup> and ‘little hemispherical covers’ in *Bugula* (as *Cellaria*)<sup>21</sup> ‘appear rather to be what we have called Ovaries’. Ellis mentioned that Pallas called ovicells and avicularia ‘Nectariums’ comparing them with ‘the flowers of some plants’. At the same time, he suggested that ovicells could be the shell-bearing larvae in ‘*Cellaria*’, that detach from the branch, ‘drops and adheres to a proper substance as a base, beginning to form a Coralline like the parent animal’.<sup>22</sup>

Later authors followed Pallas,<sup>23</sup> calling ovicells ‘corps vesiculaires’, ‘corps globuleux’,<sup>24</sup> ‘vesicules gemmifères’, ‘capsules gemmifères’,<sup>25</sup> ‘vesiculae gemmiferae’,<sup>26</sup> ‘ovary-capsules’,<sup>27</sup> and considered them as ovaries.<sup>28</sup>



Figure 3. Thomas Huxley (photograph courtesy Patrick Wyse Jackson).

One of the first observations that contradicted this view was made by Robert Grant.<sup>29</sup> Studying *Carbasea carbasea* (Ellis and Solander, 1786) (as *Flustra*) and *Flustra foliacea* (Linnaeus, 1758), he recorded the growing egg inside the zooid, whereas, when mature, it is surrounded by a helmet-shaped capsule [ovicell], that separates the egg “from the cavity of the cell [zooid]” in *Flustra*.

George Busk introduced the term ‘ovicells’,<sup>30</sup> augmenting for them such descriptive terms as ‘subglobose and terminal’, ‘galeriform’ [*Scrupocellaria*], ‘globose, subpedunculate’ [*Bicellaria*], ‘arcuate’ [*Caberea*], ‘conical’ [*Diachoris*], and ‘subglobular’<sup>31</sup> [*Cellepora*].

However, the older view that ovicells are capsules, containing the ovaries, was first altered by Thomas Huxley (Figure 3).<sup>32</sup> Huxley, who observed eggs inside autozooids and with empty ovicells that were seen to contain the egg later on in *Bugula avicularia* (as *B. avicularis*), proposed that an ovicell should be the ‘marsupial pouch’ [brood chamber].<sup>33</sup> Thomas Hincks,<sup>34</sup> who investigated *Bugula flabellata* (Thompson in Gray, 1848), *B. turbinata* Alder, 1857 and *Bicellariella ciliata* (Linnaeus, 1758) (as *Bicellaria*), challenged Huxley’s opinion, but was forced to admit the truth of Huxley’s observations afterwards.<sup>35-</sup>  
<sup>36</sup> However, Hincks stressed that he had ‘grounds for believing that in some cases, and under conditions which [he could not] explain, ova are also produced within [ovicells]’.<sup>37-</sup>  
<sup>38</sup> Hincks suggested that there are two kinds of eggs formed in gymnolaemates: some eggs are produced in the ovicells, whereas others in the autozooids, being ‘the equivalent of the statoblast[s] of the Phylactolaemata’.<sup>39</sup> For evidence he used Fredrik Smitt’s data,<sup>40-41</sup> who

first recorded embryonal development inside the gonozooid (at that time also called ovicells) in the cyclostome, *Crisia eburnea* (Linnaeus, 1758), and inside the autozooid in the cheilostome, *Cryptosula pallasiana* (Moll, 1803) (as *Lepralia*).<sup>42</sup> In the same 1880 monograph Hincks expressed the opinion that ‘its [ovicell] interior is in direct communication with the perigastric cavity’ of the maternal autozooid,<sup>43</sup> but was in doubt concerning the method of the oviposition. He observed the very beginning of this process in *Bugula*, when ‘it seemed as if a vigorous movement [of the polypide] might at any moment discharge it [an egg] into the ovicell,’<sup>44</sup> and in *Chartella papyracea* (Ellis and Solander, 1786) (as *Flustra*).<sup>45</sup> Hincks introduced the term ‘oecium’<sup>46</sup> that he used as synonymous with ‘ovicell’, and indicated that the ovicells can be ‘prominent’, ‘subimmersed’ or ‘immersed’, depending how they protrude on the surface of the colony.<sup>47</sup>

The first investigation of the structure and development of hyperstomial ovicells was made by Hinrich Nitsche on *Bicellariella ciliata* (as *Bicellaria*),<sup>48</sup> and one of his figures<sup>49</sup> was schematically redrawn by Vigelius.<sup>50</sup> Nitsche found that each ovicell formed as two outgrowths - ‘helmförmige Blase’ (oecium) and ‘rundliche Blase’ or ‘Deckelblase’ (oecial vesicle) on the distal margin of the maternal zooid in this species.<sup>51</sup> The inner vesicle serves as an operculum for the helmet-shaped part, and can be contracted by the work of special muscles during larval release (rhythmical contractions of the oecial vesicle was described first by John Reid in *Bugula flabellata* (as *Flustra avicularis*)<sup>52</sup>).<sup>53</sup> Similar to the opinion of Huxley,<sup>54</sup> Nitsche independently came to the conclusion that ovicells are merely brood chambers,<sup>55-56</sup> and ‘the ovicells or oecia in the Chilostomata’ were suggested to be modified individuals, but in a special sense.<sup>57-58</sup> Following Allman,<sup>59</sup> Nitsche believed that bryozoan colonies were ‘composed of two different classes of zooids, the “cystoid zooïds” [cystide] and the “polypoid zooïds” [polypide]’, and the latter were produced by budding inside the former. Accordingly, he considered ovicells as a variety of “cystoid zooïd”. Busk believed that ovicells ‘are clearly transformed cells [zooids]’.<sup>60-61</sup> Nitsche proposed a possible mechanism for oviposition through the hypothetical pore, placed between the basal parts of the oecium and the oecial vesicle.<sup>62</sup>

Édouard Claparède<sup>63</sup> and Lucien Joliet<sup>64</sup> made some observations on ovicells in several cheilostomes, but comparing with Nitsche,<sup>65</sup> they provided no new information about oecial structure in their publications. In *Scrupocellaria scruposa* Claparède noted that the development of the ovicell began when the first mature egg and sperm were seen in the maternal zooid.<sup>66</sup> This statement was later criticised by Vigelius,<sup>67</sup> who observed the earliest stages of the ovicellogenesis in the zooids with the incipient ovary and stated that the growth of the first egg was accompanied by the formation of the brood chamber in *Terminoflustra membranaceotruncata* (Smitt, 1868) (as *Flustra membranaceo-truncata*).<sup>68</sup> Interestingly, Claparède and Nitsche also used the data of Smitt,<sup>69</sup> but to argue against the hypothesis of Hincks (see above), since they were sure that egg had to be moved to the ovicell for further development.

