MACROPHTHALMUS (DECAPODA, BRACHYURA) OF THE SEAS OF CHINA

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INTRODUCTION

Macrophthalmus belongs to the family Ocypodidae, subfamily Macrophthalminae, a dominant group of crabs inhabiting the intertidal zone along the coast of China, including the Yellow-Bo Sea, East China Sea, and South China Sea (Shen, 1932, 1936, 1940; Lin, 1949). Members of the genus are also widely distributed in the coastal waters of Japan (Sakai, 1976). Australia (Barnes, 1967, 1968, 1968a, 1970, 1971, 1976, 1977), the Indonesian-Malaysian region (Tesch, 1918; Tweedie, 1937; Serène, 1973), Indian Peninsula (Alcock, 1900; Kemp, 1919; Chhapgar, 1957), and East and South Africa (Barnard, 1950; Crosnier, 1965, 1975; Kensley, 1981).

This study reviews all *Macrophthalmus* species inhabiting the Chinese sea shore, and includes descriptions of a new subspecies from China.

MATERIAL AND METHODS

The first author examined all material collected by the Institute of Zoology, Academia Sinica from coastal waters of China in 1928-1932, 1954-1963, and 1973-1981. Off the 17 species of *Macrophthalmus* known from this area, *M.* (*Hemiplax*) boteltobagoe (Sakai, 1939), *M.* (Mopsocarcinus) dentatus Stimpson, 1858, and *M.* (Mareotis) pacificus Dana, 1851, were not available in the Institute's collection. All of these last three species, but *M.* (*Hemiplax*) boteltobagoe, have been examined in the crustacean collections of the Museum of Comparative Zoology at Harvard University and of the Smithsonian Institution. Among the 17 species reported here, one subspecies is new to science. The type of this new taxon is deposited in the Institute of Zoology, Academia Sinica, Beijing, People's Republic of China.

All line drawings were prepared by using a camera lucida. Calipers are used to measure the carapace length at the midline and the carapace breadth at the greatest width.

SYSTEMATIC ACCOUNT

Macrophthalmus Latreille, 1879

Diagnosis. Carapace depressed, 1.2 to 2.0 times as long as broad, front narrow. Proportion of breadth of front to carapace breadth, 1: 3.0-12.0. Orbit long, occupying whole anterior margin of carapace. Epistome long and narrow, its central region concave, straight, or convex. Ocular peduncle slender, cornea reaching to or beyond outer orbital angle. First pleopod of male straight to slightly curved.

Barnes (1967) proposed separating the genus Macrophthalmus into six subgenera: Macrophthalmus, Mareotis, Mopsocarcinus, Venitus, Hemiplax, and Tasmanoplax. The last subgenus has not been found in the seas of China.



Fig. 1. Chelae of male. a, left chela of Macrophthalmus (Mareotis) japonicus frequens subsp. nov.; b, right chela of Macrophthalmus (Macrophthalmus) crassipes H. Milne Edwards; c, left chela of Macrophthalmus (Venitus) latreillei (Desmarest).

Macrophthalmus (Mareotis) japonicus frequens subsp. nov. (figs. 1a, 2a, 3a-c)

Material examined: Holotype: O(No. 78-14771), Hangu, Hebei Province, May 1978. Allotype: O(No. 78-14772), same collection as holotype. Paratypes: 1O(No. 78-14773), same collection as holotype. 1O, 1O(No. 62-14774), Haimen, Zhejiang Province, July 12, 1962. 8OO, 7OO(No. 30-72900), Qangdang, Shangdong Province, July 29, 1930. 16OO, 13OO(No. 30-62400), Beidaihe, Hebei Province, June 24, 1930. 5OO, 7OO(No. 29-72000), Yanmadao, Shangdong Province, July 20, 1929.

Description. — Carapace 1.5 times as broad as long, central regions smooth, with deep longitudinal groove separating branchial regions. Branchial

region, lateral part with granules; anterior part with two parallel transverse grooves; posterior part with two longitudinal granular lines. Front narrow, central surface with deep longitudinal groove. Orbit broad, dorsal margin arched, dorsal and ventral margins with blunt serrations, First antero-lateral tooth (external orbital angle) triangular, separated from second tooth by a wide incision; third tooth very small. Central region of epistome distinctly concave. Cheliped of male stout, carpus comparatively small, 2.1 times as long as broad; manus strong in large specimens, and weak in juveniles, in adults shape of manus similar to that of M. (Mareotis) japonicus japonicus; movable finger slender, inner margin with a blunt tooth one fourth of distance from base; inner margin of immovable finger with a larger tooth near base, and fine teeth in distal half. Ambulatory legs stout, especially merus of second and third legs; anterior and posterior margins with fine serrations, subdistal teeth slightly protruded, directed forward. Merus of third legs 2.8 times as long as broad. Sixth segment of abdomen of male 1.4 times as broad as long. First pleopod of male slightly arched with a blunt distal horny process. Males 18.8-27.6 mm long, 27.7-42.0 mm wide. Females 19.3-24.8 mm long, 28.9-39.3 mm wide.

