

The status of *Callianira hexagona* (Slabber, 1778) (Ctenophora)

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In 1768, Martinus Slabber collected the only specimen ever found of the ctenophore species mostly cited as *Callianira hexagona* (Slabber, 1778). After analysing the international confusing literature on this species, we conclude the nomenclatural correct name should be *Callianira slabberi* De Haan, 1827. The designation to *Callianira* was done by 19th-century taxonomists, who did not realize that Slabber's drawing lacks most of the transparent outer part of the animal, as indicated in the accompanying Dutch text. Moreover, Slabber's description contains details not consistent with ctenophore morphology. Most probably, Slabber described a juvenile specimen of *Pleurobrachia pileus* (O.F. Müller, 1776), and *C. slabberi* may be considered a junior synonym of the latter species. A copy of Slabber's drawing has been used in the allocation of another ctenophore species in *Callianira*. Combined with the fact that this genus was based on a poorly described specimen, this throws doubts on the validity of the genus *Callianira*.

Introduction

New techniques in sampling and genetics promise a better understanding of biodiversity and taxonomy. However, these techniques do not offer a solution for the evaluation of inadequate historic species descriptions when type material is lacking, especially in case only one specimen of the species was collected (Mianzan *et al.*, 2009). In this paper, we evaluate the case of the ctenophore *Callianira hexagona*.

From 15.vi to 6.viii.1768, the Dutch civil servant Martinus Slabber collected marine species with a dip net from the Scheldt estuary in the southwestern part of the Netherlands. He described 39 local specimens in a book entitled *Natuurlijke Verlustingen* (Natural Delights). This work appeared in 18 different parts between 1769 and 1778, but since the date of appearance of the separate pieces is not known, the complete work is mostly cited as Slabber (1778). In four cases, Slabber is cited as the author of a species.

One of these species, described and depicted in part seven of his book, is the 'Zes-hoekige (hexagonal) Beroë'. This ctenophore is nowadays often cited as *Callianira hexagona* (Slabber, 1778) *e.g.* in the World Register of Marine Species (WoRMS) (Collins, 2010), The Taxonomicon (Brands, 1989-present) and Mills (1998-present). Slabber found this ctenophore only once, and remarkably, no subsequent occurrence has been reported in the vicinity of the Scheldt estuary, a well-studied European marine region, or elsewhere. This triggered our suspicion. In order to examine the validity of this species we studied Slabber's description and accompanying illustrations and reviewed the nomenclature. Finally we dealt with the question whether Slabber's observation concerned a separate species.

Slabber's description and illustrations

Plate 7 fig. 3 ('natural size'), accompanying Slabber's description (fig. 1a), illustrates the small size of the specimen, *viz.* about four mm in diameter.

A 20-fold magnification in fig. 4 of plate 7 (fig. 1b) has a somewhat strange appearance due to very strongly protruding ribs. However, Slabber indicates in his text that he omitted the 'vlies' (membrane) around the animal, since it was not visible in the same light conditions he used to draw the figure. With a certain light direction under his Cuff's microscope, he was able to see the body wall. It would have taken very special skills indeed to illustrate this transparent feature adequately. Comparing this image to other ctenophores, we may conclude Slabber omitted almost all transparent parts of the ectoderm, mesoderm and mesogloea. As a result, we have to guess about the exact external appearance of the comb jelly.

Another strange aspect of the animal is the number of costae carrying ciliary plates, Slabber's 'rolronde lichamen' (= tube-shaped bodies). Superficially, the animal seems to possess only six costae. This impression may even be confirmed by the epithet 'zes-hoekig' used by Slabber. Six costae is a very odd number in ctenophores, and besides, it is not in accordance with the drawing: although Slabber emphasized six rows, denoted by g in fig. 1b, two additional rows indicated by f are present as well. From Slabber's description one might conclude that two of the 'g' costae are present in the sagittal plane, a non-existent phenomenon in ctenophores. Also, the deep position of the 'f' costae is aberrant, as costae are always present on the animal's outer surface. We conclude that Slabber either may have dealt with a damaged specimen, or that he was not able to see or visualize the three-dimensional aspect of the specimen properly.

