Larval development of *Sesarma catenata* Ortmann (Brachyura, Grapsidae, Sesarminae) reared in the laboratory

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Sesarma catenata larvae were raised in the laboratory and the development stages described in detail. Larval development comprises four zoea and one megalopa stage. Morphological features of the first zoea and megalopa stages of *Sesarma catenata* are compared with those of other Sesarminae species described in the literature. The genera *Sesarma, Metasesarma,* and *Bresedium* appear to be closely related taxa within the subfamily. The diagnostic value of some features of larval morphology is briefly discussed.

Die larvale stadia van Sesarma catenata is in die laboratorium aangehou en is in detail beskryf. Larvale ontwikkeling bestaan uit vier zoea- en een megalopa-stadium. In hierdie studie word die morfologie van die eerste zoea- en die megalopa-stadium van Sesarma catenata met die van ander Sesarminae-spesies, soos in die literatuur beskryf, vergelyk. Die genera Sesarma, Metasesarma en Bresedium blyk om naby verwante taksa binne die subfamilie te wees. Die diagnostiese waarde van sommige larvale morfologiese eienskappe word kortliks bespreek.

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Brachyuran crabs of the family Grapsidae are widespread inhabitants of shallow coastal and estuarine environments in tropical and subtropical areas. Within the four families recognized by Balss (1957), Barnard (1950) lists 10 genera and 20 species of grapsid crabs for Southern African waters. The genus Sesarma is the most conspicuous of them and includes eight species (Kensley 1981). Sesarma catenata is endemic to the southern and south-eastern coasts of Africa, inhabiting estuaries from the Breede River to Inhaca Island (Day 1974). The Sesarma catenata population of the Swartkops estuary saltmarshes reaches densities of up to 80 individuals m⁻² with an annual production of 109,2 kj m⁻² year⁻¹ (Els 1982). This paper describes S. catenata larval stages and considers the species' taxonomic relationships with other grapsid crabs on the basis of larval morphology.

Material and Methods

Gravid Sesarma catenata females were collected from the Swartkops estuary (Figure 1) in November- December 1983. Females were individually placed in 1 ℓ plastic containers filled with sea water (35 °/ ∞ salinity) and kept at 20 °C constant temperature under a 12 h light-dark cycle.

After hatching, groups of 10 larvae were placed in glass dishes containing 40 ml sea water (35 $^{\circ}/_{\infty}$ salinity) filtered to remove large particles, and kept in similar conditions to adult females. No more than 100 sibling larvae (10 culture dishes containing 10 larvae each) were kept at any time. Larvae were supplied with newly hatched (less than 24 h) *Artemia* sp. nauplii (origin San Francisco Bay, USA) which had been fed *Dunaliella* sp. and *Thalassiosira* sp. for 6 h beforehand. Every 24 h, dead larvae were removed from the culture dishes, the water exchanged and fresh food (300–500 nauplii per

dish) supplied.

Larvae used for illustration were anaesthetized with MgCl₂ and fixed in 4% buffered formalin. Specimens were dissected in a 25% lactic acid solution and drawn with the aid of a camera lucida attached to a compound microscope. Measurements were made with an ocular micrometer. Illustrations were based on a sample of 10 individuals from at least three different broods. All features illustrated belonged to the same specimen. This specimen was considered to be an 'average animal' and possessed the characteristics most commonly encountered in the sample.

Measurements of zoeal features were made according



Figure 1 Geographical situation of the Swartkops river. The arrow indicates the locality of collection of *Sesarma catenata* ovigerous females.

to Webber & Wear (1981). Descriptions and illustrations follow Rice (1979). Secondary setation, although not always illustrated, is tabulated using the same nomenclature as Bookhout & Costlow (1974), Greenwood & Fielder (1979) and Fielder & Greenwood (1983).

Tables 5 and 6 were constructed in the following manner. The setation pattern of multi-segmented appendages is given as a series of figures representing the number of setae on each segment starting with the proximal one. In Table 6, the setation of the endites of the maxilla is given as the number of setae on the distal lobe plus the number of setae on the proximal lobe. Setation of the epipodite of the third maxilliped is given as the number of basal setae plus the number of distal setae.

