Postilla

Published from 1950 to 2004, the short papers of the *Postilla* series reported on original research by the Yale Peabody Museum of Natural History's curators, staff, and research associates, and their colleagues, in the natural science disciplines represented by the collections of the Museum's curatorial divisions.

The *Postilla* series, which ceased publication with Number 232 (2004), was incorporated into the journal *Bulletin of the Peabody Museum of Natural History*, available from BioOne Complete at https://bioone.org/.

Yale Peabody Museum scholarly publications are archived through EliScholar, a digital platform for scholarly publishing provided by Yale University Library at https://elischolar.library.yale.edu/.

Yale PEABODY MUSEUM OF NATURAL HISTORY

P.O. Box 208118 | New Haven CT 06520-8118 USA | peabody.yale.edu

Postilla

YALE PEABODY MUSEUM

OF NATURAL HISTORY

No. 36 June 27, 1958 New Haven, Conn.

ON THE DOUBTFUL VALIDITY OF *TACHYPLEUS HOEVENI* POCOCK, AN INDONESIAN HORSESHOE CRAB (XIPHOSURA)[1,2]

TALBOT H. WATERMAN

Department of Zoology, Yale University

There are four undoubtedly valid species of living xiphosurans. One of these, *Limulus polyphemus* (L.), is from the western North Atlantic. The other three have different distributions in the western Pacific and the Bay of Bengal. They comprise *Carcinoscorpius rotundicauda* (Latreille), *Tachypleus tridentatus* Leach and *Tachypleus gigas* (Müller). All of these are well represented and recognized in collections. A third species of *Tachypleus*, *T. hoeveni*, was named by Pocock (1902) for certain figures in van der Hoeven's monograph on the Xiphosura (1838; Plate I, figs. 2, 10; Plate II, fig. 14). A key to recent species of Xiphosura is presented as an Appendix and in figs. 9-11.

[1] Respectfully dedicated to my colleague and friend Dr. Alexander Petrunkevitch.

[2] These studies were aided by a contract between the Office of Naval Research, Department of the Navy, and Yale University, NR163-091, and by a grant from the Pacific Science Board of the National Research Council.

According to its definition *Tachypleus hoeveni* resembles *T. gigas* in all known respects except that the median terminal segments of the genital operculum in *hoeveni* are separate and overlap asymmetrically, instead of being united, symmetrical and contiguous as in *gigas*. Apparently Pocock himself never saw a specimen of his species, and none have since been reported either in the field or in museums. It is of interest, therefore, to inquire whether or not *Tachypleus hoeveni* is a valid species, closely related to, but distinct from *T. gigas*. Doubt of such validity has already been raised on rather general grounds by Gravier (1929) in his review of specimens of Xiphosura in the Paris Muséum National d'Histoire Naturelle. Present attention to the problem was stimulated by the author's interest in speciation and distribution of horseshoe crabs particularly with relation to their eyes and visual physiology (Waterman, 1951; 1953a,b; 1954a,b,c; 1955; Waterman and Enami, 1953; Waterman and Wiersma, 1954).

In an attempt to settle this moot taxonomic point, a large number of *Tachypleus gigas* have been studied to determine whether any individuals could be found attributable to *T. hoeveni* as defined by Pocock. Specimens examined include the author's own material collected on Singapore Island in 1952; the collections of the Raffles Museum, Singapore; the Zoologisch Museum, Amsterdam; the Rijksmuseum van Natuurlijke Historie, Leiden; the Universitets Zoologisk Museum, Copenhagen; and the Museum of Comparative Zoology, Harvard University[3]. Relevant material was found in only three of

[3] It should be mentioned that visits or inquiries addressed to a number of other museums revealed that no specimens either of *Tachypleus gigas* or *Tachypleus hoeveni* were present: U.S. National Museum, Washington, D.C.; Peabody Museum, Yale University; American Museum of Natural History, New York; Museum Zoologicum Bogoriense, Bogor (formerly Buitenzorg), Indonesia; Institut Océanographique de Nhatrang, Vietnam; Natural History Museum, Manila, Philippine Republic; the National Museum, Sydney and National Museum of Victoria, Melbourne, Australia. In addition, review of the present collections in the British Museum (Natural History) and the Muséum National d'Histoire Naturelle in Paris shows that no relevant material has been acquired since the classic papers of Pocock (1902) and Gravier (1929) which are mainstays of our present knowledge of horseshoe crab taxonomy and distribution. The author is much indebted to the Directors and staffs of these institutions, as well as

these; the museums at Amsterdam, Copenhagen and Leiden.