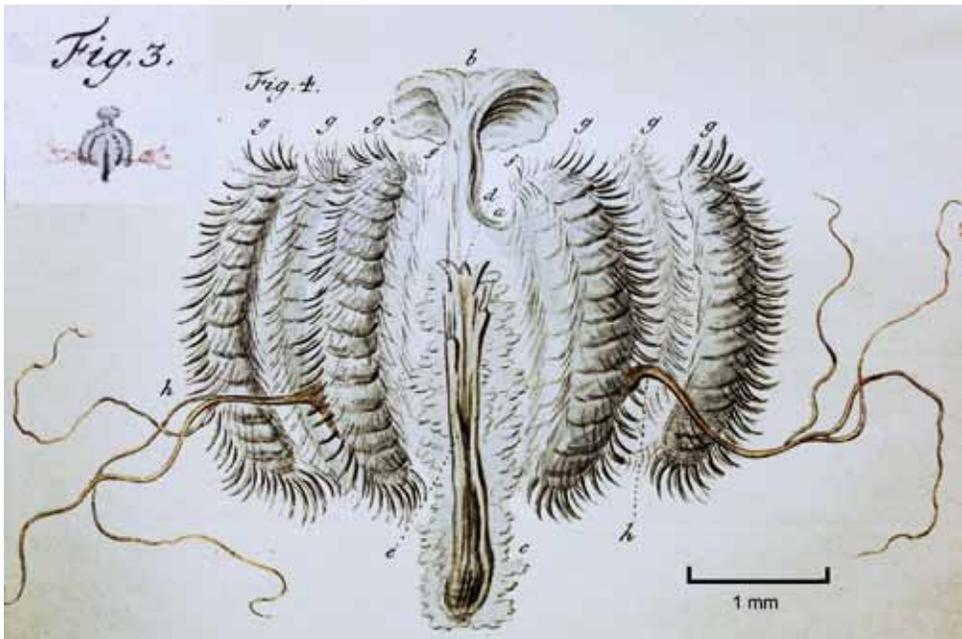


Fig. 1. Zeshoekig Beroë by Slabber (1778) plate 7. a (inset): fig. 3 'natural size', b: fig. 4 enlarged.

Table 1. History of names of the first three species assigned to *Callianira*. Rectangles denote use of figs 3, 4 on plate 7 of Slabber (1778) and its copies (fig. 5 & 6) on plate 90 in Tableau Encyclopédique (Bruguière 1791).

year	author	<i>Callianira slabberi</i>	fig. 4	fig. 3	<i>Callianira triploptera</i>	<i>Callianira diploptera</i>	Remark
1769- (Netherlands)	Slabber	Zeshoekige Beroë	4	3			Fig. 3 natural size, 1778 Fig. 4 enlarged
1789	Bruguière				<i>Beroë hexagonus</i> (Madagascar)		First 344 pp. of Hist. Naturelle des Vets; name should be <i>B. hexagona</i>
1790	Modeer	<i>Beroë hexagona</i>					Name not available
1791	Bruguière		6	5			Slabber's figs 3, 4 copied in Tableau Encyclopédique without referring to Slabber
?	Péron				<i>Sophia diploptera</i> (Australia)		Unpublished manuscript
1810	Péron & Lesueur				<i>Callianira diploptère</i>		Definition genus <i>Callianira</i> (as pteropod mollusc)
1816	Lamarck		6	5	<i>Callianira triploptera</i>	<i>Callianira diploptera</i>	Lamarck links figs 5, 6 of Bruguière to <i>C. triploptera</i>
1827	Bory de St. Vincent		6	5	<i>Callianira triploptera</i> <i>Beroë hexagonus</i>		Legend to Plate 90 published on p. 139 of Tableau Encyclopédique
1827	De Haan	<i>Callianira slabberi</i>			*		*De Haan objects to assignment of <i>Beroë hexagonus</i> to <i>Callianira</i>
1829	Eschscholtz	<i>Callianira hexagona</i>	6	5	<i>Callianira triploptera</i>	<i>Callianira diploptera</i>	<i>C. hexagona</i> (in recent use); junior synonym

Slabber described two 'armen' (arms) with tube-like bases. These tentacles divided in three tentilla and 'were moving to catch their prey'. Fig. 1b shows a position of the tentacles unusual for tentaculate ctenophores, as they are not on opposite sides of the animal. According to Slabber's text, they are on the 'frontal side' and he even notes that tentacles lack at the 'back side'. This corroborates our impression that Slabber's drawing has some deficiencies.