Remarks. — This new subspecies is widely distributed in northern Chinese seas, including the Yellow-Bo Sea and the northern part of East China Sea. Morphologically and geographically, it is closely related to *M. (Mareotis) japonicus japonicus* (de Haan). It is, however, distinguished from the latter by the broader merus and the finer serrations on the anterior and posterior margins of the second and third ambulatory legs, and by the relatively indistinct subdistal teeth on the third leg. The distal process of the first pleopod of the male is truncate. The last segment of the abdomen in the female is 2.4 times as broad as long (fig. 3c), as compared to three times in *M. (Mareotis) japonicus japonicus* (fig. 3d). In many areas, there are intermediate forms. Absolute separation of these forms is often impossible. For this reason *frequens* is designated as a subspecies of *japonicus*.

Macrophthalmus (Macrophthalmus) crassipes H. Milne Edwards, 1852 (figs. 1b, 2b, 3e, f)

Material examined: 200 (No. 60-11200), Beigang, Hainan Island, January 12, 1960. 500 (1 juv.), 300 (2 ovi.) (No. 58-52301), Beigang, Hainan Island, May 23, 1958. 10, 10 (juv.) (No. 59-11300), Haikou, November 3, 1959. 10 (No. 58-51900), Beigang, Hainan Island, May 19, 1958.

Comments. — The specimens of this species from the Chinese Sea differ from the type by having the manus of cheliped comparatively higher and shorter. The tooth of the cutting edge of the immovable finger is placed nearer to the distal end, and the ventro-anterior margin of the merus is with 7 or 8 teeth.



Fig. 2. a, Macrophthalmus (Mareotis) japonicus frequens subsp. nov.; b, Macrophthalmus (Macrophthalmus) crassipes H. Milne Edwards; c, Macrophthalmus (Venitus) latreillei (Desmarest).

Macrophthalmus (Venitus) latreillei (Desmarest, 1822) (figs. 1c, 2c, 3g, h) Material examined: 1° (No. 57-14256), Guanghai, Guandong Province, July 7, 1957. 1° (No. 57-14257), Beihai, Hainan Island, June 13, 1957.

Comments. — According to the description by Barnes (1967, 1971, 1977) the central region of the epistome in the subgenus *Venitus* is straight or excavated. But in M. (*Venitus*) latreillei, this region is slightly protruded. Therefore in that characteristic the definition of this subgenus should be emended to: The central region of epistome straight, excavated or slightly protruded.



Fig. 3. a-c, Macrophthalmus (Mareotis) japonicus frequens subsp. nov.; d, Macrophthalmus (Mareotis) japonicus japonicus (De Haan); e, f, Macrophthalmus (Macrophthalmus) crassipes H. Milne Edwards; g, h, Macrophthalmus (Venitus) latreillei (Desmarest). a, e, g, epistome; b, f, h, first male pleopod and enlarged tip; c, d, apex of female abdomen.

Key to the subgenera and species of Macrophthalmus occurring in Chinese seas:

1.	Central region of epistome distinctly convex
	Subgenus Macrophthalmus Latreille 2
—	Central region of epistome straight, concave or slightly protruded 7
2.	Ocular peduncle with one third or more of cornea projecting beyond tip of external orbital angle
	Ocular peduncle with cornea not projecting beyond tip of external orbital
3.	External orbital angle not projecting beyond tip of second and third antero-lateral teeth; first pleopod of male slightly curved with a rather long distal process
—	External orbital angle projecting beyond tip of second and third antero- lateral teeth; first pleopod of male distinctly curved with a longer distal process
4.	Inner surface of manus of cheliped of male without a spine near articula-
_	Inner surface of manus of cheliped of male with a spine near articulation with carpus
5.	Movable finger of cheliped bent downward, inner margin without teeth
_	Movable finger of cheliped slightly bent downward, inner margin with
6.	Manus 1.5 times as long as high M. (Macrophthalmus) crassipes H. Milne Edwards
_	Manus more than three times as long as high
7.	Merus and ischium of external maxilliped subequal in length
—	Merus of external maxilliped markedly shorter than ischium 10
8.	Carapace 1.2 times as broad as long; without transverse and oblique granular rows on each branchial region
—	Carapace 1.5 times as broad as long; with transverse and oblique granular rows on each branchial region (Subgenus <i>Hemiplax</i> Heller). Greatest
	breadth of carapace situated between external orbital angles; movable finger straight in male M. (Hemiplax) boteltobagoe (Sakai)
9.	Antero-lateral margin with 4 or 5 teeth; external orbital teeth long and protruded; greatest breadth of carapace between external orbital angles
	Antero-lateral margin with 2 teeth, external orbital teeth long and triangular; greatest breadth of carapace not between external orbital
10	angles
10.	of carapace length to breadth around 1:1.4-1.5 (Subgenus Venitus Barnes).