Willem Johann Vigelius<sup>70-71</sup> described the structure and the development of the ‘endozoecial’ (according to Levinsen<sup>72</sup>) ovicells in *Terminoflustra membranaceotruncata* in sections, and clearly showed that two successive zooids contribute to the formation of

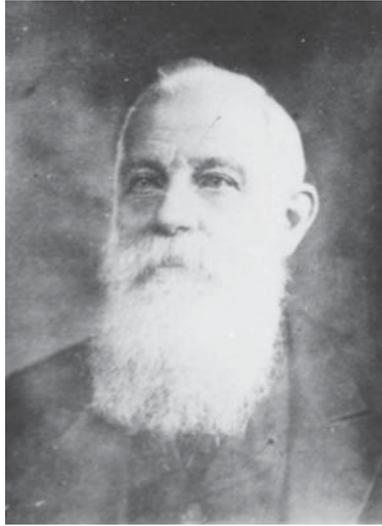


Figure 4. Arthur Waters (photograph courtesy of Mary Spencer Jones).

the brood chamber: ‘Helm’ (ooecium) originates from the daughter zooid whereas ‘Deckel’ (ooecial vesicle) from the maternal zooid.<sup>73</sup> Vigelius believed that, despite the different origin of ‘external’ (in *Bicellariella ciliata*) and the ‘internal’ (in *Terminoflustra membranaceotruncata*) brood chambers,<sup>74</sup> the ovicell structure shows obvious similarities in these species. He held the opinion that, an ovicell with its simple structure is more likely a specialised organ in *Terminoflustra*, not a ‘Cystidindividuen’ like Nitsche stated for *Bicellariella*. He also suggested a possible mechanism for oviposition through the rupture hole in the inner vesicle, and this idea was accepted by Delage and Hérouard<sup>75</sup> and by Calvet.<sup>76</sup> Later a similar idea was also suggested by Arthur Waters (Figure 4).<sup>77</sup> In his later paper, Vigelius described the ovicell structure and briefly outlined its formation in *Bugula calathus* Norman, 1868, where he thought that the brood chamber developed ‘from the free distal wall of the sexually mature animal’ [maternal zooid].<sup>78</sup> Vigelius also found ‘Cylinderzellenschicht’ (cylindrical epithelium) on the inner surface of the distal wall of the ooecial vesicle, and described precisely the musculature of the ooecial plug, which consisted of two groups of bands perpendicular to each other. He thought that one of the muscle groups was responsible for the rupture of the ooecial vesicle wall during oviposition. Interestingly, the hypertrophied cell layer (mentioned above) that serves as an embryophore<sup>79-82</sup> was probably discovered first by Reid, who wrote that the ‘membranous partition [ooecial vesicle] was much thickened, especially at the central part ..., and contained a number of nucleated cells’ in *B. flabellata*.<sup>83-84</sup>

Jules Jullien<sup>85</sup> used the terms ‘coïtis’ (Greek, ‘cradle’) for the thick external ovicellar wall, and ‘sparganile’ (Greek, ‘swaddling-cloth’) for the thin internal one in the description of cheilostome *Exochella longirostris* Jullien, 1888.<sup>86</sup> Classifying cheilostomes, he introduced the new ‘tribes’ Inovicellata, Subovicellata and Suproovicellata based on the

presence and position of the ovicell opening in relation to the orifice of the maternal autozoid, and proposed the terms ‘aneucleithral’ and ‘cleithral’ for different types of the closure of the ovicell opening by the zooidal operculum.<sup>87</sup> Jullien also illustrated larvae, developing inside zooids in *Beania* sp. (as *Diachoris costata*), and suggested that oviposition might occur with the help of the tentacle sheath in *Celleporella hyalina* (as *Hippothoa*).

Eduard Pergens<sup>88</sup> was the first to record oviposition in cheilostomes, but his paper was overlooked and forgotten by later authors. Studying *Fenestrulina malusii* (Audouin, 1826) (described as *Microporella*), he noted that this was accompanied by a strong compression of the egg and occurred when the polypide degenerated.

Ives Delage and Edgar Hérouard in their book<sup>89</sup> mentioned both opinions concerning the origin of the ovicells (Nitsche’s,<sup>90</sup> that these brood chambers were formed by the maternal zooid, and Vigeliuss’s,<sup>91</sup> that they originated from both the maternal zooid and the daughter zooid), but favoured Nitsche’s point of view. Sidney Harmer<sup>92</sup> first noted that the oecium can also be either a part of the ‘fertile (proximal)’ zooid or belong ‘to the distal’ zooid. As a third possibility he mentioned ‘that it is a modified individual, as believed by Nitsche and others’. He suggested that the oecium as seen in *Euthyroides episcopalis* (Busk, 1852), should communicate with a maternal zooid, although he could not prove this. Harmer’s idea was that ‘the ovicell is formed by the fusion a pair of greatly expanded oral spines, the bases of which should communicate with the fertile zooecium on each side of the operculum’. On the other hand, he wrote<sup>93</sup> that ‘it is impossible not to be struck by the resemblance between the development of the ovicell and that of the frontal bars’ in this species.<sup>94</sup> This contradiction and Harmer’s doubts overshadowed the true nature of these structures for a long time.

Harmer<sup>95</sup> was the first to describe extraembryonic nutrition in cheilostomes when he stated that the embryo “receives ...yolk while in the [brooding] sac” in *Retiflustra schoenau* Levinsen, 1909 (described as *Flustra cribriformis* Busk).

Waters made sections of the ovicells in a number of cheilostome species. His descriptions and figures show that there are two ways of the ooecial formation, and the ooecium can be formed either by the maternal, or by the daughter zooid in the different taxa.<sup>96-100</sup> One of the most informative papers was published in 1913.<sup>101</sup> In this work, Waters depicted the ovicell consisting of the small kenozooidal ooecium (budded from the fertile zooid) and brooding sac in *Halysisis diaphanus* (Busk, 1860) (as *Catenaria diaphana*). Here he also applied the ovicell shape and position for classification of Catenicellidae, and described the developmental stages of the ovicell in *Retepora umbonata* MacGillivray, 1885. These data were later supported and verified by Yaichiro Okada,<sup>102</sup> Paul Buchner<sup>103</sup> and Sidney Harmer<sup>104</sup> who described ovicellogenesis in several phidoloporids.<sup>105</sup>

Louis Calvet carefully investigated anatomy of brooding chambers in several species, including cheilostomes, making sections of decalcified specimens.<sup>106</sup> He noted that there are marine bryozoans (cheilostomes as well as ctenostomes) that do not brood their youth, whereas the majority of them are brooders. In *Bugula simplex* Hincks, 1886 (as *B.*

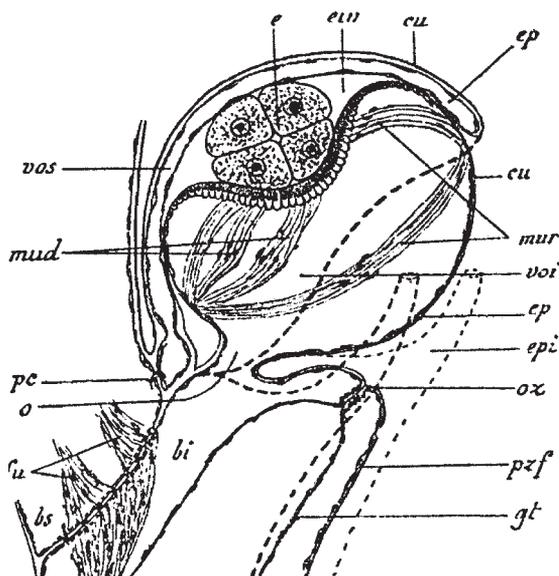


Figure 5. Ovicell structure in *Bugula simplex*: bi – visceral coelom of the maternal autozooid, bs – visceral coelom of the daughter autozooid, cu – cuticle, e – embryo, eiv – brooding cavity, ep – epidermis, epi – oral spine, fu – funicular strands, gt – wall of the tentacle sheath, mud – muscles-depressors, mur – muscles of the ooecial vesicle, o – communication between the ooecial vesicle and the maternal autozooid, oz – zooidal orifice, pc – communication pore, pzf – frontal wall of the maternal autozooid, voi – ooecial vesicle cavity, vos – ooecial coelomic cavity (from Calvet, 1900, figure 10).