On top of the animal, Slabber saw a protruding fan. He compared this structure to the rudder of a ship. The fan may have been reflectance of light off the ectoderm as it curved backwards out of sight. The lines that radiate out from a central point on the fan may have been the ciliary tracks that run between the comb rows and the apical organ. Possibly the statocyst is visible as a small oval structure at the central base of the fan (right from *f* in fig. 1b).

Nomenclatural history

To support the below-mentioned complicated and confusing nomenclatural history of Slabber's ctenophore, a time-line is presented in table 1.

Unlike the majority of species in his book, Slabber did not ascribe a scientific name to the specimen. Maybe he was not convinced of dealing with a separate species. He confined himself to the Dutch description 'Zeshoekige Beroë'. In our opinion Slabber's approach should be considered as a violation of ICZN article 11.4: consistent application of binominal nomenclature. As a result, Slabber, 1778 is not the correct author/year designation of the species.

The Swedish scientist Modeer referred to Slabber's specimen (Modeer, 1790: 46) and described it as *Beroe hexagona*. Since Modeer was the first to assign a Latin binominal name, one would expect him to be the author of the species. However, the name *B. hexagona* was not available: one year earlier, Bruguière published the first 344 pages of his *Histoire Naturelle des Vers* (Evenhuis & Petit, 2003) including a description of *B. hexagonus*, a ctenophore encountered in 1774 in Antongil Bay, Madagascar (Bruguière, 1789: 176). In this name, the species epithet *hexagonus* violates ICZN article 32.1; it should end in *-gona*. Therefore, for Slabber's specimen, *Callianira slabberi* De Haan, 1827, the next available name, should apply.

Finally, Eschscholtz (1829: 28), unaware of De Haan's paper, referred to Slabber's specimen (see below) and transferred *Beroe hexagona* Modeer, 1790 to *Callianira*, but the resulting name, *Callianira hexagona* (Modeer, 1790) should be considered a junior synonym of *C. slabberi* De Haan, 1827.



Fig. 2. Peron & Lesueur (1810) plate 2 fig. 16. The authors considered this *Callianira* to be a pteropod mollusc.

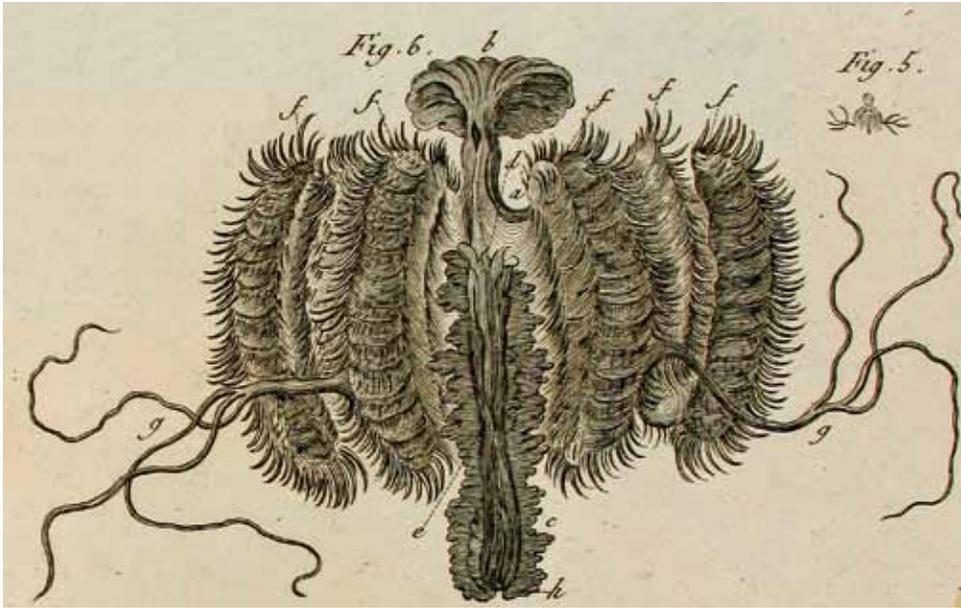


Fig. 3. Bruguière (1791) plate 90 figs 5, 6. Lamarck (1816) referred to this drawing as *Callianira triploptera*.

Callianira, a valid genus?