Results

The larval development of *Sesarma catenata* consists of four zoeal stages and one megalopa stage. Development times of zoeal stages reared at 20 °C are shown in

Figure 2. Measurements of zoeal morphological features are summarized in Table 1. Setation pattern of appendages of zoeae and megalopa are shown in Tables 2 and 3 respectively.

Zoea I (Figures 3a, 4a-4i)

Carapace subcircular and globose. Dorsal spine curved posteriorly, with a slight anterior depression midway along its length. Rostral spine projecting downwards, with a convex anterior outline. No lateral spines present. Eyes sessile. Pairs of small setae present laterally at the base of the dorsal spine and frontally above the eyes. Abdomen consists of five segments plus telson. One pair of dorsolateral knobs present on second and third segments. Posterolateral margin of second to fifth segments extended into small projections. Second to fourth segments subquadrate, as broad as long. Fifth segment longer, about 0,25 times longer than broad. Telson strongly bifurcate with a median notch. Posteromedial margin with three pairs of stout spines fringed laterally



Figure 2 Percentage of survival and duration of Sesarma catenata larval stages reared at 20 °C and 35 % salinity. Initial N = 100. Roman numerals = zoeae I to IV. M = megalopa.

Table 1 Dimensions and proportions of some morphological features of *Sesarma catenata* zoeal stages; all measurements are in mm; CL = length of the carapace; DL = length of dorsal spine; DR = length from tip of dorsal spine to tip of rostral spine; RL = length of rostral spine; LTC = length of telson cornua; AP = length of protopodite of the antenna; AE = length of exopodite of the antenna; F = feature; mean values from 10 individuals; range given in parentheses

	Zoea I		Zoea II		2	Zoea III	Zoea IV		
F	mean	range	mean	range	mean	range	mean	range	
CL	0,23	(0,20-0,29)	0,26	(0,21-0,30)	0,28	(0,22–0,31)	0,41	(0,36-0,49)	
DL	0,16	(0,13-0,20)	0,18	(0,15-0,23)	0,20	(0,17-0,24)	0,28	(0,23-0,31)	
DR	0,44	(0,39-0,47)	0,98	(0,84-1,12)	1,09	(0,92-1,14)	1,50	(1,40-1,56)	
RL	0,24	(0,220,27)	0,27	(0,24-0,32)	0,30	(0,26-0,30)	0,40	(0,36-0,44)	
LTC	0,26	(0,24-0,27)	0,26	(0,26-0,28)	0,31	(0,28-0,31)	0,33	(0,26-0,38)	
AP	0,17	(0,14-0,20)	0,16	(0,14-0,18)	0,26	(0,22-0,28)	0,24	(0,20-0,36)	
AE	0,06	(0,06-0,08)	0,06	—	0,06	_	0,10	(0,08-0,10)	
DR/DL	2,7		5,6		5,4		5,3		
DR/CL	1,9		3,7		3,7		3,6		
AP/AE	2,8		2,6		4,3		2,4		
RL/AP	1,4		1,6			1,1	1,6		

Table 2 Segmentation and setation of appendages of *Sesarma catenata* zoeal stages; A = aesthetacs; S = simple; SP = sparcely plumose; HP = highly plumose; D = denticulate; hp = hirsute proximal; pdt = plumodenticulate terminal; all symbols except 'A' refer to setae