Of greatest interest was finding that the Leiden museum has what is undoubtedly the original specimen of a male operculum from which van der Hoeven's Plate II, fig. 14 was drawn (reproduced fig. 1). Because this particular figure was a crucial one cited by Pocock in establishing *Tachypleus hoeveni*, the specimen in question is presumptive type material for that species. It is hereby designated the lectotype (figs. 3,4). This operculum, which is in alcohol, had been Number 1038 in the Collection of the Zoological Laboratory, University of Leiden. It was transferred to the museum when that collection was dispersed. Other records show that van der Hoeven's anatomical collections were given by him to the Zoological Laboratory at Leiden so that this evidence fits well with the identification of the specimen.

When examined by the author in August 1953, the jar containing this interesting operculum held among several other labels, a note in the handwriting of Dr. H. D. Blöte, Assistant Director of the Leiden Museum. Translated from the Dutch this reads, "This preparation most probably is the original of Plate II, fig. 14 in J. van der Hoeven's Recherches sur l'Histoire Naturelle, etc. des Lumules, Leiden 1838. See Pocock, Ann. Mag. Nat. Hist. VII, Ser. IX, 1902, p. 264."

Careful comparison of this specimen with the figure in question leaves little doubt of the correctness of Dr. Blöte's attribution (figs. 1,3). Note particularly that even the edges where the appendage was cut from the rest of the body and the slight scar on the lateral margin at the right agree almost perfectly. Only in the exact proportions of the appendage and degree of overlap between the terminal medial elements does the specimen differ from the figure. But as the specimen itself had been stapled to a slab of soapstone, some changes in its shape and in the position of its parts would not be surprising in the course of the 115 years since it was drawn. The maximum

all those mentioned in the text, for their generous cooperation and assistance in examining available material. Thanks are also due to Dr. Fenner A. Chace, Jr. of the U.S. National Museum and Dr. Charles L. Remington of the Yale University Zoology Department for their helpful suggestions concerning the manuscript.

width of this Leiden specimen was 70.5 millimeters while that of the drawing, stated to be natural size, is about 70 millimeters which provides another important point of agreement.

It should be pointed out that Pocock's interpretation of van der Hoeven's figures does not agree with the original specimen in certain respects not visible in the plates. The British zoologist believed that the opercular elements which overlap in *T. hoeveni* were separated medially, unlike those of *T. gigas* which are normally united (fig. 8). However, in the Leiden Museum operculum they are, in fact, not separate in the midline. The edges appear to overlap, not because they are free medially, but merely because the appendage is pleated with a double fold in that region. Whether this fold was present in the living animal is not obvious from its appearance.

Unfortunately, this single xiphosuran fragment is all that is known to remain of van der Hoeven's original material. Consequently, it is not possible to settle the point directly whether this unique opercular detail is really a valid species character or merely an individual idiosyncrasy. As Pocock correctly pointed out, however, three of the four drawings of the operculum labelled *Limulus moluccanus* Latreille (= *Tachypleus gigas*) in van der Hoeven's monograph show identical overlapping elements in both adult male and adult female specimens (reproduced figs. 1,2,5,6). At its face value this does make the peculiarity seem taxonomically significant. Van der Hoeven's failure to comment in any way on this anomaly is accordingly the more exasperating.

