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NOTE ON THE ZUIDERZEE CRAB, *RITHROpanopeus harrisii* (GOULD) SUBSPECIES *TRIDENTATUS* (MAITLAND)

by

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In the former Zuiderzee, the large brackish inland sea of the Netherlands, a species of crab was commonly met with, which species generally was considered to be endemic in the Dutch inland waters, and was named by most authors *Heteropanope tridentata* (Maitland). Examination of material and literature convinced us that the crab does not belong to the genus *Heteropanope* at all, but is a *Rithropanopeus*, while it is so closely related to the American *Rithropanopeus harrisii* (Gould), that we only can consider it to be a subspecies of that species.

The synonymy of the Dutch form is as follows:

- Pilumnus tridentatus* Maitland, 1874, Tijdschr. Nederl. dierk. Ver., vol. 1, p. 232.
non *Pilumnus tridentatus* Maitland, 1876, Tijdschr. Nederl. dierk. Ver., vol. 2, p. 11.
Pilumnus tridentatus Hoek, 1876, Tijdschr. Nederl. dierk. Ver., vol. 2, p. 243, pl. 14 fig. 12-16.
Pilumnus tridentatus Miers, 1886, Rep. Voy. Challenger, Zool., vol. 17, pp. 146, 149, 227.
Pilumnus tridentatus Hoek, 1887, Tijdschr. Nederl. dierk. Ver., ser. 2 vol. 1, p. 96.
Pilumnus tridentatus De Man, 1889, Zool. Jb. Syst., vol. 4, p. 422.
Heteropanope tridentata De Man, 1892, Notes Leyden Mus., vol. 14, p. 228, pl. 7 figs. 1, 1a-1d.
Pilumnus tridentatus A. Milne Edwards & Bouvier, 1894, Rés. Camp. sci. Monaco, vol. 7, p. 39.