The genus *Callianira* has a striking history. It was described by Péron & Lesueur (1810) as a genus of pteropod molluscs *without* tentacles and with three fins (nageoires), one caudal and two lateral. The latter carried cilia and were considered gills. Péron and Lesueur added a rather non-descriptive picture of their ‘Callianire Diploptère’ (fig. 2). Remarkably they noted a resemblance of the ‘gills’ to those of ‘beroës’.

Lamarck (1816: 467)¹ noted the similarity of *Callianira* of Péron and Lesueur (1810) and *Beroe* and placed *Callianira* in his ‘Radiaires anormales’. He assigned two species to *Callianira*: *C. diploptera*, i.e. the non-tentaculate Australian Callianire Diploptère of Péron and Lesueur, and *C. triploptera* Lamarck, 1816, a species with short tentacles. The latter was the above-mentioned *Beroe hexagonus* of Bruguière (1789: 176)², an animal with six ‘angles longitudinaux’. In his treatment of *C. triploptera*, Lamarck (1816) referred to plate 90 figs 5-6 in Bruguière’s *Tableau Encyclopédique et Méthodique des trois Règnes de la Nature* (1791) depicted in fig. 3. In doing so, Lamarck created a link between the description and an illustration, a link not made by Bruguière (1789). This action was clearly erroneous as figures 5 and 6 in Bruguière (1791) are an almost exact copy of Slab

¹ This is Lamarck’s *Histoire naturelle des animaux sans vertèbres*, not his contribution to the *Tableau encyclopédique et méthodique* which also appeared in 1816.

² Before Lamarck renamed *Beroe hexagonus*, both Slabber’s *Beroe hexagona* and its congener *B. hexagonus* existed simultaneously, a confusing situation lasting from 1790-1816.

ber's drawing, a fact also mentioned in De Haan (1827) and De Blainville (1834: 152)³. De Haan (1827) opposed the assignment of *B. hexagonus* Bruguière, 1789 to *Callianira*, not only because a wrong illustration (fig. 3) was used, but also because the original description did not mention any keels – on the contrary, it reported convex intervals between the longitudinal angles. The suggestion of De Haan to retain *B. hexagonus* of Bruguière in *Beroë* was neglected, perhaps because he wrote his paper in Dutch.

In the opinion of De Haan (1827), Slabber's specimen belongs to the genus *Callianira*, and he proposed the name *Callianira slabberi*.

Eschscholtz (1829) placed the genus *Callianira* Péron & Lesueur (1810) in his new Class Tentaculata. Apart from its keel-shaped costae now also the presence of tentacles characterized the genus. Although Eschscholtz stated that he never saw an example of *Callianira*, he claimed *C. diploptera* to fit well within the genus and that its tentacles must have been overlooked (without any reference he stated this species to withdraw its tentacles upon catchment and to protrude them only after the animal was left untouched for some time!). Slabber's comb jelly was added as a third species, *Callianira hexagona*, based on the protruding comb rows in the incomplete drawing. Later on, four more species were discerned within the genus. Remarkably, Eschscholtz (1829) refers to plate 90 fig. 5 in Bruguière (1791) for *C. triploptera* and - unlike Lamarck (1816) - to fig. 6 for *C. hexagona*. Clearly, Eschscholtz was not aware of the fact that both figures illustrated the same (*viz.* Slabber's) specimen.

³ Yet another copy of Slabber's drawing exists on plate 7 of the atlas of De Blainville (1834). It is strange that it carries the name *Callianire triploptère*, since De Blainville himself mentions the error of using Slabber's drawing for the Madagascan ctenophore of Bruguière.



Fig. 4. *Pleurobrachia pileus* juvenile of 3-4 mm. Photo rotated 180° in order to match fig. 1. Photo Peter Parks.

The arguments used to join the first three species in *Callianira* are arbitrary and do not meet modern standards. One species was poorly described and lacked tentacles, whereas the other two lacked the characteristic keels. Clearly, as suggested earlier (Mertens, 1833: 499; Chun, 1880: 278; Moser, 1910: 164; Agassiz, 1860: 193), the genus *Callianira* needs a thorough revision. Recent work, using molecular techniques to study phylogenetic relationships of ctenophores, indicates that the present classification needs to be radically revised (Mills, 1998-2010; Mills & Haddock, 2007). Hopefully this solves the problematic status of the genus *Callianira*.