On the other hand, close reading of van der Hoeven's text reveals (1838, p. 2) that only two spirit specimens of *T. gigas* were available to him for the anatomical work reported. Yet measurements of three specimens are given (1838, p. 10). It is not explicit whether two of these are the anatomical subjects, which of them may be merely dried examples, or what the total number of individuals studied may have been. If two complete specimens only were available for the four drawings concerned, it is possible that the same operculum may have been used as a model for the figures of more than one animal. The fact that the operculum, still extant, was already detached from the

whole specimen, when drawn for van der Hoeven's Plate II, fig. 14, adds some likelihood to this possibility.

Further circumstantial evidence is provided by the mirror image similarity of the opercula in figs. 2 and 10, Plate I. This is carried even to the peculiar extra plates present in the proximal lateral margins of the overlapping sections in both drawings (reproduced figs. 5,6). The collaboration of another artist in drafting Plate I in contrast to the anatomical Plates II and III drawn entirely by van der Hoeven himself may also lend credibility to this notion. The extra opercular plates mentioned above, which are not symmetrical, could also be taken as evidence that this operculum is abnormal; in general all normal xiphosuran external anatomical features are bilaterally symmetrical.

One must, therefore, entertain the possibility of *Tachypleus hoeveni* being merely an abnormal *T. gigas*. Some independent but congruent evidence has been found that abnormalities of the median distal plates of the genital operculum are not rare in this animal. In the Amsterdam Museum there is a *Tachypleus gigas* (No. Xi 1001), collected in East Sumatra by J. C. van der Meer Mohr, which also has overlapping elements at the margin of the operculum (fig. 7), although the specimen is otherwise normal. The overlapping plates are not, however, the median distal elements as in the Leiden specimen but are the lateral distal elements. These are so lobed along their medial margins that the edges lie over one another for a short distance. None of the 8 other specimens of *T. gigas* in the Amsterdam collection show any similar opercular anomalies.

Another *T. gigas* with a deformed operculum is present among the 11 specimens of this species in the Copenhagen Museum, a male from Penang Island on the west coast of Malaya (collected by the research ship "Galathea"). As in the Amsterdam specimen, there is a small medial overlap in the lateral distal opercular plates in this animal. In this case, though, the reason for the anomaly is more obvious, since there is a considerable healed wound in the edge of the operculum on the left side, and both prosoma and opisthosoma show distorted or missing parts. Further evidence for a widespread occurrence of structural abnormalities in *Tachypleus gigas* is

given by van der Meer Mohr (1934), but no opercular deviations are mentioned specifically. In *T. tridentatus*, however, Smedley (1931) reported that various specimens differ considerably in the degree of separation of the internal opercular branches at their tips.

From the specimens examined and here discussed one would conclude that the peculiar fold and other unique details of the van der Hoeven *Tachypleus* operculum in Leiden are but minor teratological variants of *Tachypleus gigas.*

On the other hand the geographical origin of van der Hoeven's material in the Moluccas is an element that in all fairness should weigh on the side of the validity of *T. hoeveni.* Few, if any, specimens of Xiphosura from these islands are known in museum collections. Consequently, study of *Tachypleus* from Ceram, Halmahera, and adjacent islands might indeed show that *T. hoeveni* exists as a taxonomically distinct form in these regions.

Yet such a circumscript distribution would be unique for a xiphosuran species, since the four definitely known recent forms have wide ranges. *Limulus polyphemus* (L.) occurs from Nova Scotia to Yucatan on the east coast of North America, a large spread in latitude, covering a shore line several thousand miles long. *Tachypleus tridentatus* Leach occurs south from the Inland Sea of Japan, along the China coast, in the western islands of the Philippine Republic, in Hainan and at least as far south as Nhatrang in south central Vietnam (Flower, 1901; Smedley, 1929, 1931; Shoji, 1932; Asano, 1942; Waterman, 1953a)[4]. *Tachypleus gigas* (Müller) overlaps the latter species by occurring in northern Vietnam (Prof. C. Boisson, University of Hanoi, personal communication) and North Borneo, extends west to the Orissa coast on the Bay of Bengal and east as far as Torres Strait (Pocock, 1902; Annandale, 1909). *Carcinoscorpius rotundicauda* (Latreille) has been reported in the southern Philippines, Indonesia, Malaya, the Gulf of Siam, and the Bay of Bengal.