	Outer surface of manus smooth, upper and distal part of inner surface with					
	thick hairs, lower and proximal parts with compact granules, immovable					
	finger without teeth M. (Venitus) latreillii (Desmarest)					
	Central region of epistome distinctly concave; ratio of carapace length to					
	breadth around 1:1.2-1.3 Subgenus Mareotis Barnes 11					
11.	Inner surface of manus with a spine near articulation of carpus					
	M. (Mareotis) erato de Man					
—	Inner surface of manus without spine near articulation of carpus 12					
12.	Inner margin of movable finger of cheliped of male without teeth 13					
—	Inner margin of movable finger of cheliped of male with teeth					
13. Merus, carpus and propodus of ambulatory legs with few hairs;						
	pleopod of male with a short distal protruded lobe					
—	Merus, carpus and propodus of ambulatory legs with many hairs; first					
	pleopod of male with a well developed distal protruded lobe					
	M. (Mareotis) depressus Rüppell					
14.	Inner surface of manus of cheliped of male with hairs					
	M. (Mareotis) definitus Adams & White					
	Inner surface of manus of cheliped of male without hairs					
15.	Anterior part of lateral margin distinctly convergent; greatest breadth of					
	carapace between third teeth					
	Anterior part of lateral margin not distinctly convergent; greatest breadth					
	of carapace between second teeth					
16.	Merus of second and third ambulatory legs comparatively slender, serra-					
	tions of anterior and posterior margins stout and sparse; subdistal tooth of					
	merus protruded <i>M. (Mareotis) japonicus japonicus (de Haan)</i>					
_	Merus of second and third ambulatory legs comparatively broad, serra-					
	tions of anterior and posterior margins fine and compact; subdistal tooth of					
	anterior margin not very protruded					

DISCUSSION

Evolutionary relationship. — Fossil evidence indicates that *Macrophthalmus* originated in the Mediterranean in the later Tertiary period (Remy, 1952). According to the optimal conditions for the habitat of *Macrophthalmus* in the geological period, Barnes (1967, 1968a) suggested that it originated in the Indo-West Pacific in late Eocene-Oligocene epoch. It is our opinion that material available at the present is insufficient to trace the ancestral history of these animals. According to the fossil record, the order of primitive characteristics in this genus is as follows: 1, carapace subquadrate; 2, front broad with no constriction at its base; 3, ocular peduncles stout; 4, central region of epistome straight; 5, merus and ischium of external maxilliped almost equal in length (Barnes, 1967).

A comparison of characters of the five subgenera found in the seas of China indicates three different evolutionary groupings, with the *Hemiplax-Mopsocarcinus* group as the most primitive. Species of this group have more plesiomorphic characters such as: a subquadrate carapace (length/breath proportion of 1 to 1.2-1.5); broad front; stout ocular peduncle; straight central region of the epistome; external maxilliped with the merus and ischium subequal in size. This group includes *M. (Hemiplax) boteltobagoe, M. (Mopsocarcinus) boscii* and *M. (Mopsocarcinus) dentatus.*

The intermediate group is the Venitus-group. Although almost all of the fossil records of the genus pertain to this subgenus, it represents a transitional stage, having both primitive (plesiomorphic) and specialized (apomorphic) characters. The primitive characters exhibited in this subgenus are subquadrate carapace; stout ocular peduncle; straight central region of epistome. The apomorphic characters found in this group are narrow front; external maxilliped with merus shorter than ischium. This group has only one species in Chinese waters, M. (Venitus) latreillei.