- Pilumnus tridentatus* Maitland, 1897, Prodr. Faune Pays-Bas, p. 36.
- Pilumnus tridentatus* A. Milne Edwards & Bouvier, 1900, Expéd. sci. Travailleur & Talisman, Crust. Décap., pt. 1, p. 72.
- Pilumnus tridentatus* Horst, 1903, Maandbl. Nederl. natuurk. Ver., vol. 2, p. 40.
- Pilumnus tridentatus* Van Breemen & Redeke, 1907, Redeke's Zuiderzee Rapport, app. 5, p. 12.
- Pilumnus tridentatus* Tesch, 1909, Jaarb. Rijksinst. Onderz. Zee, 1908, p. 80.
- Pilumnus tridentatus* Tesch, 1912, De Levende Natuur, vol. 17, p. 76, fig.
- Pilumnus tridentatus* Dorsman, 1913, Langs Strand en Dijken, p. 171, fig.
- Heteropanope tridentata* Heinsius & Jaspers, 1913, Strandboekje, vol. 1 pt. 2, pp. 67, 93, fig. 10 D.
- Pilumnus hirtellus* var. *tridentatus* Blohm, 1915, Wiss. Meeresunters. Kiel, n. ser. vol. 17, p. 72.
- Heteropanope tridentata* Van der Sleen, 1920, Tijdschr. Nederl. dierk. Ver., ser. 2, vol. 18, p. xxxiv.
- Heteropanope tridentata* Thijssse, 1921, Flevo, vol. 1, p. 188, fig.
- Heteropanope tridentata* Redeke, 1922, Bijdr. Dierk., vol. 22, p. 332.
- Heteropanope tridentata* Tesch, 1922, Redeke's Flora Fauna Zuiderzee, p. 346, figs. 7-19.
- Heteropanope tridentata* De Vos, 1922, Tijdschr. Nederl. dierk. Ver., ser. 2 vol. 18, p.c.
- Heteropanope tridentata* Balss, 1926, Tierw. Nord- und Ostsee, vol. 10 pt. h2, p. 44.
- Heteropanope tridentata* Schellenberg, 1928, Tierw. Deutschl., vol. 10 pt. 2, p. 135, figs. 106, 107.
- Heteropanope tridentata* Redeke, 1929, Verh. Int. Ver. Limnol., vol. 4, p. 537.
- Heteropanope tridentata* Redeke, 1932, Publ. Hydrobiol. Cl., vol. 1, p. 34.
- Heteropanope tridentata* Balss, 1933, Capita Zool., vol. 4 pt. 3, p. 33.
- Heteropanope tridentata* Kamps & Otto, 1933, De Levende Natuur, vol. 38, p. 168.
- Heteropanope tridentata* Sybrandi, 1933, Aquarium, vol. 3, p. 201, fig. 4.
- Zuiderzeekrab* Tinbergen, 1933, De Levende Natuur, vol. 38, p. 262.
- Heteropanope tridentata* Otto, 1934, Onze Zoetwatervisscherij, vol. 30 app. 9, p. 35.
- Heteropanope tridentata* Otto, 1934a, Zool. Anz., vol. 108, p. 130, fig. 1.
- Heteropanope tridentata* Anonymus, 1935, Onze Zoetwatervisscherij, vol. 31, p. 93.
- Heteropanope tridentata* Redeke, 1935, Hand. Nederl. natuur- en geneesk. Congr., vol. 25, p. 169.
- Heteropanope tridentata* Havinga, 1936, Biologie Zuiderzee tijdens Drooglegging, vol. 4, p. 11.
- Heteropanope tridentata* Korringa, 1936, De Levende Natuur, vol. 41, pp. 89, 154, fig.
- Pilumnopeus tridentatus* Schubert, 1936, Zool. Anz., vol. 116, p. 320, figs. 1, 2.
- Heteropanope tridentata* Anonymus, 1937, Onze Zoetwatervisscherij, vol. 33, p. 6.
- Heteropanope tridentata* Redeke, 1937, Int. Rev. Hydrobiol. Hydrogr., vol. 35, p. 226.
- Heteropanope tridentata* Makarov, 1939, C. R. (Doklady) Acad. Sci. URSS, vol. 23, p. 819, figs. 1, 2, 1 map.
- Pilumnopeus tridentatus* Vorstman, 1939, Bijdr. Dierk., vol. 27, p. 369, figs. 1, 1, 1-5, phot. 1, tabs. 1-7.
- Heteropanope tridentatus* Bouvier, 1940, Faune de France, vol. 37, p. 259, fig. 167.
- Heteropanope tridentata* Havinga, 1941, Biologie Zuiderzee tijdens Drooglegging, vol. 5, p. 11.
- Heteropanope tridentata* De Vos, 1941, Biologie Zuiderzee tijdens Drooglegging, vol. 5, p. 47.
- Heteropanope tridentata* Prud'homme van Reine, 1941, Wat vind ik aan het Strand?, p. 80, pl. 24 fig. 8.

The species was described for the first time by Maitland (1874) after material from the Zuiderzee and from near Haarlem. He (Maitland, 1874, 1876) also identifies the crab figured by Baster (1765) on his pl. 2 figs. 4, 5, with the present species. This, however, is not correct. The carapace of the specimen figured by Baster has the anterolateral border provided with 4 instead of with 3 teeth, while also the frontal margin is differently shaped. In our opinion Baster is right in referring his specimen to the same species as the shore crab (*Carcinus maenas* (L.)), which he figures on his pl. 2 figs. 1-3. We cannot agree with Hoek (1876), who refers the specimen figured on Baster's pl. 2 figs. 4, 5 to *Pilumnus hirtellus* (L.).