[4] If the specimens of *Limulus longispinus* (sic) (= *Tachypleus tridentatus*) reported (in lit.) in the Australian Museum, Sydney, are correctly identified, this species occasionally reaches as far as the west coast of Malaya.

On the basis of the evidence at hand one must conclude that *Tachypleus hoeveni* is a dubious species at best and most likely was named for an abnormal operculum of *Tachypleus gigas*. But since the original material does not permit a definitive solution of the problem, it is to be hoped that the interest and opportunity of studying the xiphosurans of the Moluccas will develop in the near future to resolve the dilemma more decisively. However, a recent attempt to do this failed. At the author's request, Dr. Dillon Ripley of the Peabody Museum at Yale University, who spent three months of 1954 in the Moluccas collecting specimens of various animals, particularly birds, tried to obtain horseshoe crabs from these islands.

According to information he most kindly gathered, *ikan mimi* or *imi imi*, as these animals are called in Indonesia, were known to fishermen in the Moluccas but were said not to occur there. According to these sources the nearest place where such crabs were ordinarily caught was Menado. This is a town on the northern arm of Celebes more than 200 miles westward across the Molucca Passage from Ternate, Tidore, Halmahera and other islands in the group. Not only were no specimens of *T. hoeveni* to be obtained even in Menado, but no evidence for the occurrence of any species of Xiphosura in the Moluccas themselves was found despite the fact that *T. gigas* and *Carcinoscorpius* are well known from other parts of Indonesia.

The reported complete absence of these forms in the area concerned is the more baffling since the Moluccas are the first place of occurrence cited for the xiphosurans in the East Indies. L'Écluse in 1605 figured specimens of *Cancer moluccanus*, a horseshoe crab sent to Holland reputedly from the Moluccas. Rumphius (1705) in his famous book about the natural history of these islands illustrates a horseshoe crab under the name of *Cancer perversus*. This animal, he states, was well known by him to occur in the Moluccas (he was working in Amboina in the southern part of the archipelago) and he also had received a specimen of it from Menado.

Summary

1. In reviewing material suitable for determining the validity of *Tachypleus hoeveni* Pocock, an original fragmentary

specimen apparently used by van der Hoeven for one of the figures cited as the type by Pocock was re-examined in the Rijksmuseum van Natuurlijke Historie in Leiden. This specimen itself, here designated the lectotype, and Pocock's monograph do not alone permit a decisive conclusion whether the material represents an anomalous *Tachypleus gigas* or another valid species.

2. Evidence has been obtained from single specimens in the Amsterdam and Copenhagen zoological museums that opercular anomalies, comparable to but distinct from the one for which *Tachypleus hoeveni* was erected, are not rare in *Tachypleus gigas*.

3. The fact that van der Hoeven's material came from the Moluccas, a region from which few, if any, xiphosuran specimens have since been studied, leaves open the possibility of a taxonomically significant geographic variation in this area. However, a recent search failed to find any Xiphosura in the Moluccas.

4. It is concluded that *Tachypleus hoeveni* is probably a synonym of *T. gigas*, but this synonymy can only receive its decisive test when substantial series of Indonesian xiphosurans have been studied.

5. A key to recent species of Xiphosura is presented as an Appendix.

References Cited

Annandale, N. 1909. The habits of king crabs. *Rec. Ind. Mus., 3*:294-295.

Asano, U. 1942. On the life history of *Tachypleus tridentatus*. (In Japanese) *Botany and Zoology, Pure and Applied. 10*:120-124.

L'Écluse, C. de 1605. Exoticorum Libri Decem. (Antverpae) ex officinâ Plantiniana Raphalengii, pp. 1-378.

Flower, S. S. 1901. Notes on the millipedes, centipedes, scorpions, etc. of the Malay Peninsula and Siam. *J. Straits Branch Roy. Asiatic Soc., 36*:1-48.