*sabatieri* Calvet, 1900) he described early ovicellogenesis as the formation of two hollow vesicles, one of which, being formed from a maternal zooid, was a rudiment of the ooecial vesicle ('vésicule ovicellienne inférieure'), whereas the second, originating from a daughter zooid, was a rudiment of the ooecium ('vésicule ovicellienne supérieure').<sup>107</sup> Calvet suggested that this ovicell type in which its two parts (ooecium and inner vesicle) belong to the different subsequent zooids, is most common among cheilostomes. However, he thought that *Bicellariella ciliata*, in which ovicells were studied by Nitsche,<sup>108</sup> should not be an exception from this rule, (despite an absence of the terminally budded distal zooid in this species<sup>109-110</sup>), and this was later recognized by Harmer.<sup>111</sup> One of Calvet's most important findings was a communication pore in the septum between ooecial and daughter zooid coeloms (Figure 5).<sup>112</sup> In the ooecial vesicle of the ovicells of *B. simplex* he found a sclerite - circular thickening of its cuticle corresponding to the place of contact between ooecium and ooecial vesicle, plexus of the mesenchymatous cells (obviously, funicular strands), and following Vigelius, complex musculature and embryophore.<sup>113</sup> Calvet described growth of the embryo accompanied by the enlargement of the cells in the ooecial vesicle. It is also well seen in his illustrations: for instance, in the ovicell containing the zygote, the epithelium of the ooecial vesicle is not hypertrophied, whereas its cells have a cylindrical shape when there is the large embryo in the brood chamber. However, Calvet did not explain this.<sup>114</sup> He described and illustrated the structure of the endozooidal ovicell in *Securiflustra securifrons* (Pallas, 1766) (as *Flustra*), also depicting the longitudinal sections of the hyperstomial ovicells in *Amphiblestrum flemingi* (Busk, 1854) (as *Membranipora*) and *Fenestulina malusii* (Audouin, 1826) (as *Microporella*). Until now Calvet is the only researcher who has studied the anatomy of endotoichal ovicells in the genus *Cellaria* (in *Cellaria fistulosa* (Linnaeus, 1758) and *C. salicornioides* Lamouroux, 1816). One of the most interesting characters found in these peculiar internal brood

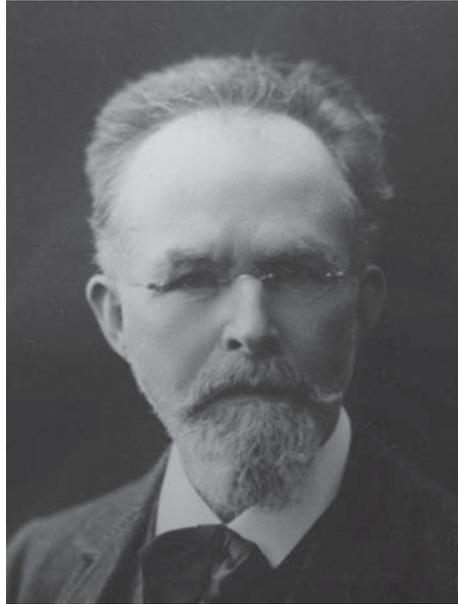


Figure 6. Georg Levinsen (photograph courtesy of the Library of the Zoological Museum, University of Copenhagen).

chambers was a hypertrophied epithelium of the brooding sac and an additional operculum, closing the ovicell opening. Calvet wrote that the brooding cavity [as he called the space around the brooding sac] is connected with a cavity of the maternal zooid, and considered it as a part of the latter. He recorded the enlargement of the embryophore cells accompanying the growth of the embryo, but, again, failed to recognize its true function.

Waters<sup>115</sup> studied tube-like brood chambers ('peristomial oecia' according to Levinsen<sup>116</sup>) in *Margaretta chuakensis* Waters, 1907 (as *Tubucellaria ceroides* var. *chuakensis*), and found a peculiar modified polypide with a special terminal plug, closing the entrance to the ovicell in the maternal zooid.

Harmer<sup>117</sup> described 'somewhat hood-like external ovicells' and an 'ovisac' with associated muscles in 'fertile zoecia' of *Cheiloporina haddoni* (Harmer, 1902) (as *Lepralia*), but was not able to ascertain if the sac was a diverticulum of the vestibulum.

The comprehensive studies of Georg Levinsen (Figure 6),<sup>118-123</sup> who intentionally did not use the term 'ovicell',<sup>124</sup> revealed 'numerous modifications' of 'hyperstomial oecia' and showed a basic similarity in their structure, where 'the two layers [walls] of the actual oecium are formed by the frontal membrane [wall] of the distal zoecium [daughter zooid]'.<sup>125</sup> Levinsen also described and depicted some bryozoans with the oecia formed either by the distal kenozooids or avicularia, but stated that the above mentioned 'type of the oecium ... appears in the majority of the Cheilostomata'.<sup>126</sup> Similarly, considering endozooidal ovicells, he divided them on the "oecia which are enclosed in autozoecia", and "oecia which are surrounded by kenozoecia".<sup>127</sup> In contrast with Calvet,<sup>128</sup> Levinsen did not mention the communication between the oecial and distal zooidal coeloms. He

did not picture it in the scheme of a *Bugula* ovicell,<sup>129</sup> but carefully illustrated it in many other cases instead.<sup>130-132</sup> Levinsen described the ovicell structure and development in more than 80 cheilostome species, but, except for his terminology, his data were almost never used and were not revised.

Levinsen classified cheilostome brood chambers according to their structure and a position of the ovicell relative to the distal zooid (ovicell immersion), introducing the terms ‘endozoecial’, ‘hyperstomial’, ‘peristomial’, ‘endotoichal’, ‘double-valved’ and ‘acanthostegous’<sup>133-134</sup> that are currently in use. He also divided hyperstomial ovicells into (1) ‘oecia without a cryptocyst’ and ‘oecia with a cryptocyst’,<sup>135</sup> and (2) ‘dependent’ and ‘independent’ according to the size of the wall contact between the oocial base and the distal zooid.<sup>136</sup> For the entire oocium he often used the term ‘oocial fold’, for the oocial vesicle - ‘oocial operculum’, and for the external and internal oocial walls ‘ectoOocium’ and ‘endoOocium’<sup>137</sup> (‘coitis’ and ‘sparganile’ of Jullien<sup>138</sup>). He also described the earliest stages of ovicellogenesis (in dried specimens) which, according to him, in different taxa starts from the development of either ‘two small distal calcareous plates’ or ‘a continuous plate’, arising ‘from the frontal edge of the distal [zooidal] wall’.<sup>139</sup> Levinsen suggested that the egg should leave the maternal zooid before entering the ovicell, however, oviposition has a place under the closed zooidal operculum in some species.<sup>140</sup>

Subsequent authors either accepted without discussion, or supported or just ignored the data of the previous workers on the oocial structure. Eugen Korschelt and Karl Heider<sup>141</sup> briefly described the ovicell structure in *Bugula* after Calvet and copied the scheme of the ovicell saggital section from his monograph<sup>142</sup> with no comments. Ferdinand Canu and Ray Bassler,<sup>143</sup> although criticizing Levinsen, gave very similar schemes of the different ovicellar types.<sup>144-145</sup> They sectioned a number of species with ovicells,<sup>146-147</sup> and proposed modified terms ‘aneucleithrian’ (for the hyperstomial ovicells not closed by a zooidal operculum), ‘cleithrian’ (closed by the operculum), and introduced ‘subcleithrian’ (the ovicells is closed with the operculum risen).<sup>148</sup> These authors substituted Levinsen’s term ‘independent oecia’ for the ‘recumbent’ ones<sup>149</sup> (criticized by Ryland<sup>150</sup>), and they also copied Calvet’s scheme of the *Bugula* ovicell.<sup>151</sup>