Appendage	Zoea I	Zoea II	Zoea III	Zoea IV	
Antennule					
terminal	4A + 1S	4A + 1S	4A + 2S	3A + 3S	
subterminal	0	0	0	1	
Antenna					
Protopodite	13-14 teeth	14-20 teeth	16-20 teeth	15-25 teeth	
Exopodite	2S	2S	2S	2S	
Endopodite	absent	bud	present	present	
Maxillule					
Coxopodite	0	1 HP	1 HP	1HP	
Basal endite	5PD	7PD	6PD,1S	9PD,2S	
Coxal endite	5PD	5PD	4PD,1S	6PD	
Endopodite prox. seg.	1S	1PD	1 S	1S	
dist. seg.	1S,1SPpdt,3SPhp	3SP,1PD,1SPpdt	1PD,4SPpdt	5SPpdt	
Maxilla					
Basal endite prox.	4PD	5PD	3PD,1S,1D	7S	
dist.	4PD	4PD	3PD,1S	5PD	
Coxal endite prox.	5PD	5PD	4PD,1S	6PD	
dist.	3PD	3PD	3PD	3PD } + IPD	
Endopodite prox.	2SP	2SPpdt	2SP	2SPpdt	
dist.	3SP	3SPpdt	3SP	3SPpdt	
Scaphognathite	4HP	5HP + 3HP	7HP + 4HP	19-20HP	
Maxilliped I					
Basipodite	2SP,2PD,6S	6SP,2PD,2S	9PD,1S	5SP,5PD	
Endopodite prox. seg.	1SP,1S	1SP,1S	1SP,1S	1SP,1S	
2 seg.	1SP,1S	1SP,1S	1SP,1S	1SP,1S	
3 seg.	1SP	1SP	2SP	2SP	
4 seg.	2PD	IS,1PD	2PD	2PD	
5 seg.	2SP,3SPpdt	1PD,2SP,2SPpdt	1PD,2SP,4SPpdt	2SP,4SPpdt	
Exopodite	4HP	6HP	8HP	9HP	
Maxilliped II					
Basipodite	3SP,1S	1SP,1PD,2S	1SP,1PD,2S	2SP,2S	
Endopodite prox. seg.	0	0	0	0	
2 seg.	1PD	1PD	1PD	1PD	
3 seg.	1PD,5S	2PD,4S	1PD,5S	1PD,5S	
Exopodite	4HP	6HP	8HP	10 HP	

with spinules. Dorsal surface of telson and abdominal segments covered with minute spinules arranged in groups (Figure 4b).

Setation of appendages is illustrated in Figure 4 and listed in Table 2.

Zoea II (Figures 3b, 5a-5i)

Carapace with two small setae on midfrontal region and two large plumose setae on posteroventral margin. Small pereiopod buds present ventrally. Eyes slightly stalked. Abdomen with single setae present dorsally on posterior margin of first segment. Telson cornua bent slightly outwards on distal section.

Setation of appendages is illustrated in Figure 5 and listed in Table 2.

Zoea III (Figures 3c; 6a-6i)

Carapace more elongate posteriorly than in preceding

stages. Dorsal spine proportionally broader along most of its length. Four (occasionally five) plumose setae present on each side of posterior margin. Eyes fully stalked. Pereiopods further developed with first pereiopod showing the beginning of chelae segmentation. Abdomen with six segments plus telson. Pleopod buds present.

Setation of appendages is illustrated in Figure 6 and listed in Table 2.

Zoea IV (Figures 3d, 7a-7i)

Carapace subquadrate. Dorsal spine distal portion recurved. Rostral spine with broadened base extending over the same length as the antennule. Eight plumose setae present on both sides of posterolateral margin. Pereiopods further developed, protruding beneath carapace. Third maxilliped bud present. Abdomen with six segments plus telson. Pleopods well developed but not Table 3 Segmentation and setation of appendages of Sesarma catenata megalopa stage; symbols as in Table 2

Appendage and segmentation	Setation
Antennule	
Peduncle	1,0,0
Terminal flagellum prox. seg.	1\$
2 seg.	4A,1S
3 seg.	2 A ,2S
Antenna	
prox. seg.	15
2 seg.	15
3 seg.	15
4 seg.	0
5 seg.	25
0 seg.	28.58
/ seg.	23,55
o seg. Maxillule	23
Rasal endite	3S-13PD
Coxal endite	2P.10PD
Endopodite	6PD
Basinodite	2PD
Maxilla	
Basal endite prox.	7PD
dist.	5PD
Coxal endite	2P,9PD
Endopodite	1P
Scaphognathite	37HP,1P + 3F
First maxilliped	
Basal endite	8PD,1S
Coxal endite	8PD,1P
Endopodite	15
Endopodite prox. seg.	3HP
2 seg.	3HP
Epipodite	5P
Second maxilliped	
Endopodite prox. seg.	0
2 seg.	15
3 seg.	3PD 10
4 seg.	5PD,15
Exopodite prox. seg.	
2 seg.	JHP
Endopodite prov. seg	6PD 15
2 seg	2SP 3PD 2S
2 sog. 3 seg.	2S. 1PD
4 seg.	2PD,2S
5 seg.	4PD
Exopodite prox. seg.	1 S
2 seg.	4HP
Epipodite prox. seg.	3P
dist. seg.	13SP
Basipodite	7PD