Gravier, C. 1929. Révision de la collection des Limules du Muséum National d'Histoire Naturelle. *Bull. Mus. Nat. Hist. Nat. Paris,* Ser. 2, *1*:313-331.

van der Hoeven, J. 1838. *Recherches sur l'Histoire Naturelle et l'Anatomie des Limules.* Leyden, Luchtmans, pp. 1-48.

van der Meer Mohr, J. C. 1934. Sur quelques malformations chez la limule, *Tachypleus gigas. Miscell. Zool. Sumatrana, 87*:1-3.

Pocock, R. I. 1902. The taxonomy of recent species of *Limulus. Ann. Mag Nat. Hist., 9*:256-266.

Rumphius, G. E. 1705. *D'Amboinische Rariteitkamer.* Amsterdam, Halma, pp. 1-340.

Shoji, K. 1932. Morphology and biology of Xiphosura. (In Japanese) *Fukuoka Nat. Hist. J. 7*:28-52.

Smedley, N. 1929. Malaysian king crabs. *Bull. Raffles Mus., 2*:73-78.

————. 1931. Notes on king crabs (Xiphosura). *Bull. Raffles Mus., 5*:71-74.

Waterman, T. H. 1951. Polarized light navigation by arthropods. *Trans. N.Y. Acad. Sci., 14*:11-14.

————. 1953a. Xiphosura from Xuong-Ha. *Amer. Scientist, 41*:292-302.

————. 1953b. Action potentials from an arthropod ocellus: the median eye of *Limulus. Proc. Nat. Acad. Sci., 39*:687-694.

————. 1954a. Directional sensitivity of single ommatidia in the compound eye of *Limulus. Proc. Nat. Acad. Sci., 40*:252-257.

————. 1954b. Polarized light and angle of stimulus incidence in the compound eye of *Limulus. Proc. Nat. Acad. Sci., 40*:258-262.

————. 1954c. Relative growth and the compound eye in Xiphosura. *J. Morph., 95*:125-158.

Waterman, T. H. 1955. Polarized light and animal navigation. *Sci. Amer. 193*: 88-94.

Waterman, T. H. and M. Enami. 1953. Neurosecretion in the lateral rudimentary eye of *Tachypleus*, a xiphosuran. (Abstr.) Convegno sulla Neurosecrezione, *Pubbl. Staz. Zool. Napoli, 24*: Suppl., 81-82.

Waterman, T. H. and C. A. G. Wiersma. 1954. The functional relation between retinal cells and optic nerve in *Limulus*. *J. Exp. Zool., 126*:59-86.

Appendix

KEY TO RECENT XIPHOSURA

1. Tail spine oval or circular in cross section with no marked dorsal ridge. Adult sexual characteristics: Male, first two pairs of walking legs modified as chelate claspers (fig. 11A) ..... *Carcinoscorpius rotundicauda* (Latreille)
Tail spine triangular in cross section with marked dorsal ridge along most of its length ..... 2.

2. Genital operculum (first opisthosomal appendage) with three endopodite segments on each side (including tab-like terminal element) (fig. 10A). Adult sexual characteristics: Male, first pair of walking legs modified as hemichelate claspers (fig. 11B) ..... *Limulus polyphemus* Linnaeus
Genital operculum with two endopodite segments on each side (fig. 10C) ..... 3.

3. Distal endopodite segments of genital operculum overlapping in midline (according to Pocock not united in midline but are so in lectotype; see text) (fig. 10B). Adult sexual characteristics: Male, presumably first two pairs of walking legs modified as hemichelate claspers. Female, presumably first three movable lateral opisthosomal spines long, other three short stubs (fig. 9B) ..... *Tachypleus hoeveni* Pocock
Distal endopodite segments of genital operculum united and not overlapping along midline (fig. 10C). Adult sexual characteristics: Male, first two pairs of walking legs modified as hemichelate claspers; anterior margin of prosoma scalloped (fig. 9A). Female, first three movable lateral opisthosomal spines long, other three short stubs (fig. 9B) ..... 4.