Harmer considered the ovicell structure in all three cheilostome volumes of his famous monograph *The Polyzoa of the Siboga Expedition*. Following Levinsen,<sup>152</sup> he depicted several schemes of the ovicell structure with the oecia consisting of two external non-calcified walls (ecto- and entoecium),<sup>153</sup> and the oecia with a double inner wall (cryptocyst) inbetween.<sup>154</sup> In both cases the oocium is a continuation of the daughter zooid frontal wall. Copying Calvet’s scheme for *Bugula*,<sup>155</sup> Harmer<sup>156</sup> did not mention or illustrate the communication pore of the oocium for some reason. It is even more strange, since he discussed Calvet’s findings in his previous work,<sup>157</sup> and stressed that “the vestigial ... ovicell is ... definitely shown to be a derivative of the distal zoocium” in *B. longicauda* Harmer, 1926. In contrast, Ernst Marcus<sup>158</sup> figured this pore, using the modified scheme of *B. avicularia* from the work of Adolf Gerwerzhagen.<sup>159</sup> After Pergens,<sup>160</sup> Gerwerzhagen was the first to observe the oviposition in cheilostomes, and this

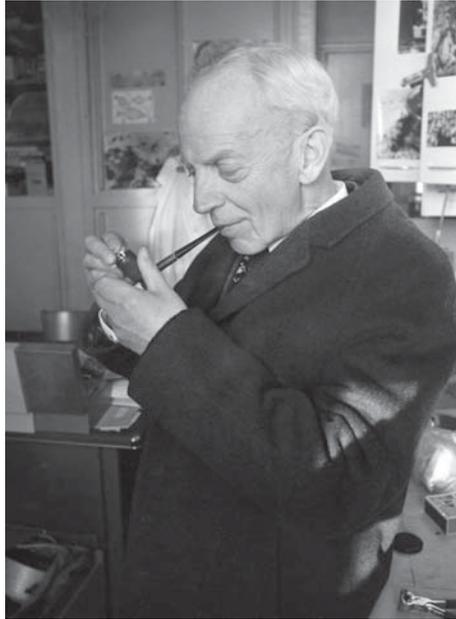


Figure 7. Lars Silén (photograph courtesy of Jean-George Harmelin).

question was finally answered. Later the oviposition was also observed by several researchers.<sup>161-168</sup>

Marcus<sup>169</sup> depicted the stages of ovicellogenesis and presented the scheme of the longitudinal section of ovicellated autozooid of *Thalamoporella evelinae* Marcus, 1941. Looking at this scheme, one has an impression that the oocidium consists of three walls in this species. However, the epithelial lining shows that there are actually two walls. Marcus did not illustrate any communication organs between oocial and zooidal coeloms.<sup>170</sup>

Contrary to all previous authors, Carl Cori<sup>171</sup> modified the scheme of Calvet<sup>172</sup> and pictured the communication between oocial and maternal zooid coeloms instead. The reason for this is unclear, since Cori did not make the sections of the ovicells by himself. However, Cori's figure was approved by Lars Silén (Figure 7).<sup>173-174</sup> It should be noted that the last researcher was, probably, the first who realized the importance of communication between coelomic cavities (instead of a continuity of zooidal walls) to reveal the source of oocial origin. After making sections, Silén reconstructed the ovicell anatomy of *Scrupocellaria scabra* (van Beneden, 1848).<sup>175</sup> According to him, the oocial coelom is confluent with the coelom of the maternal autozooid.

In 1945 Silén published his famous paper 'The main features of the development of the ovum, embryo and oocidium in the oociferous Bryozoa Gymnolaemata'.<sup>176</sup> This prominent study investigated many aspects of bryozoan structure and reproductive biology, including the development and structure of the oocidia of three cheilostome species: *Callopora dumerilii* (Audouin, 1826), *Escharella immersa* (Fleming, 1828) and *Fenestrulina malusii*. As a result of his work, Silén refuted the point of view of earlier scientists about

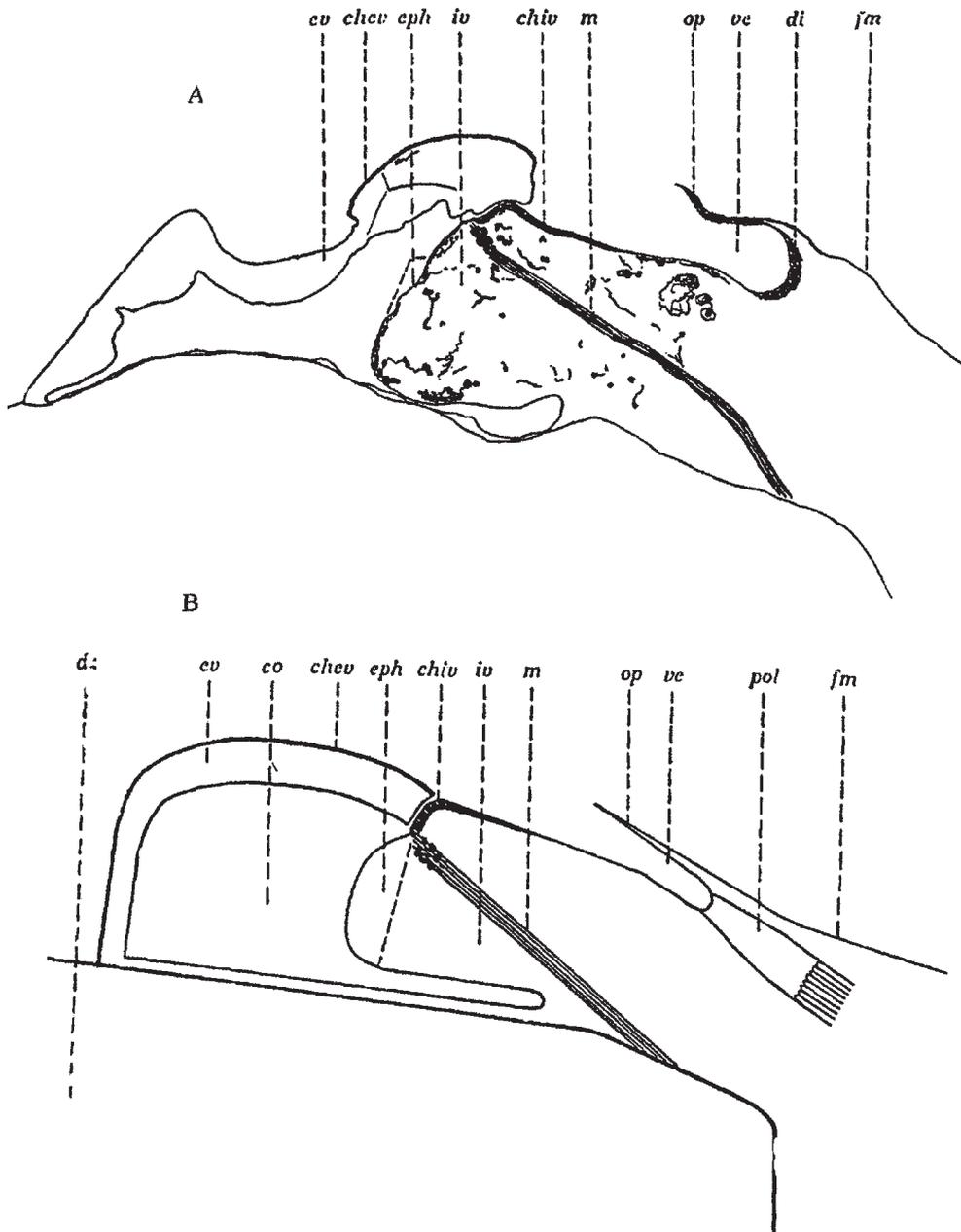


Figure 8. *Scrupocellaria scabra*. (A) Drawing of the decalcified specimen longitudinal section.