(*) Only some stages described.

(**) As Sesarma intermedium by Baba & Fukuda (1975).

(***) As S. erythrodactylum by Baba & Fukuda (1975).

yet setose. One larger median and two shorter lateral plumose setae present dorsally on first segment. Setation of appendages is illustrated in Figure 7 and listed in Table 2.

Megalopa (Figures 3e, 3f, 8a-8h, 9a-9g)

Carapace smooth and globose. Anterior region narrow

and depressed, ending in a short rostrum bent ventrally. Orbicular edge broad, ending in a rounded angle. Lateral and posterior margins with numerous setae.

Abdomen has six segments plus telson. Fifth segment with two rounded posterolateral projections. Posterior margin of telson convexly rounded with five small indentations, and four spinules present on its dorsal surface (Figure 9a). Pleopods with a small endopodite bearing two hook-like setae distolaterally. Exopodite onesegmented, bearing 13,12,12,12 plumose setae on pleopods one to four respectively. Uropods uniramous and bisegmented, with one plumose seta on external margin of proximal segment and six plumose setae on terminal segment.

Setation of other appendages is illustrated in Figures 8 and 9 and listed in Table 3.

Table 4 Published larval descriptions of species belonging to the Sesarminae subfamily

Aratus pisonii (Warner 1968)
Bresedium brevipes (Fielder & Greenwood 1983)
Chasmagnathus convexus (Baba & Fukuda 1972)
C. granulata (Boschi et al. 1967)
C. laevis (Green & Anderson 1973) (*)
Chiromantes bidens (Fukuda & Baba 1976)
Cyclograpsus punctatus (Fagetti & Campodonico 1971)
C. cinereus (Costlow & Fagetti 1967)
C. insularum (Wear 1970) (*)
C. lavauxi (Wear 1970) $(*)$
Helice crassa (Wear 1970) (*)
H. tridens wnana (Baba & Morivama 1972) (*)
H. tridens tridens (Baba & Moriyama 1972) (*)
H. leachi (Baba et al. 1984) (*)
Helograpsus hanswellanus (Green & Anderson 1973) (*)
Holometopus haematochaeir (Fukuda & Baba 1976) (*)
Metasesarma rubripes (Diaz & Ewald 1968)
M. rousseauxii (Rajabai 1961) (*)
Parasesarma plicatum (Fukuda & Baba 1976) (*)
Sesarmops intermedius (Fukuda & Baba 1976) (*)(**)
Sesarma bidentatus (Hartno11 1964)
S. cinereus (Costlow & Bookhout 1960)
S. dehaani (Baba & Minyata 1971)
S. erythrodactyla (Green & Anderson 1973) (*)(***)
S. lanatum (Kakati & Sankolli 1975)
S. perracae (Soh 1969)
S. picta (Aikawa 1937) (*)
S. plicatum (Baba & Fukuda 1975) (*)
S. reticulatum (Costlow & Bookhout 1962) (*)
S. ricordi (Diaz & Ewald 1968)
S. tetragonum (Rajabai 1961) (*)

Discussion

Wear (1970) distinguished four groups of grapsid zoea larvae based on the presence of lateral spines on the carapace and the relative lengths of the endopodite and exopodite of the antenna. This grouping agrees with the



Figure 3 Sesarma catenata larval stages. A = zoea I. B = zoea II. C = zoea III. D = zoea IV. E = megalopa, dorsal view. F = megalopa, lateral view.