Alternative classification of Slabber's comb jelly

We are not the first to cast doubt on the status of Slabber's *Callianira* (Römer, 1904: 86; Chun, 1910: 241). Louis Agassiz (1860: 293) tried to solve the ambiguity by claiming that *Callianira hexagona* was a synonym of *Pleurobrachia pileus* (O.F. Müller, 1776). As he did not provide any evidence, we will discuss the probability of his assumption that in fact Slabber described a sea gooseberry (*P. pileus*). Solving this matter could prevent Slabber's *Callianira* from reappearing in literature as a separate species.

As mentioned above, Slabber's specimen was about four mm in diameter. Such a small size suggests he described a juvenile comb jelly. Searching for a potential candidate, it seems logical to look at juveniles of tentaculate ctenophores in Dutch coastal waters. The genus *Bolinopsis* is rare in the Netherlands; also its tentaculate juveniles can be excluded because of the placement of costae, nearing in pairs at the aboral end (Greve, 1975). *Mnemiopsis leidyi* A. Agassiz, 1865 can be ruled out because it did not appear in Dutch waters before 2005. Only one species deserves consideration: the ubiquitous *Pleurobrachia pileus*.

Slabber's specimen probably is a juvenile *Pleurobrachia pileus*. Its developmental stage is comparable to the 3-4 mm juvenile in fig. 4.

Pleurobrachia juveniles have much in common with Slabber's 'Zeshoekige Beroë'. Considering that Slabber (1778) omitted most of the outer transparent parts, the general appearance resembles juveniles of the same size. The proportions and placement of the costae and the gastro-vascular system fit well. Other details, for instance the number of ctenes (13-14) in each costa, match a four-mm *P. pileus* as well.

However, not all details perfectly match: the tentacles in Slabber's illustration are too short and do not show enough tentilla characteristic for a four-mm juvenile. It is possible that some parts of the tentacles were broken off during microscopical preparation, as easily happens in juveniles. The tentacles in Slabber's illustration are situated too far from the aboral pole. However, the curvature of the visible part of the tentacle's bases nicely matches the same part of the bulb structure as can be seen in fig. 4, especially on the right side.

Slabber was aware of the existence of *Pleurobrachia*, since he knew it at least as *Beroë* from Baster (1765, Vol. 1, plate 14 figs 6, 7). Most likely, he did not recognize his specimen as a juvenile of this species. It is not the first time to notice that the original description of a ctenophore is not accurate and that the 'species' turns out to be a juvenile of a different animal. Many original descriptions of ctenophores are based on distorted or damaged specimens or on juveniles (Mianzan *et al.* 2009).

Conclusion

Following ICZN rules, Slabber's Zeshoekige Beroë should not be cited as *Callianira hexagona* (Slabber, 1778) but as *Callianira slabberi* De Haan, 1827.

However, we question if this is really an extant species. Slabber's specimen was observed only once in a well-studied region, *viz.* the southern North Sea, and the species characteristics he mentions are unusual. The description and drawing (Slabber, 1778) leave many doubts on the accuracy of his observations. Most probably, Slabber described a juvenile of *Pleurobrachia pileus*, a very common species in his area.

The genus *Callianira* has a doubtful pedigree, and its rationale is questionable. Several species were added, based on dubious characteristics. Slabber's 'Zeshoekige Beroë' was placed in *Callianira* on account of an incomplete drawing.

Acknowledgements

We like to thank Arnold Tulp for thinking along with us on the probability that Slabber described a juvenile *Pleurobrachia pileus*. He confirmed several characteristics to match 4 mm juveniles of *P. pileus*: the proportions and placement of the costae, the gastro-vascular system and the number of ctenes (13-14) in each costa. He also noticed the short tentilla. Also thanks to Neal Evenhuis (Bishop Museum, Hawai'i) and Jip Binsbergen of Artis Library, Special collections, University of Amsterdam for leading us through the contents and publication dates of the different parts of Bruguière's *Histoire Naturelle des Vers* and *Tableau Encyclopédique*. Rob van Soest (University of Amsterdam) was helpful with taxonomical suggestions. Special thanks go to Claudia Mills (Friday Harbor laboratories and Department of Biology, University of Washington) for her valuable comments and suggestions on an earlier version of this paper. She explained the fan and suggested the visibility of the statocyst in Slabber's drawing. She also noticed the resemblance of the curvature of the basis of the tentacles in the drawing with the curvature of *P. pileus*. Finally, we appreciate the reviewers suggestions.

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