(B) Reconstructed ovicell structure based on the above drawing. Abbreviations: chev - ectooecium, chiv - sclerit of the ooecial vesicle, co - brooding cavity, cv - ooecial coelomic cavity, di - diaphragm, dz - daughter (distal) autozoooid, eph - embryophore, fm - frontal wall of the daughter autozoooid, iv - ooecial (inner) vesicle, m - muscles of the ooecial vesicle, op - operculum, pol - polypide, ve - vestibulum (from Silén, 1944, figures 18-19).

the existence of a connection between the ooeial coelom and the perigastric cavity of the daughter zooid. Referring to his sections of *Scrupocellaria scabra* (Figure 8),<sup>177</sup> he stated that in all three species studied an ooeial fold originates from the maternal zooid, and its cavity communicates with that of the latter. It was shown that the ooeium starts its development when the first oocyte begins to grow in the ovary, and this was suggested as being regulated by hormones. Silén obviously implied that if the oovicellogenesis is triggered by the maternal zooid (its ovary), the ooeium is formed at the expense of it too. Calvet's<sup>178</sup> finding of the communication pore in *Bugula simplex* as well as Levinsen's illustrations of the oovicell structure and development in *S. scabra*,<sup>179-181</sup> *E. immersa*,<sup>182</sup> and calloporids *Callopora dumerilii*,<sup>183</sup> *C. aurita* (Hincks, 1877),<sup>184</sup> *Tegella unicornis* (Fleming, 1828) (as *Membranipora*)<sup>185-187</sup> and *T. arctica* (d'Orbigny, 1853) (as *T. sophiae* (Busk, 1855)),<sup>188</sup> where an ooeial origin from the daughter zooid is clearly seen, were either criticized or ignored. The earliest stage of oovicellogenesis was described as 'a flat and narrow prominence from the frontal part of distal wall [of the mother zooid] ... composed of two separate knobs', and the inner wall of the ooeial fold was said to be membranous.<sup>189-190</sup> Finally, Silén extrapolated these statements to all bryozoans with hyperstomial and endozooidal oovicells.<sup>191</sup> It is noteworthy, that in his previous paper Silén wrote that the ooeium is formed by the distal zooid in endozooidal oovicells.<sup>192</sup>

It should be mentioned here that the statement on the ooeial origin from the maternal zooid was influenced by the early idea of Harmer,<sup>193</sup> who suggested that the ooeium originates from the two oral spines in the cribrimorph *Euthyroides episcopalis* (see above). Based on this and his own inferences concerning evolution of the spines in Gymnolaemata,<sup>194</sup> Silén speculated that the ooeium 'is possibly a structure composed of transformed zoid-buds'.<sup>195</sup> Later this author<sup>196</sup> advocated these opinions in one of his following papers.<sup>197</sup>

Silén's study was so comprehensive, and his arguments were so convincing, that they have been accepted or mentioned by the authors of most large reviews and handbooks on Bryozoa up to the present time (Brown,<sup>198</sup> Hyman,<sup>199</sup> Brien,<sup>200</sup> Larwood,<sup>201</sup> Kluge,<sup>202-203</sup> Prenant and Bobin,<sup>204</sup> Powell,<sup>205</sup> Ryland,<sup>206-209</sup> Ryland & Hayward,<sup>210</sup> Ström,<sup>211</sup> Hayward & Ryland,<sup>212-213</sup> Reed,<sup>214</sup> Viskova,<sup>215</sup> Mukai *et al.*<sup>216</sup>). Some authors<sup>217-218</sup> also accepted the changes in terminology made by Silén, who used the term 'ectooecium' for the entire ooeial fold and 'entooecium' for the inner vesicle.<sup>219-220</sup> Interestingly, figures 1-8a from Silén's paper,<sup>221</sup> that have often been reproduced elsewhere, have never been subsequently modified, whereas a communication pore of the oovicell in the text-figure 10 by Calvet<sup>222</sup> has been often omitted without comment.<sup>223-225</sup> It could possibly have happened because Calvet stressed that he did not find this pore in any of the species with hyperstomial oovicells other than in *Bugula simplex* (in the endozooidal oovicell of the *Securiflustra securifrons* the connection between the ooeial and visceral coeloms was described and depicted).<sup>226</sup>

Nobody challenged Silén's generally accepted opinion during next three decades,<sup>227-228</sup> except Hans Hass<sup>229</sup> who provided very diagrammatical shemes of the 'reteporid' ooeicia, formed by the daughter zooid.

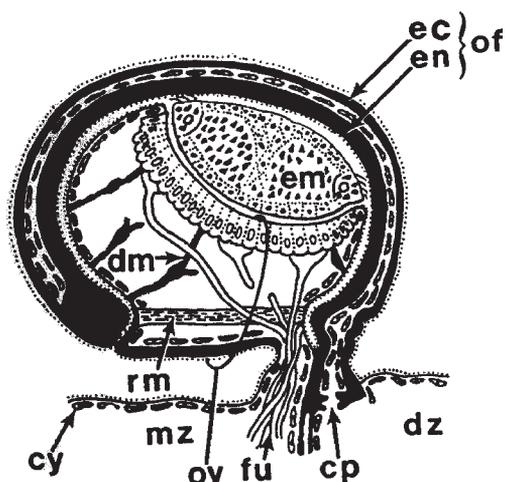
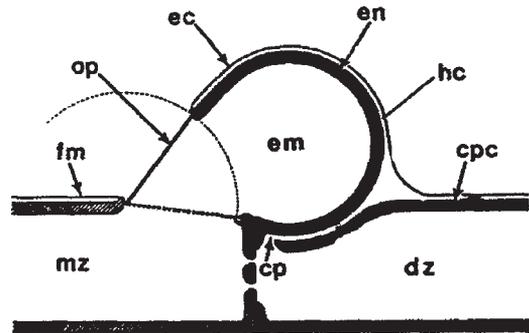


Figure 9. Ovicell structure in *Bugula neritina*. Abbreviations: cp – communication pore, cy – cystid wall, dm – depressor muscles of the oocial vesicle, dz – daughter (distal) autozooid, em – embryo, ec – ectoocium, en – entoocium, fu – funicular strands, mz – maternal autozooid, of – oocium, ov – oocial vesicle, rm – retractor-muscle of the oocial vesicle (after Woollacott and Zimmer, 1972, figure 2, abbreviations modified).

Anna Hastings discussed interesting points concerning the simultaneous presence of the hyperstomial and the ‘reduced and vestigial ovicells’ within the same cheilostome genera.<sup>230</sup> Hugo Moyano presented the diagrammatical schemes of the ovicells from four ascophoran genera, but gave not much detail on their structure.<sup>231</sup> John Ryland<sup>232</sup> discussed terminological problems accumulated since the works of Jullien,<sup>233</sup> Levinsen,<sup>234-235</sup> Canu and Bassler<sup>236</sup> and Silén,<sup>237-238</sup> and selected the most appropriate terms that are currently in use.<sup>239</sup>

Robert Woollacott and Russel Zimmer<sup>240</sup> investigated ovicell structure in *Bugula neritina* (Figure 9) and completely verified the data of Calvet.<sup>241</sup> They also studied a placental analogue.<sup>242</sup> After this, Silén was forced to admit the correctness of Calvet in respect of the species mentioned.<sup>243</sup> However, he stressed that the oocium inevitably should be formed by the maternal zooid in forms where the daughter zooid is absent in a longitudinal zooidal row (series). Silén suggested that the oocium is formed in different ways in different taxa. Subsequently, Alan Cheetham,<sup>244</sup> William Banta,<sup>245</sup> Philip Sandberg,<sup>246</sup> Renate Carson,<sup>247</sup> Claus Nielsen,<sup>248-249</sup> Patricia Cook and Jim Chimonides,<sup>250</sup> Alan Cheetham and Patricia Cook,<sup>251</sup> Ekaterina Lobastova and Andrew Ostrovsky<sup>252</sup> and Scott Santagata and William Banta<sup>253</sup> presented further evidence in favour of oocium formation from the daughter zooid in several cheilostome families (Calloporidae, Phidoloporidae, Bitectiporidae, Candidae, Bugulidae, Microporellidae, Cribrilinidae, Petraliellidae). Among others, the representatives of the same genera and, sometimes, the same species, which have been studied by Silén, were investigated. Nielsen<sup>254-255</sup> studied, amongst others, *Scrupocellaria varians* Hincks, 1882, *Bugula pacifica* Robertson, 1905 and *Fenestulina miramara* Soule, Soule & Chaney, 1995 (described as *F. malusii*) (Figure 10).<sup>256</sup> Following Levinsen,<sup>257</sup> he showed that the initial stage of ovicell formation can be either bilobate or single in different taxa. Lobastova and Ostrovsky<sup>258</sup> and Santagata and Banta<sup>259</sup> studied sections of *S. scabra*, *Callopora aurita* and *S. ferox* Busk, 1852 correspondingly. In all these cases the oocia formed by the daughter zooid were found,