Figure 4 Sesarma catenata zoea I appendages. A = frontal view of carapace. B = telson, dorsal view. C = antennule. D = antenna. E = mandible. F = maxillule. G = maxilla. H = first maxilliped. I = second maxilliped.

subdivision of the family into four subfamilies recognized by Balss (1957). Two of these groups are homogeneous and well defined, and include larvae from subfamilies Grapsinae (no lateral spines and and very short antennal exopodite) and Plagusinae (lateral spines present and comparatively long antennal exopodite). The other two groups are more heterogeneous and share taxa from Sesarminae and Varuninae subfamilies. Although



Figure 5 Sesarma catenata zoea II appendages. A = frontal view of carapace. B = telson, dorsal view. C = antennule. D = antenna. E = mandible. F = maxillule. G = maxilla. H = first maxilliped. I = second maxilliped.

Schlotterbeck (1976) showed that lateral spines on the carapace could be an acquired feature during the larval

development of grapsids, and recent revision of brachyuran zoeal morphology and classification by Rice (1980)



Figure 6 Sesarma catenata zoea III appendages. A = frontal view of carapace. B = posterior view of the carapace (first maxilliped and mouth-parts omitted). C = antennule. D = antenna. E = mandible. F = maxillule. G = maxilla. H = first maxilliped. I = second maxilliped.



Figure 7 Sesarma catenata zoea IV appendages. A =frontal view of carapace. B =pereiopods. C =third maxilliped. D =antennule. E =antenna. F =mandible. G =maxillue. H =maxilla. I =first maxilliped. J =second maxilliped.

comfirms the validity of Wear's (1970) grouping.

Rice (1980) groups the genus Sesarma together with Metasesarma, Aratus and Chiromantes. These four genera share the following features: (a) absence of lat-

eral spines on the carapace, (b) 2 + 3 setae on the exopodite of the maxilla, and (c) almost always only three pairs of posterior telson spines. The genera *Bresedium* (*Bresedium brevipes*, Fielder & Greenwood 1983) and



Figure 8 Sesarma catenata megalopa stage appendages. A = antennule. B = antenna. C = mandible. D = maxillule. E = maxilla. F = first maxilliped. G = second maxilliped. H = third maxilliped.



Figure 9 Sesarma catenata megalopa stage appendages. A = dorsal view of telson. B = second pleopod. C = first pereiopod. D = second pereiopod. E = third pereiopod. F = fourth pereiopod. G = fifth pereiopod.

Sesarmops (Sesarmops intermedius, Fukuda & Baba 1976) could be added to this list following the revision of the genus Sesarma by Serene & Soh (1970). Descriptions of *B. brevipes* and *S. intermedius* larvae are, however, the only ones published for their respective genera (see Table 4) and more information is needed before forming a definite opinion about their relationship with other Sesarminae species.

Morphological features of Sesarminae spp. first zoeal and megalopa stages are shown in Tables 5 and 6. Comparison of first zoeae (Table 5) suggests that Sesarma, Metasesarma, and Bresedium (sensu Serene & Soh 1970) are closely related taxa. The setation pattern of the maxilla endites is mostly 7–8,9 with the exception of S. lanatum, S. tetragonum and M. rousseauxii. The latter two species also differ in their setation pattern of the maxillule endites, which is otherwise a uniform character in all species listed in Table 5. S. tetragonum and M. rousseauxii (Rajabai 1961) share other features which disagree with Rice's (1980, p.339, Table XI) definition of the first zoea of the Grapsidae and with the characteristics of the group containing the genera Sesarma and Metasesarma (Rice 1980, p.341).

The close similarity of Sesarma, Metasesarma and Bresedium is also evident when comparing the megalopa stage in these three genera, relative to that of Chasmagnathus and Cyclograpsus. The first segment of the endopodite of the second maxilliped bears no setae. This is a common feature of Sesarma, Metasesarma and Bresedium (except for S. reticulatum). In addition, all species except S. lanatum and S. reticulatum have the setal formula 0,1,3,6 in this appendage. The absence of setae on the fourth segment of the antenna is a common feature of all megalopa listed in Table 6. A distinctive feature of *S. catenata* megalopa is the one-segmented endopodite of the maxillule. In this, *S. catenata* differs from other *Sesarma, Metasesarma* and *Bresedium* species and is similar to *Chasmagnathus* and *Cyclograpsus*.