The most specialized of the three groups is the Mareotis-Macrophthalmus group. Possibly due to adaptations to the environment, almost all the characters are specialized, such as broad carapace; narrow front with constriction at the base; slender ocular peduncle; concave or convex central region of epistome; external maxilliped with merus shorter than ischium. The species of this group are diverse. They include M. (Mareotis) erato, M. (Mareotis) pacificus, M. (Mareotis) tomentosus, M. (Mareotis) depressus, M. (Mareotis) definitus, M. (Mareotis) japonicus japonicus, M. (Mareotis) japonicus frequens, M. (Macrophthalmus) telescopicus, M. (Macrophthalmus) verreauxi, M. (Macrophthalmus) dilatatus dilatatus, M_{\cdot} (Macrophthalmus) brevis, M. (Macrophthalmus) convexus, and M_{\cdot} (Macrophthalmus) crassipes. These taxa constitute 76% of the total number of species of *Macrophthalmus* in Chinese seas. The morphological diversity and the wide geographic distribution suggest that this group has undergone an adaptive radiation. The presence of subspecies indicates that it is comparatively more specialized and a higher evolutionary stage than the other two groups.

Species distribution. — The Macrophthalmus fauna is generally tropical and subtropical in nature. All but M. (Mareotis) japonicus frequens are widely distributed in the South China Sea. Only M. (Mareotis) japonicus japonicus and M. (Macrophthalmus) dilatatus dilatatus extend further northward to the Yellow-Bo Sea and M. (Mopsocarcinus) erato to the East China Sea. M. (Mareotis) japonicus frequens is exceptional in that it is found only in the Yellow-Bo Sea and in the northern part of the East China Sea. Most species are also widely distributed in the Indo-West Pacific region, namely, M. (Mopsocarcinus) boscii, M. (Venitus) latreillei, M. (Mareotis) pacificus, M. (Mareotis) japonicus japonicus, M. (Macrophthalmus) telescopicus, M. (Macrophthalmus) verreauxi, M. (Macrophthalmus) convexus, and M. (Macrophthalmus) crassipes. A small number of species occur in

TABLE I

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	а	b	с	d	e	f	g	h	i
M. (Hemiplax) boteltobagoe (Sakai, 1939)	+								
M. (Mopsocarcinus) boscii Audouin, 1826	+				+	+		+	+
M. (Mopsocarcinus) dentatus Stimpson, 1858	+								
M. (Venitus) latreillei (Desmarest, 1822)	+				+	+	+	+	+
M. (Mareotis) erato de Man, 1888	+	+				+			
M. (Mareotis) pacificus Dana, 1851	+			+	+	+	+	+	
M. (Mareotis) tomentosus Souleyet, 1841	+					+			
M. (Mareotis) depressus Rüppell, 1830	+								
M. (Mareotis) definitus Adams &									
White, 1848	+					+			
M. (Mareotis) japonicus japonicus									
(de Haan, 1835)	+	+	+		+	+			
M. (Mareotis) japonicus frequens subsp. nov.		+	+						
M. (Macrophthalmus) telescopicus Owen, 1839	+			+		+			+
M. (Macrophthalmus) verreauxi H. Milne									
Edwards, 1848	+			+	+		+	+	+
M. (Macrophthalmus) dilatatus dilatatus									
de Haan, 1835	+	+	+		+				
M. (Macrophthalmus) brevis (Herbst, 1804)	+					+			
M. (Macrophthalmus) convexus Stimpson, 1854	+			+	+	+		+	+

Distribution of Chinese Macrophthalmus

a-c, China: a, South China Sea and southern East China Sea; b, northern East China Sea and southern Yellow-Bo Sea; c, Yellow-Bo Sea; d, Hawaii and Indo-West Pacific Islands; e, Japan and Korea; f, Indonesia, Malaysian Peninsula; g, Australia; h, India; i, Madagascar; East and South Africa.

the Indonesian-Malaysian tropics; they are M. (Mareotis) erato, M. (Mareotis) tomentosus, M. (Mareotis) definitus, and M. (Macrophthalmus) brevis. M. (Hemiplax) boteltobagae and M. (Mareotis) japonicus frequens represent the endemic species in Chinese seas. In addition, probably M. (Macrophthalmus) dilatatus dilatatus is a stenothermal warm-water species. Outside of China it is found in Japanese and Korean waters. However, the disjunct distribution of M. (Mareotis) depressus which is found only in the South China Sea and Indian Ocean east of Africa, is probably attributable to incomplete collecting.

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SUMMARY

The Macrophthalmus species of the seas of China are dealt with and a key is presented to the 17 species (in 5 subgenera) known from Chinese waters. A new subspecies, Macrophthalmus (Mareotis) japonicus frequens, is described. M. (Venitus) latreillei (Desmarest) and M. (M.) crassipes H. Milne Edwards are discussed in more detail. Speculations on the evolutionary relationships are made, based on morphological characters and geographical distribution.

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