Figure. 10. Ovicell structure in *Fenestrulina miramara*. Abbreviations: *cp* – communication pore, *cpc* – cryptocyst, *dz* – daughter (distal) autozoid, *ec* – non-calcified ectooecium, *em* – brooding cavity, *en* – calcified entoecium, *fm* – frontal membrane, *hc* – hypostegal coelom, *mz* – maternal (proximal) autozoid, *op* – operculum (after Nielsen, 1981, figure 20, abbreviations modified).



(regarded as basic<sup>260</sup>), and oocial coelom is connected with a visceral one through the communication pore(s) or slit. As a consequence of this, the dominance of one point of view in the literature changed to a co-existence of both Silén's and Levinsen-Calvet's opinions.<sup>261-263</sup>

Because calcification of the incipient entoecium starts from the transversal wall between the maternal (proximal) zooid and the distal bud (or zooid), and thus, the wall and the entoecium are continuous, one more explanation of the oocial formation has been raised. It was suggested that the entoecium derives from the maternal zooid, and the ectooecium from the daughter zooid. The first mention of this, one can find in the paper of Levinsen,<sup>264</sup> who wrote that 'it is obvious that the inner layer (the endooecium) can be regarded as a continuation of the distal [transversal] wall while the outer layer (the ectooecium) is formed from the front wall of the distal zoecium'. Since the papers of Dorothy Soule<sup>265</sup> and Jean-Georges Harmelin,<sup>266</sup> this point of view has reappeared in the literature as a compromise between the two earlier conflicting opinions.<sup>267-276</sup> For instance, Harmelin suggested this in the calloporid, *Corbulella maderensis* (Waters, 1898) (as *Crassimarginatella*),<sup>277</sup> and Cook did the same for *Doryporella alcicornis* (O'Donoghue and O'Donoghue, 1923) and *Scrupocellaria* (Candidae).<sup>278</sup> Nonetheless, Ostrovsky<sup>279</sup> came to the conclusion that although the entoecium and transverse wall are continuous, one should consider the oocial fold as a whole structure, and all the authors mentioned have dealt with oocia formed by the daughter zooid.<sup>280-281</sup>

Patricia Cook<sup>282</sup> and Peter Hayward<sup>283</sup> outlined different variants of the brood chamber formation within Cheilostomata, describing and illustrating the ovicells in some Lekythoporidae with unusual zooidal orientation. Judging from their figure, the oocium is formed by the maternal autozoid in this case, although the polypide orientation shows that the oocium obviously originated at the expense of the distal zooid in the ancestral forms.

As important landmark the paper of John Bishop and Bridgette Househam should be considered.<sup>284</sup> In the genus *Puellina* they found the ovicells of three categories 'based on the timing of production of the ovicell in relation to the budding of the maternal autozoid and of the zooid distal to it'.<sup>285</sup> The ovicell 'is a proximal component of the distal zooid' in category A, and 'of the kenozooid ... distal to the maternal autozoid' in category B. 'The ovicell appears to be a distal component of the maternal zooid' in category C.<sup>286</sup>

Ostrovsky<sup>287</sup> investigated the structure and development of the ovicells in *Cribrilina annulata* (Fabricius, 1780) and *Celleporella hyalina* (Linnaeus, 1767), and analysed the current state of the ovicell research in detail. He recognized two main types of ovicells among the Cheilostomata, assigning ovicells of categories A and B<sup>288</sup> to the 1<sup>st</sup> type, and of category C to the 2<sup>nd</sup> type.

However, since *Callopora dumerilii* has not been restudied, it was impossible to deny or ignore the statements of Silén,<sup>289-290</sup> who sectioned *Scrupocellaria scabra* and reported on the oecia formed by the maternal autozoid in this and other cheilostomes. Andrew Ostrovsky and Priska Schäfer investigated ovicell structure (anatomy and external morphology) in two calloporid bryozoans, *C. dumerilii* and *C. lineata* (Linnaeus, 1767) (the type species of the genus *Callopora* Gray, 1848), with the aim to finally resolve the long-term controversy described.<sup>291</sup> It was confirmed that ovicells are formed by the daughter zooids in both these species. The early stages of ovicellogenesis in *C. lineata* were studied, and there were no knobs or any other outgrowths found. An analysis of text-figure 18 of Silén<sup>292</sup> (representing a longitudinal section of the ovicell in *Scrupocellaria scabra*), and the accompanying description, showed that Silén could not find communication between an oecial fold and a distal zooid because of the strong shrinkage of the specimen fixed in alcohol. Studying three other species, Silén<sup>293</sup> did not make sections and referred to the wrongly interpreted structure of *Scrupocellaria*. Interestingly, Silén himself explained the difference between his and Calvet's results using the same reason: he suggested that the latter author worked with shrunked material. On the basis of these and previous findings (see above) Silén's<sup>294-295</sup> conclusions concerning the ovicell structure were regarded as incorrect, and his generalization was rejected. It was stressed that both ovicell types exist among Cheilostomata,<sup>296-297</sup> and sometimes within one and the same taxa, and further research is necessary to verify which types are characteristic for different taxa. Ostrovsky and Schäfer came to the conclusion that since there are no special pore-cell complexes associated with the oecial communication pore(s), there is only a formal reason to credit oecium as being a heterozoid. It is not a true kenozoid.

It should be mentioned here, that there is no clear distinction between the oecia formed by the distal kenozoid and by the maternal zooid in many instances, since the kenozoid can be flat, non-prominent distally and not seen from the above. In such cases, the maternal zooid forms the flat, distal kenozooidal bud that, in its turn, forms the oecium. Thus, the kenozooidal frontal wall serves as a floor of the brooding cavity, and the oecium itself is an outgrowth of this basal kenozoid. The majority of so-called 'terminal' ovicells have such structure, but they are traditionally considered as being formed by the maternal autozoid.<sup>298</sup> However, it would be better to reserve this definition for oecia, where the distal kenozoid is strongly reduced (like in *Cribrilina annulata* and *Cauloramphus spinifer*).