A major problem concerning the classification of brachyuran larvae is the difficulty of attributing diagnostic value to morphological features (Rice 1979,1980). Some features considered in this discussion have not yet been 'tested' in this respect. According to Kensley (1981) eight Sesarma species inhabit Southern African coastal and estuarine waters. It is to be expected that detailed descriptions of larval stages of local species, will in future, increase our knowledge of larval morphology within the genus and help to identify those morphological features with clear diagnostic value.

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References

- AIKAWA, H. 1937. Further notes on Brachyuran larvae. Rec. Oceanogr. Wks. Japan. 9: 87-162.
- BABA, K. & FUKUDA, Y. 1972. Larval development of *Chasmagnathus convexus* de Haan (Crustacea, Brachyura) reared under laboratory conditions. *Mem. Fac. Educ. Kumamoto Univ.* 21: 90–96.
- BABA, K. & FUKUDA, Y. 1975. Newly obtained first zoeae of three species of Sesarma (Crustacea, Brachyura). Mem. Fac. Educ. Kumamoto Univ. 24: 63-68.
- BABA, K., FUKUDA, Y. & NAKASONE, Y. 1984. Zoeal development of the Sesarminae crab *Helice leachi* (Hess) (Crustacea: Decapoda: Brachyura). *Mem. Fac. Educ. Kumamoto Univ.* 33: 5-10.
- BABA, K. & MINYATA, K. 1971. Larval development of Sesarma (Holometopus) dehaani H. Milne-Edwards (Crustacea, Brachyura) reared in the laboratory. Mem. Fac. Educ. Kumamoto Univ. 19: 54-64.
- BABA, K. & MORIYAMA, M. 1972. Larval development of Helice tridens wnana Rathbun and Helice tridens tridens de Haan (Crustacea, Brachyura) reared in the laboratory. Mem. Fac. Educ. Kumamoto Univ. 20: 49-68.
- BALSS, H. 1957. Decapoda. VIII. Systematik. Bronn's Kl. Ordn. Tierreichs Bd. 5, Abt. 1, Buch 7. Leif. 12: 1505-1672.
- BARNARD, K.H. 1950. Descriptive catalog of South African decapod Crustacea. Ann. S. Afr. Mus. Vol. 37, 864 pp.
- BOOKHOUT, C.G. & COSTLOW, J.D. 1974. Larval development of *Portunus spinicarpus* reared in the laboratory. *Bull. Mar. Sci.* 24: 20–51.
- BOSCHI, E., SCHELZO, M.A. & GOLDSTEIN, B. 1967. Desarrollo larval de dos especies de crustáceos decápodos

 Table 5
 Comparison of morphological features of first zoeal stages of species belonging to the Sesarminae subfamily: (?) no data; (*) according to illustrations; references as in Table 4