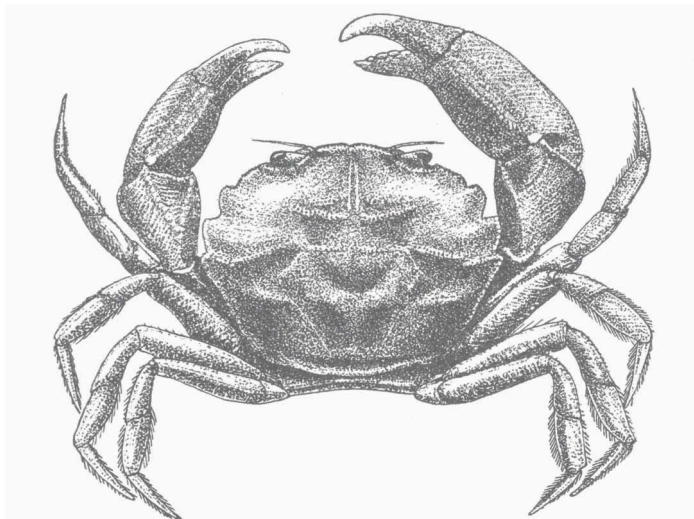


Fig. 1. *Rithropanopeus harrisii* (Gould) ssp. *tridentatus* (Maitland), animal in dorsal view. $\times 2$.

Maitland (1874) named his new species *Pilumnus tridentatus*, and many subsequent authors followed him in considering the species to belong to *Pilumnus*. Hoek (1876) is the first to give figures of the form. His drawing shows the male abdomen consisting of seven separate joints. Miers (1886), who doubts that the Zuiderzee crab is correctly placed in *Pilumnus*, thinks it possible that the species is a *Pilumnoplax* or a *Heteroplax*. De Man (1889) places the species in the genus *Heteropanope* and in 1892 the same author gives an extensive description and good figures of the animal. De Man figures the male abdomen correctly as five-jointed, having the third, fourth and fifth joints fused to one large segment. In the description he states: "The abdomen of the male seems to be five-jointed, as the third,

fourth and fifth segments are probably coalescent, but Hoek figures it (l.c.) as seven-jointed". A. Milne-Edwards and Bouvier (1894 and 1900) consider the present form to be nothing but a variety of *Pilumnus hirtellus*; this opinion also is shared by Blohm (1915). Most authors, however, consider it to be a distinct species and name it *Pilumnus tridentatus* or *Heteropanope tridentata*. In various descriptions the male abdomen is described having the third to fifth joints fused. So Tesch (1912, p. 77) states: "Het smalle, schijnbaar 5-ledige achterlijf, waarbij gewoonlijk het 3e, 4e en 5e segment met elkander vergroeid zijn..." [The narrow, seemingly 5-jointed abdomen, of which usually the third, fourth and fifth segments are fused...]. In his 1922 article, however, Tesch gives a figure of the male abdomen and states: "Abdomen van ♂ niet geheel overeenstemmend met Hoek's afbeelding (wellicht heeft hij een afwijkend exemplaar onderzocht); aan het 3e segment is het abdomen sterk ingesnoerd, en het 4e en 5e segment zijn geheel versmolten; ook vond ik het laatste segment iets langer dan het voorgaande, en de zijranden veel meer evenwijdig verlopend, dan Hoek teekent." [Abdomen of ♂ not entirely agreeing with Hoek's figure (probably he has examined an aberrant specimen); the abdomen is strongly constricted at the third segment, and the fourth and fifth segments are wholly coalesced; moreover I found the last segment slightly longer than the previous and the lateral margins are much more parallel than figured by Hoek]. That part of the abdomen, which is considered by Tesch to be formed by the first and second segments, in reality proves to be nothing but the anterior and posterior parts of one segment (the first), these two parts being separated by a sharp ridge. Consequently the narrowly constricted segment considered by Tesch to be the third is the second, while the large joint, which according to Tesch is formed by the fusion of the fourth and fifth segments, also includes the third. In many specimens the lines between the original third, fourth and fifth segments still may be seen as pits and grooves. Schellenberg (1928) follows Tesch (1922), and in his definition of the genus *Heteropanope* he states the male abdomen to be six-jointed. Balss (1933) separates the genera *Heteropanope* and *Pilumnopeus*, which by most authors were considered synonymous. *Heteropanope* should differ from *Pilumnopeus* in the shape of the frontal margin of the carapace and in the convexity, breadth and structure of the carapace. Balss places the present form in the genus *Pilumnopeus*. Schubert (1936) gives a good figure of the male abdomen, but he follows Tesch in considering it 6-jointed. Also Makarov (1939) figures the fused third, fourth and fifth segments of the male abdomen in his material from the Black Sea coast. Finally Bouvier (1940) described and figured the form in his volume on