Ultrastructure and development of the ovicells in a few more calloporids (*Callopora*, *Tegella*, *Corbulella*) have been further studied by Ostrovsky, Schäfer and Gordon.<sup>299</sup>

Paul Taylor and Ken MacKinney,<sup>300</sup> and Ostrovsky<sup>301</sup> investigated the structure of so-called 'costate' ovicells in some fossil and Recent Microporidae and Cribrilinidae

correspondingly, and discussed the origin of ovicells in cheilostomes. Ostrovsky and Taylor<sup>302</sup> described four calloporid species with brood chambers formed by spines of the daughter zooid in the Mid-Cretaceous deposits of England and Germany. Such primitive ovicells looked like a cage, on one hand, supporting Harmer's hypothesis on the ovicell originated from mural spines,<sup>303</sup> and, on the other, mirrored Nielsen's view<sup>304</sup> about ovicells of the category A (ooecium is formed by the distal autozooid) as a basic form in ovicell evolution. Further more these authors published a detailed survey on all fossil and Recent forms known, whose brood chambers consists of spines or costae.<sup>305</sup> Evolutionary scenarios on the ooecial transformations in Calloporoidae, Monoporellidae, Macroporidae and Cribrilinidae were proposed. The acanthostegal brood chambers of *Tendra* were stated to be an example of independent evolution of brooding in the Cheilostomata.<sup>306</sup>

The development of the ooecium has additionally been investigated in the earliest cheilostome brooders belonging to the genus *Wilbertopora*. Interestingly, it is different from ovicellogenesis in the Recent calloporids, more reminiscent of ooecial formation in some Recent cribrimorphs, for example, *Puellina*.<sup>307</sup>

## 2. Other types of external brood chambers with calcified walls

Wassiliy Repiahoff<sup>308</sup>, Vladimir Reingard<sup>309</sup> and Alexandr Ostroumoff<sup>310</sup> investigated unusual brood-chambers from flattened mural spines ('acanthostegous ooecia' according to Levinsen<sup>311</sup>) in *Tendra zostericola* Nordmann, 1839, that were described first by M. Alexander Nordmann in 1839.<sup>312-314</sup> Although being mistaken in the understanding of the construction of these brood-chambers and believing that embryos were developed inside the body cavity of specialized zooids, Repiahoff suggested that they play the role of ovicells, and Reingard was the first who stated that '...*Tendra* will represent a transition between bryozoans without ovicells to those, that possess them...'.<sup>315</sup> Ostroumoff<sup>316</sup> first understood that embryos are brooded in the space [episteg] between the frontal membrane and the over-arching spines in *T. zostericola*.

Busk<sup>317</sup> recorded brood chambers in *Alysidium parasiticum* Busk, 1852, that were later studied by Levinsen<sup>318-319</sup> in detail. Such an 'ovicell' consists of two semispherical hollow plates or 'valves', forming a protecting chamber in the distal part of the maternal zooid. Each 'valve' is connected with the maternal zooid by the cuticular base that permits them to bend outwards. Levinsen called these brood chambers 'bivalvular' or 'double-valved ooecia', suggesting first that they correspond to two [oral] spines in non-fertile zooids.<sup>320</sup> However, in his next paper he showed that ooecial 'valves' are true kenozooids whose cavity is separated from the visceral coelom of the maternal zooid by the pore-plate.<sup>321</sup>

The 'bivalve' appearance of the brood-chambers is also characteristic of the genera *Scruparia*, *Alysidium* and *Thalamoporella*, and that is why Libbie Hyman<sup>322</sup> united them in the group of 'two-valved' ovicells.<sup>323-324</sup> She also believed that the 'synecium' – an unusually complexed brood chamber of eight hollow flat plates discovered by O'Donoghue in *Catenicula*<sup>325-326</sup> was 'related to the two-valved type'.<sup>327</sup> Later Cook<sup>328</sup> modified the term to 'synoecium'.

Levinsen first called the ovicells of *Thalamoporella* ‘epistomial’,<sup>329</sup> but later considered them as being hyperstomial.<sup>330</sup> In his turn, Harmer<sup>331</sup> suggested that ovicells in *Thalamoporella* are non-homologous to hyperstomial ovicells in other Cheilostomata, proposing that they evolved from the ‘adoral tubercles’ of the maternal zooid. Waters<sup>332</sup> called ovicells ‘bilobate’ in this genus, but stated that ‘there is no complete divisional wall in’ them.

### 3. Internal brood chambers<sup>333</sup> and intracoelomic brooding

The first observations of internal brooding in Cheilostomata were made by Grant in *Carbasa carbasa*.<sup>334</sup> Grant saw eggs, developing embryos and larval release, but did not recognize the brooding sac, which has not been studied yet. Similarly intrazooidal development of the embryo was recorded by Smitt in *Cryptosula pallasiana* (as *Lepralia*).<sup>335</sup> Later Louis Calvet described the internal brood chamber (pouch or diverticulum of the vestibulum), recording the muscles attached to its walls and the fertilisation envelope surrounding the early embryo in this species.<sup>336</sup> It was stated that the envelope disappears later in development.

Waters<sup>337-338</sup> recorded the internal brooding in several species from the genera *Watersipora* (as *Lepralia*), *Adeona*, *Adeonella*, *Adeonellopsis*, *Laminopora* and *Beania*, and discussed the possible value of such brood chambers for bryozoan classification. Embryos were said to be brooded inside the internal sac, placed in the distal part of the zooid (a specialized, and often enlarged ‘gonoecium’ in Adeonidae and Adeonellidae). In contrast with *Watersipora*, in which embryos were described and depicted being enveloped by the ‘thin-walled [brooding] sac’,<sup>339</sup> all other cheilostomes mentioned have been characterized by the ‘thick-walled sac’. Judging from Waters data (that embryos occupied half or even most part of the zooidal cavity in four ‘adeonid’ genera, but the eggs found were from small to moderate size), there should be extraembryonic nutrition in them. In the following paper Waters<sup>340</sup> described and depicted hypertrophied epithelium of the brooding sac in *Adeonella platalea* (Busk, 1854). In *Poricellaria ratoniensis* (Waters, 1887) (as *Diplodidymia complicata*) the small egg begins growth within the small brooding sac, hanging below the zooidal operculum. Further more they both enlarge to such an extent that they fill most of the zooidal cavity, but Waters did not understand that he had discovered an extraembryonic nutrition in both these species. However, he obviously realised this in the case of *Catenicella elegans* (Busk, 1852) (as *Vitaticella*), since he wrote that there are ‘several fleshy bands or tubes by which ... material for growth is transferred to the ovicell’, containing large embryo in this species.<sup>341</sup>

Additionally, Waters found embryos surrounded by a membrane inside some zooids of *Steginoporella magnilabris* (Busk, 1854) (as *Steganoporella*), calling such brooding structures ‘internal ovicells’.<sup>342</sup> He also found an embryo brooded internally in *Chlidonia pyriformis* (Bertolini, 1810) (as *C. cordieri*) in sections, but did not mentioned the brooding organs in his paper. Marcus made a similar finding while studying *Steginoporella haddoni* (Harmer, 1900) (as *Steganoporella*).<sup>343</sup> Later, Harmer<sup>344</sup> described internal

brooding in ‘a spacious, thin-walled ovisac’ in *S. magnilabris*. He mentioned that it extends nearly to the zooidal basal wall, attaching ‘to the lateral walls ... by a number of muscle-fibres’, but was not able to recognize whether it was connected with a vestibulum. Studying *S. buskii* (Harmer, 1900) (as *Steganoporella*), Cook<sup>345</sup> recorded the internal brooding and noted that the cryptocyst is strongly reduced as the embryo grows which could be evidence of extraembryonic nutrition.

Marcus<sup>346</sup> discovered viviparity (intracoelomic embryonic development) in *Synnotum* sp. (as *S. aegyptiacum*). He stated that the embryo ‘is nourished by the follicle cells which receive alimentary material from other parts of the colony and the maternal brown body, transported by the mesenchymatous tissue-cords’.<sup>347</sup> The late embryo is 50-60 times larger than the mature ovum before cleavage, that is evidence of extraembryonic nutrition.

Hastings recorded ‘the zooecia ... [with] embryos in the body-cavity, although they had no ovicells and showed no external difference from the non-fertile zooecia’ in *Oshurkovia littoralis* Hasting, 1944 (as *Umbonula verrucosa*).<sup>348</sup> Later she mentioned ‘internal ovisacs’ in this species.<sup>349</sup> The data were confirmed by David Eggleston<sup>350</sup> who noted the internal brooding of several embryos simultaneously in *O. littoralis* (as *Umbonula*). The structure of the brooding organ is unknown, however.