		Antenna protopodite exopodite	Maxillule		Maxilla			Abdomen	
Species	Antennule		coxal end.	basal end.	coxal cnd.	basal cnd.	- Maxilliped II endopodite	lateral projections	Cornua setules
Chasmagnathus granulata	3A + 1S	2 rows teeth $\simeq 1/2$ prot.	5	6	6	10	0,1,5	short & spinous	?
Cyclograpsus punctatus	2A + 2S	2 rows teeth $> 2/3$ prot.	5	5	6	9	0,1,6,	short & rounded	present
Bresedium brevipes	4A	1 row teeth $\simeq 1/3$ prot.	5	5	7	9	0,1,6	short & spinous	present
Sesarma catenata	4A + 1S	1 row teeth $\approx 1/3$ prot	5	5	8	9	0,1,6	short & rounded	absent
Sesarma reticulatum	4A + 1S	1 row teeth $\simeq 1/3$ prot.	5	5	7	9	0,1,5	?	absent
Sesarma cinereum	3A + 2S	2 rows teeth $\simeq 1/3$ prot.	5	5	7	9	0,1,5	short & rounded	absent
Sesarma ricordi	3A + 2S	2 rows teeth $\simeq 1/3$ prot.	5	5	8	9	0,1,6	short & rounded	absent
Sesarma erythrodactyla	3A + 2S	2 rows teeth $> 1/2$ prot.	5	5	7•	9*	0,1,5	short & rounded	absent
Sesarma lanatum	3A + 1S	2 rows teeth $\approx 1/2$ prot.	5	5	8	10	0,1,6	short & rounded	present
Sesarma tetragonum	3A	2 rows teeth $\approx 3/4$ prot.	3	5	5	4	0,1,3	short & spinous	present
Metasesarma rubripes	3A + 1S	1 row teeth $< 1/3$ prot.	5	5	8	9	0,1,6	short & rounded	absent
Metasesarma rousseauxii	3A	1 row teeth $< 1/2$ prot.	2	3	4	8	0,1,4	short & rounded	absent
Chiromantes bidens	4A	1 row teeth $\approx 1/2$ prot.	5	5	7	9	0,1,6	short & rounded	absent
Sesarmops intermedius	?	1 row teeth < 1/4 prot.	5	5	5	?	0,1,6	short & spinous	absent

en el laboratorio. Pachycheles haigae Rodrigez da Costa (Porcellanidae) y Chasmagnathus granulata Dana (Grapsidae). Bol. Inst. Biol. Mar. Mar del Plata. 12: 1-46.

- COSTLOW, J.D. & BOOKHOUT, C.G. 1960. The complete larval development of *Sesarma cinereus* (Bosc) reared in the laboratory. *Biol.Bull.* 118: 203–214.
- COSTLOW, J.D. & BOOKHOUT, C.G. 1962. The larval development of *Sesarma reticulatum* Say reared in the laboratory. *Crustaceana*. 4: 281–229.
- COSTLOW, J.D. & FAGETTI, E. 1967. Larval development of the crab *Cyclograpsus cinereus* Dana, under laboratory conditions. *Pacific Sci.* 21: 166–177.
- DAY, J.H. 1974. A guide to marine life on Southern African shores. A.A. Balkema, Cape Town.
- DIAZ, H. & EWALD, J.J. 1968. A comparison of the larval development of *Metasesarma rubripes* (Rathbun) and *Sesarma ricordi* H. Milne-Edwards (Brachyura, Grapsidae) reared under similar conditions. *Crustaceana*. Suppl. II, p. 225–248.
- ELS, S. 1980. Distribution and abundance of two crab species on the Swartkops estuary saltmarshes and the

energetics of Sesarma catenata. M.Sc. thesis, University of Port Elizabeth.

- FAGETTI, E. & CAMPODONICO, G.I. 1971. The larval development of the crab Cyclograpsus punctatus H.
 Milne-Edwards under laboratory conditions (Decapoda, Brachyura, Grapsidae, Sesarminae). Crustaceana. 21: 183–195.
- FIELDER, D.R. & GREENWOOD, J.G. 1983. The zoeal stages and megalopa of *Bresedium brevipes* (de Man, 1899) (Crustacea: Decapoda: Grapsidae), reared in the laboratory. J. Plankton Res. 5: 585-598.
- FUKUDA, Y. & BABA, K. 1976. Complete larval development of the sesarminid crabs Chiromantes bidens, Holometopus haematochaeir, Parasesarma plicatum and Sesarmops intermedius reared in the laboratory. Mem. Fac. Educ. Kumamoto Univ. 25: 61-75.

GREEN, P.A. & ANDERSON, D.T. 1973. The first zoeal larvae of the estuarine crabs Sesarma erythrodactyla Hess, Helograpsus hanswellanus (Whitelegge) and Chasmagnathus laevis (Brachyura, Grapsidae, Sesarminae). Proc. Linn. Soc. N.S.W. 98: 13-28.