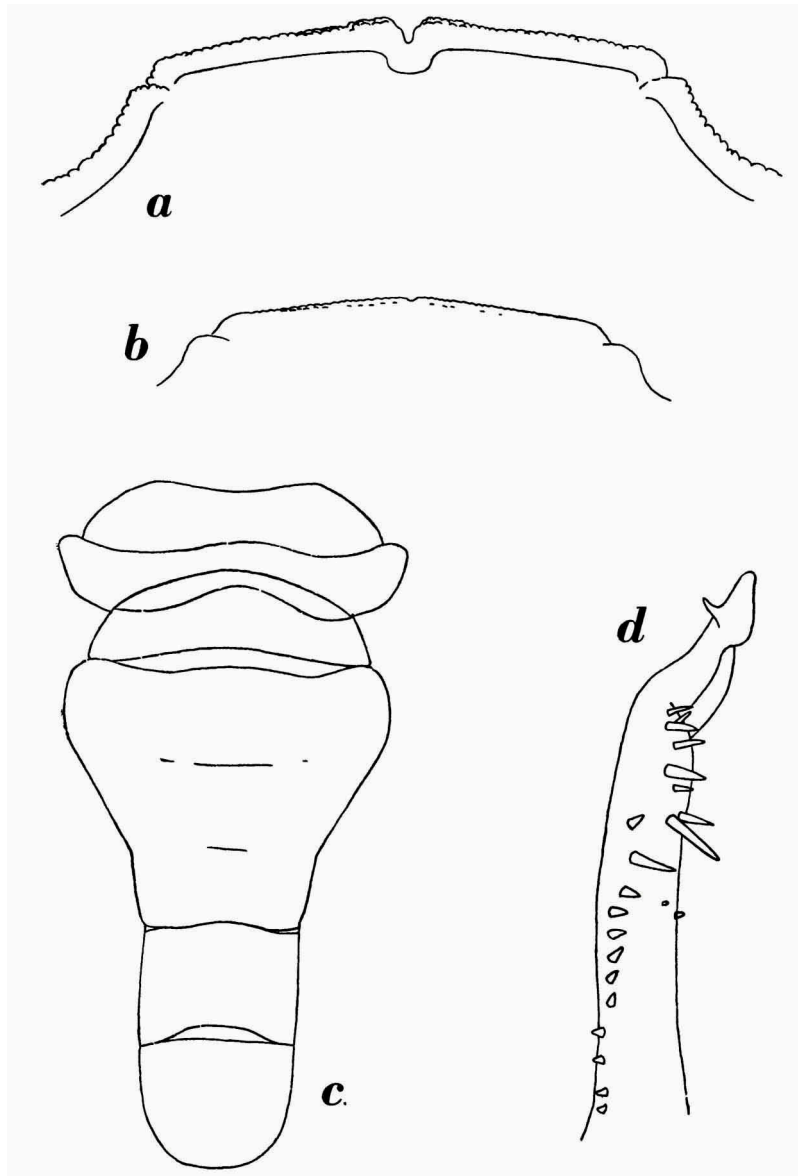


Fig. 2. a, c, d, *Rithropanopeus harrisii* (Gould) ssp. *tridentatus* (Maitland); a, frontal margin of carapace in dorsal view; c, abdomen of male; d, first pleopod of male, b, *Rithropanopeus harrisii* (Gould) ssp. *harrisii* (Gould), frontal margin of carapace in dorsal view. a, b, $\times 13$; c, $\times 9$; d, $\times 66$.

the Decapoda in the series Faune de France. He disagrees with Balss about the species belonging to *Pilumnopus* and refers it to *Heteropanope*, though he recognizes the genus *Pilumnopus*. The male abdomen is figured by Bouvier. In the definition of the genus *Heteropanope* he states: "les trois segments intermédiaires (3, 4, 5) de l'abdomen du ♂ sont soudés entre eux." Notwithstanding the fact that he includes the character of the fused joints of the abdomen in his generic definition of *Heteropanope*, he says in the description of the male abdomen of the second species treated by him in that genus, *Heteropanope laevis* (Dana): "l'abdomen est triangulaire, avec tous les segments libres."