4. Usually three spines on posterior dorsal surface of opisthosoma over base of tail spine (fig. 9B); lateral eyes black, no pseudopupil visible; lateral eye length not more than 5-6 per cent of prosoma length along the midline ..... *Tachypleus tridentatus* Leach
One spine only on posterior dorsal surface of opisthosoma over base of tail spine; lateral eye brownish, pseudopupil visible; lateral eye length more than 6.5 per cent of opisthosoma length along the midline ..... *Tachypleus gigas* (Müller)

Plate I

Fig. 1. Posterior surface of the genital operculum of a male Moluccan xiphosuran as figured by van der Hoeven (1838, Plate II, fig. 14). The original author does not mention the anomalous double fold in the midline of the central terminal segments and referred this drawing to *Limulus moluccanus* (= *Tachypleus gigas*). Pocock (1902) considered this opercular fold, which may also be seen in figs. 3, 4, 5 and 6, grounds for establishing a third species of *Tachypleus, T. hoeveni.* Maximum lateral extent (width) of this operculum 70 mm.

Fig. 2. Posterior surface of the genital operculum of a female Moluccan xiphosuran as figured by van der Hoeven (1838, Plate II, fig. 15). This also was assigned by the original author to *Limulus moluccanus* (= *Tachypleus gigas*). Note that the median margins of the inner and outer terminal segments are neither folded nor overlapping and are normal for the species like those shown in fig. 8. Maximum lateral extent of this operculum 85 mm.

Fig. 3. Posterior surface of the genital operculum of a male xiphosuran which is most likely the original specimen from which van der Hoeven's (1838) Plate II, fig. 14 (fig. 1, above) was drawn. Except for the length width ratio, the two agree closely. Photograph courtesy of the Rijksmuseum van Natuurlijke Historie, Leiden. Maximum lateral extent of this specimen 70.5 mm.

Fig. 4. Anterior surface of the same specimen as shown in Fig. 3. Since this peculiar operculum apparently was the basis for Pocock's species *Tachypleus hoeveni*, it is designated as the lectotype pending final clarification of its validity. The specimen is in the Rijksmuseum van Natuurlijke Historie, Leiden, through whose courtesy the photograph is reproduced.

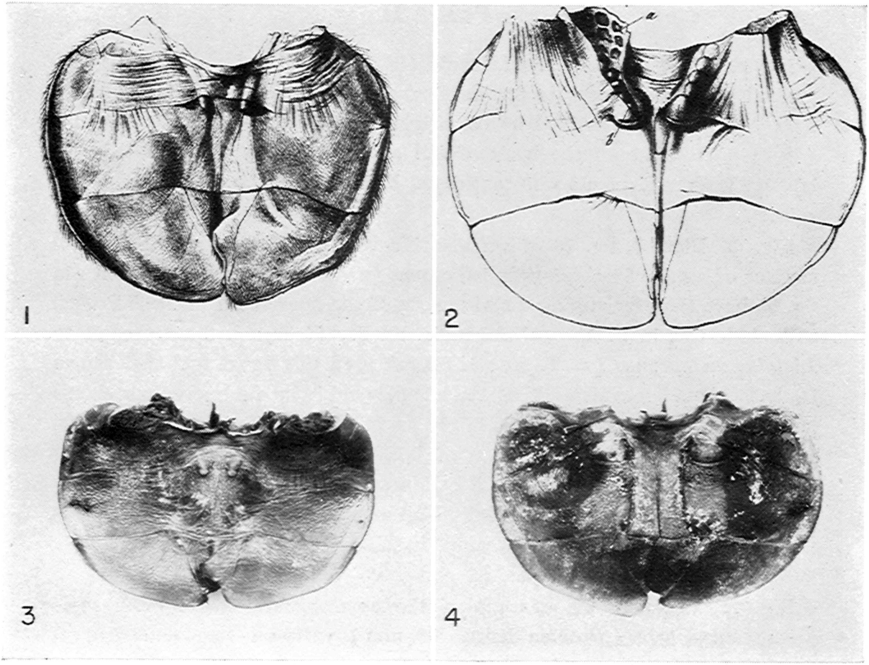


PLATE I

Plate II

Fig. 5. Part of van der Hoeven's (1838) Plate I, fig. 2 showing the ventral surface of a mature female *Tachypleus* (prosoma length 100 mm.). This drawing was identified by the original author as *Limulus moluccanus* (= *T. gigas*) but on the basis of the genital operculum with the overlapping median elements was considered by Pocock to be *T. hoeveni.*