Mawatari<sup>351</sup> studied some aspects of the sexual reproduction in *Watersipora subtorquata* (d’Orbigny, 1842) (as *W. cucullata* (Busk)). He mentioned ‘the embryo sac’, which envelops the developing embryo, and his figures 20-38 and 44 show that it is evagination of the vestibulum.<sup>352</sup> Similarly, Cook<sup>353</sup> mentioned ‘membranous diverticula housed within zooid body wall’ as a brood chamber in dimorphic female zooids of *Tropidozoum cellariiforme* Harmer, 1957.

Dyrynda discovered the intracoelomic brooding in *Epistomia bursaria* (Linnaeus, 1758).<sup>354-355</sup> The embryonic cleavage starts inside the ‘follicle’ and the embryo increases about 1000 fold in volume, which is evidence of extraembryonic feeding. Finally it was suggested that the combination of endocoelomic brooding, larval viviparity and one polypide generation per zooid may be a primitive feature from which recycling and extracoelomic brooding may have evolved.

Recently, the anatomical structure of internal sacs for embryonic incubation has been studied in three cheilostome bryozoans, *Nematoflustra flagellata*, *Gontarella* sp. and ‘*Biflustra*’ *perfragilis* by Ostrovsky *et al.*<sup>356</sup> In the evolution of brood chambers in the Cheilostomata, such internal sacs for embryonic incubation have been considered as a final step, being the result of immersion of the brooding cavity into the maternal zooid and reduction of the protective fold (oocium). Possible stages and reasons for this transformation have been discussed, and the hypothesis of Santagata and Banta<sup>357</sup> that internal brooding evolved prior to incubation in ovicells has been rejected.

#### 4. External brooding sacs

Waters<sup>358</sup> discovered the external brooding sacs (that he called ‘ovicells’) in *Aetea sica* (Couch, 1844) (as *A. anguina forma recta*) and *Aetea anguina* (Linnaeus, 1758).<sup>359</sup> He

figured them on the top of the dorsal side of the erect portion in the maternal zooids. Alice Robertson<sup>360</sup> recorded this ‘membranous bag’, being situated on the frontal side of the zooid below the operculum in the same species.<sup>361</sup> She suggested that the curvature of the tubular part of the zooid ‘afford[s]... protection to the delicate oecium and its contents’. Levinsen<sup>362</sup>, considering the unusual appearance and position of this structure, concluded that ‘the supposed ovicellular wall [is] only ... a shell membrane surrounding the egg’.<sup>363</sup> Waters<sup>364</sup> challenged Levinsen’s opinion, in saying that the position of all the brood chambers he saw, is very consistent. He referred to the paper of Raymond Osburn,<sup>365</sup> who also found the brooding sacs at the top of the zooids, distally from the operculum. Further researchers supported both opinions: in *Aetea anguina* the brooding sac (ovisac) has been described on the frontal membrane, proximally to the operculum by Hastings,<sup>366</sup> Gautier<sup>367</sup> and Mawatari,<sup>368</sup> and distally to the operculum by Marcus,<sup>369-370</sup> Eggleston<sup>371</sup> and Cook.<sup>372-373</sup> Hastings noted that embryo sacs with the early embryo are closely applied to the zooidal frontal membrane, whereas those with an advanced embryo are free from the membrane except to the distal narrow attachment. She also depicted this narrowest part in the ovisac with an embryo and in an empty one. Similar ‘commencement of the ovicell’ has been mentioned by Waters,<sup>374</sup> and depicted by Shizuo Mawatari,<sup>375</sup> who described ‘the membranous ovicelligeous sac at the distal extremity on one side of the frontal membrane just proximal to the opercular valve’.<sup>376</sup> Patricia Cook,<sup>377</sup> who observed the brood chambers on the zooidal dorsal side only, stated that they were covered by a cuticular layer. Additionally, in one population of *A. anguina* she also found the slight proximal and ventral calcification of its wall on the side apposed to the zooidal wall in sections. She suggested that the ovisac is a product of the exterior zooidal wall, and not of the external diverticulum from the tentacle sheath. Cook also noted that in a significant number of zooids two embryos were contained and released simultaneously from the same brooding sac. The inconsistency in positioning of the embryo sacs, its presence during reproductive periods only<sup>378</sup> and an absence of the opening could be considered in favour of Levinsen’s hypothesis. In contrast, partial calcification of the ovisac wall and embryonal pairs met may be evidence against this hypothesis. Information concerning the ovisacs found in other species of the genus *Aetea*, is in the books of Prenant and Bobin,<sup>379</sup> and Ryland and Hayward.<sup>380</sup>

A similar type of brooding in the ‘membrane sac above the orifice’ was recorded by Eggleston<sup>381</sup> in *Eucratea loricata* (Linnaeus, 1758). Leo Stach<sup>382</sup> discovered external ‘brood-sac’[s] in *Carbasea indivisa* Busk, 1852. Each brooding zooid possesses three to seven such sacs. The author stated that they ‘are developed from the distal portion of the tentacle-sheath forming the inner wall of the operculum.’<sup>383</sup> Larvae escape from the sacs supposedly through the rupture of its wall.<sup>384</sup> ‘1-2 membrane-bounded embryos’ attached to the frontal membrane adjacent to the zooidal opening were recorded by Dennis Gordon in *Leiosalpinx australis* (Busk, 1884).<sup>385</sup>

In conclusion, it should be admitted that in spite of two and half centuries of investigations, the general picture of cheilostome brood chamber structure and development is still very incomplete. The largest existing source of data on that topic is Levinsen’s

illustrations and, in a lesser extent, his descriptions.<sup>386</sup> As mentioned above, this prominent researcher studied the complete, sectioned and developing ovicells in more than 80 cheilostome species belonging to 62 genera, but since he worked with cleaned bryozoan skeletons only, it is often very difficult to estimate the correctness of the conclusions he made.<sup>387-388</sup> As a result, Levinsen's data were never used, and careful restudy is necessary in this case. Ovicell anatomy should also be reinvestigated in some recently studied species as well. For instance, Calvet's schematical drawing of the ovicell in *Fenestrulina malusii* (as *Microporella*) made from the section of decalcified animal,<sup>389</sup> differs from the diagram of the species *Fenestrulina miramara* (described as *F. malusii*) presented by Nielsen who only used the skeletal parts.<sup>390</sup> It is clear now that a combined approach is the only adequate method for this kind of research. Further accumulation of data on brooding structures is necessary to make progress in our understanding of bryozoan phylogeny and evolution of their reproductive patterns.

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## Notes

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- 38 Hincks, note 35.
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- 107 Calvet, note 61, page 132, Plate II, figure 14, Plate III, figure 5.
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- 112 Calvet, note 61, page 58, text-fig. 10.
- 113 Calvet (note 61) called those muscles that opened the ovicell opening - 'retractors', and those that expanded the brooding cavity - 'dilators'. He also wrote that the number of muscle bundles increased during embryonal development. It is possible that he confused a some of them with funicular strands.
- 114 In the calloporid *Amphiblestrum flemingii* Calvet (note 61, fig. 45) illustrated cells of the inner wall of the oocell vesicle as larger than all other epithelial cells. The same impression is gained from his scheme of the flustrid *Securiflustra securifrons* (fig. 44), however, this requires checking.
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- 124 The word 'ovicell' could imply a zooid [cell], producing an egg [ovum].
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- 127 Levinsen, note 14, pages 56, 59.
- 128 Calvet, note 61.
- 129 Levinsen, note 14, Plate XXIV, figure 13.
- 130 Levinsen, note 118.
- 131 Levinsen, note 119.
- 132 Levinsen, note 14.

- 133 Levinsen, note 72.
- 134 Levinsen, note 14.
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- 153 Harmer, note 111.
- 154 S.F. Harmer, 'The Polyzoa of the Siboga Expedition. IV. Cheilostomata Ascophora. II', *Reports of the Siboga Expedition*, 28d (E.J. Brill, Leiden 1957), 641-1147.
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