Examination of an abundant material of this form confirmed the statement of the majority of the authors that the third to fifth segments of the male abdomen are fused. Hoek's statement that all segments are free obviously is a mistake, while the error of Tesch, Schellenberg and Schubert, who think only the fourth and fifth segments fused, is easily explained (see above).

Stimpson (1858) in the description of his new genus *Heteropanope* gives as one of the generic characters: "Abdomen maris septem-articulatum." A. Milne Edwards (1863, p. 289) states that his new genus *Pilumnopus* is closely related to *Pilumnus* "par l'existence de sept anneaux à l'abdomen." Also later authors, when dealing with *Heteropanope* or *Pilumnopus*, give the seven-jointed male abdomen always as a generic character (the only exceptions are the above mentioned definitions of *Heteropanope* by Schellenberg, 1928, and Bouvier, 1940). It is therefore quite clear that the Zuiderzee crab does not belong to any of the genera *Pilumnus*, *Pilumnopus* or *Heteropanope*, but is much closer related to the *Panopeus* group, in which the male abdomen is five jointed by the fusion of the third to fifth abdominal joints. It certainly is surprising that this fact has been overlooked by authors as De Man, Tesch, Balss, and Bouvier.

The next question is to find out to which genus the Zuiderzee crab belongs if it is no *Pilumnus*, no *Pilumnopus* and no *Heteropanope*. Comparison of Dutch material with the description and figures given by Rathbun (1930) of *Rithropanopeus harrisi* (Gould), a crab occurring in brackish and fresh water of the Atlantic coast of America from New Brunswick to Mexico, showed the two forms to be closely related. Through the kindness of Dr. Fenner A. Chace Jr., curator of the division of Marine Invertebrates, U.S. National Museum at Washington, D.C., we were able to examine male and female specimens of *Rithropanopeus harrisi* from various localities in the U.S.A. (Creek near West Point, Hudson River N.Y., E.A. Mearns leg., Cat. No. 19632 U.S.N.M., 1 female; Rock Hall,

Md., October 29, 1936, R. V. Truitt leg., Cat. No. 75573 U.S.N.M., 3 males, 3 females; Eastern Branch, Cooper River, S.C., January 21, 1938, T. K. Ellis leg., Cat. No. 78393 U.S.N.M., 4 males, 4 females; Smith Cove, Putnam Co., Fla., June 17, 1946, W. McLane leg., Cat. No. 82372 U.S.N.M., 4 males, 4 females). Actual comparison of American and Dutch material convinced us that the two forms belong to one and the same species, and that the European form at most may be considered a subspecies of the American species. In the Dutch specimens the median incision of the frontal margin of the carapace as a whole is deeper than in the American material, while generally the lobes flanking this incision are more pronounced in our Zuiderzee specimens. Furthermore the Dutch specimens seen by us are larger than the specimens of the American material at our disposal. In literature the maximum breadth of the carapace of the Dutch specimens generally is given as 20 mm, while Vorstman (1939) records several specimens with a carapace of 23 mm wide. Gould (1841) in his original description mentions the width of the carapace of *Pilumnus Harrisii* to be 12.7 mm ("half an inch"), Benedict & Rathbun (1891) give as the width of the carapace in their material 14.5 mm, while finally Rathbun (1930) mentions a specimen with the carapace 19.4 mm wide. These characters are too small to justify the Dutch form to be considered a good species, but they are so constant that we cannot consider the two forms to be perfectly identical. Therefore the European form is made here a subspecies of the American form, and therefore must be named *Rithropanopeus harrisii* (Gould, 1841) subsp. *tridentatus* (Maitland, 1874).