Fig. 6. Plate I, fig. 10 of van der Hoeven (1838) showing the ventral surface of a male *Tachypleus* opisthosoma (prosoma length 82 mm.). As in fig. 5 above the overlapping distal moiety of the operculum induced Pocock to include this in *T. hoeveni* although van der Hoeven had referred it to *Limulus moluccanus* (= *T. gigas*). Pocock used this figure and that shown in fig. 5 above as evidence that the peculiar folds in the operculum shown here in figs. 1, 3, and 5 were not just an individual idiosyncrasy since the same thing is shown in drawings of both sexes. Note however, that the opercula in the drawings reproduced in figs. 5 and 6 are mirror images of each other and nearly identical which suggests that one operculum was used as a model in drawing two individuals.

Fig. 7. Ventral view of part of the opisthosoma of a mature male *Tachypleus gigas* (prosoma length 98 mm.) with an anomalous genital operculum showing some overlap of median elements. Note, however, that here the outer terminal segments rather than the central ones as in the Leiden specimen (fig. 3) form the overlapping pair. Also observe that the median edges of these segments are free, not fused, and just folded over as in the other case. Specimen Xi 1001 in the Zoologisch Museum, Amsterdam, through whose courtesy the photograph is reproduced.

Fig. 8. Ventral view of part of the opisthosoma of a mature *Tachypleus gigas* (prosoma length 95 mm.) with a normal genital operculum showing the smooth median fusion of the central distal segments with no folding and the free edges and absence of overlap in the lateral distal segments. Photograph courtesy of the Zoologisch Museum, Amsterdam.

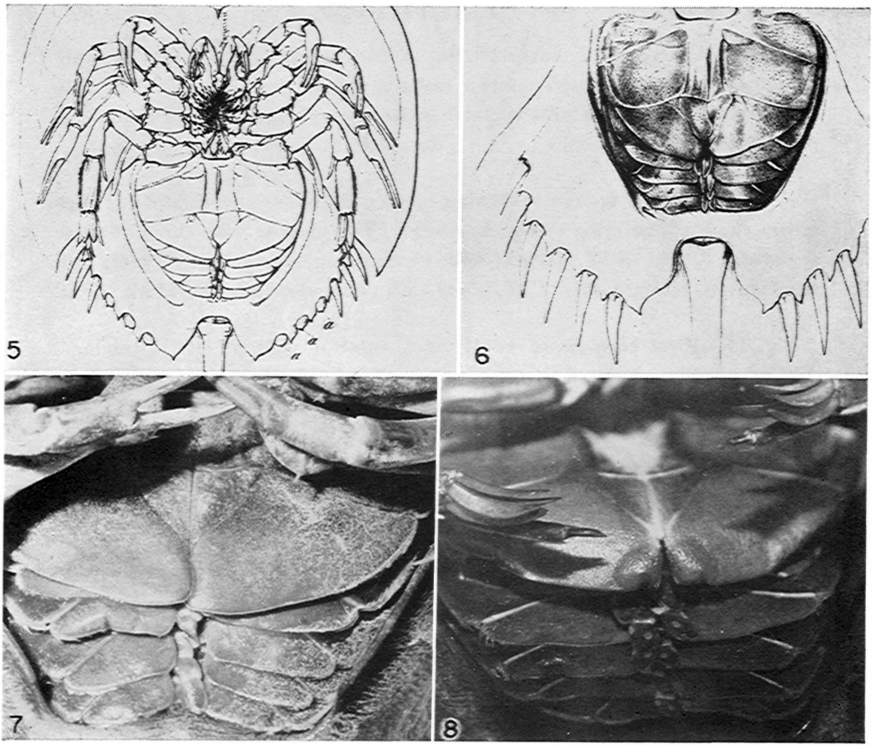


PLATE II

Plate III

Fig. 9. Adult sexual characteristics in *Tachypleus tridentatus*. A. Male prosoma showing scalloped anterior margin, dorsal view. X 0.3. B. Female opisthosoma showing lateral movable spines (*a - f*) and species characteristic posterior median ones (*g, h, i*), dorsal view. X 0.3.