Distribution. The distribution of the present form in Europe is too interesting not to be mentioned here. After the crab was discovered in the Zuiderzee and the North Holland waters, it for a very long time was known only from the Netherlands. Before the closure of the Zuiderzee it mainly inhabited the brackish southern part of that inland sea, not occurring in the northern part where the salinity was higher. It also was recorded from the brackish or almost fresh inland waters of the provinces surrounding the Zuiderzee, so for instance it was found in Amsterdam canals. Furthermore there are some records of this species from the provinces South Holland and Groningen. After the closure of the Zuiderzee (which since that time was named IJsselmeer) in 1932 and due to the diminishing salinity, the population of the crabs at first increased considerably, and its range extended more northward into that part of the Zuiderzee in which before the closure the salinity was too high. After about 1936 the number of crabs diminished gradually and at present the species does not occur any longer in the IJsselmeer, unless some specimens live near the sluices in the closing

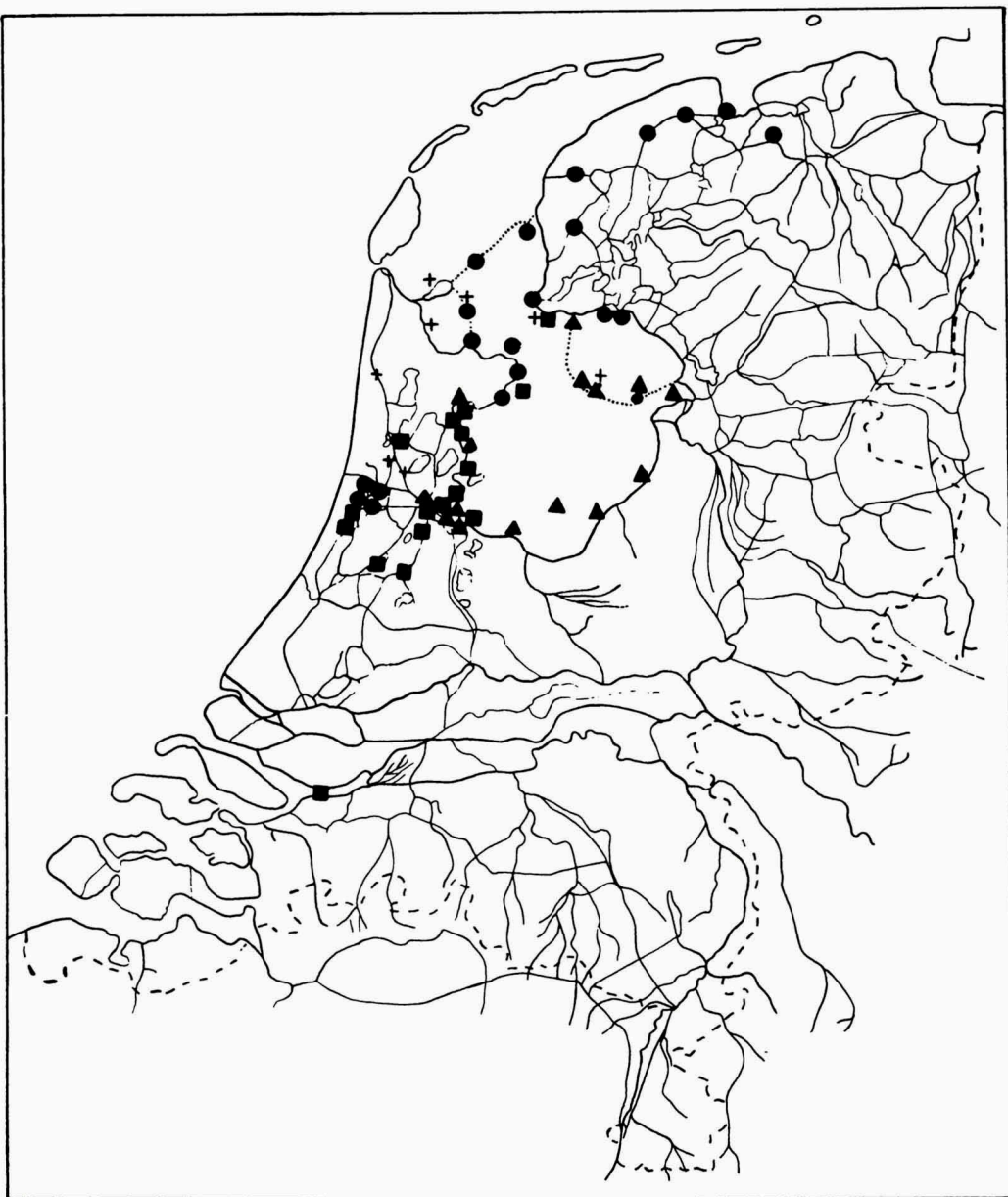


Fig. 3. Distribution of *Rithropanopeus harrisi* (Gould) ssp. *tridentatus* (Maitland) in Holland. ■, localities from where adult specimens were recorded before the closure of the Zuiderzee (1932); ●, localities from where adult specimens were recorded after 1932; ▲, localities from where adult specimens were recorded before and after 1932; +, localities from where larvae were recorded (before 1932).

dam, where the salinity is higher. In the inland waters of the province North Holland the salinity too dropped considerably due to the closing and becoming fresh of the Zuiderzee, and here too the Zuiderzee crab finally disappeared. Little is known at present about what happened with the population of crabs in those brackish inland waters, which had no direct connection with the Zuiderzee.

In 1936 the species was recorded for the first time in European waters outside the Netherlands. Schubert (1936) namely reported the crab from the Flemhuder See, a lake near the North Sea-Baltic canal in N. Germany. It was supposed that these crabs were introduced by ships from Holland. Then in 1939 Makarov reported the crab from S. Russia, where it inhabited the Dnjepr and Bug estuaries in large numbers. According to information obtained by Makarov from local fishermen the crab was observed for the first time in 1936, and the Russian author is sure that it was not present there before 1932, as the fauna of those estuaries was extensively studied in 1931¹). It is interesting to note that the crab was observed in Germany and in Russia for the first time in 1936, the year when the population of this crab in Holland reached its peak. This fact also was pointed out by Makarov.

Many speculations have been made about the origin of the Zuiderzee crab. It generally was accepted (on De Man's authority) that it was most closely related to the indo-westpacific *Heteropanope indica* De Man. Many authors supposed that either the latter species or a very closely related form was brought by merchantmen of the East India fleet from the Indies to Holland between algae attached to the ship's bottom. But it surely is very difficult to imagine a tropical marine species adapting itself to brackish and almost fresh water in a temperate region. It is much easier to suppose that the American form *Rithropanopeus harrisi*, living in the same climate, and in water of the same salinity on the American eastcoast as "*Heteropanope tridentata*" did in Holland, has been transported somehow or other over the Atlantic Ocean some time before 1874 and became acclimatized in the Zuiderzee. The largest difficulty here is to explain how a brackish water species as *Rithropanopeus* is, could stand a trip of several weeks in seawater, which it should have to do, if it had come over between the growth of a ship's bottom. But the same difficulty exists, when one will try to explain how the Zuiderzee crab reached S. Russia (probably Nikolaev, according to Makarov) from Holland, a

1) Miers's (1886) record of the species from the Black Sea is of much interest in this respect.

trip, slightly longer than a voyage from America to Holland, which had to go through the salt water of the Atlantic Ocean, the Mediterranean and the Black Sea. A still much longer trip has been made by the first specimens of *Eriocheir sinensis* H. Milne Edw., the mitten crab, which inhabits fresh and brackish water of China, and has been transported in the second decade of this century to N. Germany.

In connection with the occurrence of the American *Rithropanopeus harrisi* in the former Zuiderzee, it is interesting to draw the attention to the fact that another curious form inhabiting the Zuiderzee was the medusa *Nemopsis bachei* Agassiz, which except for the specimens caught in the Zuiderzee, only was known with certainty from the American east coast.

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ERRATUM

Zoologische Mededelingen, Deel XXX, No. 7:
pp. 95-104: for *Rithropanopeus* read *Rhithropanopeus*