Fig. 10. Genital opercula showing species characteristic endopodite segments (*a, b, c*), anterior view. A. *Limulus polyphemus* with three of these segments. X 0.5. B. *T. hoeveni* with overlapping segment (*b*) (after van der Hoeven, 1838). X 0.5. C. *T. gigas* with two endopodite segments. X 0.4.

Fig. 11. First claspers of adult male, anterior view of left appendage. A. *Carcinoscorpius rotundicauda*, chelate. X 1.5. B. *L. polyphemus*, hemichelate, X 0.7. C. *T. tridentatus*, hemichelate. X 0.7.

(Figs. 9-11 drawn by Shirley P. Glaser)

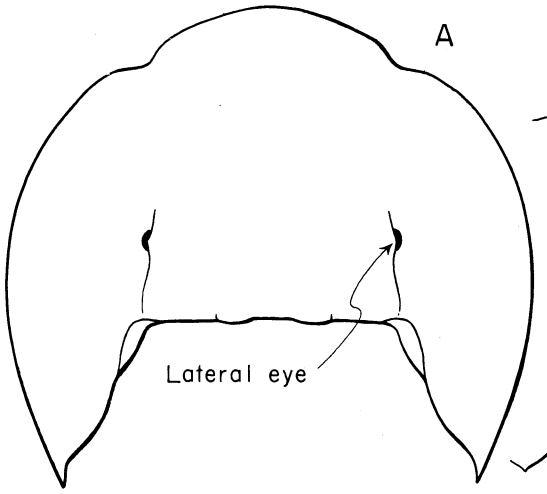
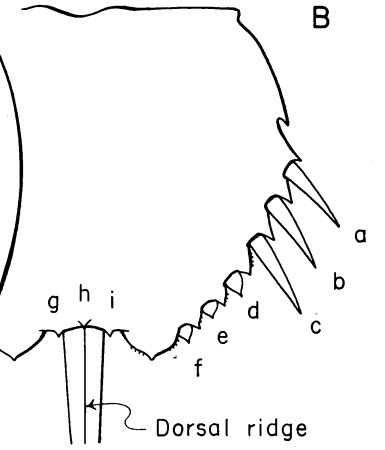


Figure 9



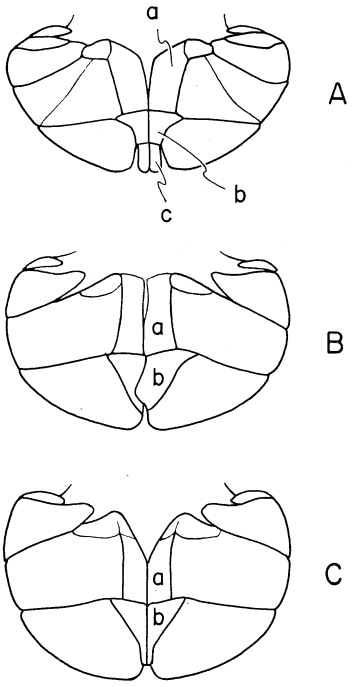


Figure 10

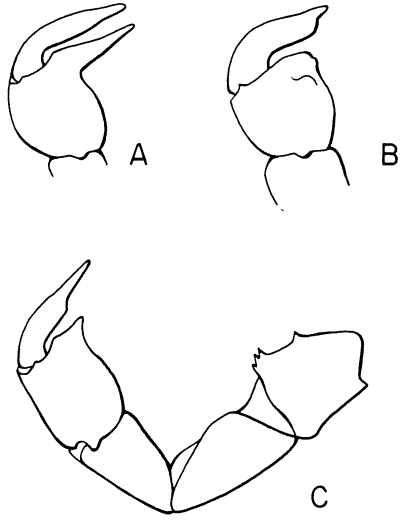


Figure 11

PLATE III