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subfamily

Table 6 Comparison of morphological features of the megalopa stages of species belonging to the Sesarminae

Feature	Chasmagnathus granulata	Cyclograpsus punctatus	Bresedium brevipes	Sesarma catenata	Sesarma reticulatum	Sesarma cinereum	Sesarma ricordi	Sesarma Ianatum	Metasesarma rubripes
Rostral spine	absent	present	absent	absent	present	absent	absent	absent	absent
Telson	3 spines *	6 setae+3 spines	1 seta	bare	8 spines	8 setae	1 seta	bare	1 seta
Antenna	2A,9A	4A.4A+2S,	4A,4A+2S	4A,2A+28	5 4A+2S,	3A,5A	3A+2S,6A	9A+1S	3A,5A
		4A+3S			5A				
Antennule	0,0,0,0,0,2,0,	1,0,0,0,4,2,	2,1,1,0,2,1,	1,1,1,0,2,	1,1,1,0,4,4	0,0,1,0,2,1,	1,1,1,0,2,1,	1,1,1,0,2,1,4	2,1,1,0,2,1,4,1,3
	0,2,4	3,2,3	4,1,3	0,5,2		2,1,2	5,1,3		
Spinous proc.	absent	absent	absent	absent	present	absent	absent	no data	absent
Maxillule									
Endopodite	4*	6	2,5	6	1,5	2,4	2,4	7	2,4
Basal endite	13*	24	17	14	15	12	18	16	17
Coxal endite	6*	16	11	12	10	9	11	10-12	11
Maxilla									
Endopodite	0*	2	1	1	2 + 2	3 + 2	0	0	0
Basal endite	12 + 8*	13 + 10	4 + 5	5 + 7	7 + 8	7 + 7	12	5 + 8	5 + 6
Coxal endite	3 + 10*	6 + 9	6 + 6	11	7 + 5	8 + 5	15	11 + 12	14
Scaphognathite	49 + 3*	65 + 8	28 + 3	37 + 4	30	30	40	34	$40 + 5(32^*)$
Maxilliped									
Endopodite	1*	4	2	1	3,2,2,5	10	2	1	2
Exopodite	4*	2,4	3,3	3,3	1,8	2,5	3,4	0,3	3,4
Epipodite	6	12	5	5	4	5	6	5	5
Basal endite	11	15*	8	9	14	8	11	9	9
Coxal endite	7	29*	6	9	15	5	8	6	6
Maxilliped 11									
Endopodite	1,0,3,8	2,1,5,10*	0,1,3,6	0,1,3,6	1,1,4,8	0,1,3,6	0,1,3,6	0,0,1,4,7	0,1,3,6
Exopodite	0,5	1,4*	4	1,5	7•	5	1,5	0,5	1,5
Maxilliped III									
Endopodite	10,6,0,6,5	19,15,11,7,8*	8,7,3,3,6	7,7,3,4,4	9,6,2,4,6	7,6,3,5,2	8,8,3,4,6	7,7,2,3,7	8,8,3,4,6
Exopodite	1,4	2,5	1,5	1,4	0,5	0,5	1,4	0,3-4	2,5
Epipodite	15 + 13	19 + 20	10 + 7	16 + 7	10 + 7	8 + 5	15 + 10	10 + 3	18 + 12

(*) According to illustrations; references as in Table 4.

stages and megalopa of Portunus rubromarginatus (Lachester) (Decapoda, Portunidae), reared in the laboratory. J. Plankton Res. 1: 191-205.

- HARTNOLL, R.G. 1964. The freshwater crabs of Jamaica. Proc. Linn. Soc. London. 175: 145-169.
- KAKATI, V.S. & SANKOLLI, K.N. 1975. Larval culture of an estuarine crab, Sesarma lanatum Alcock in the laboratory (Brachyura, Grapsidae). Bull. Dep. Mar. Sci. Univ. Cochin. 7: 384-401.
- KENSLEY, B. 1981. On the zoogeography of Southern African decapod Crustacea, with a distributional checklist of the species. Smithon. Contr. Zool. N 388, 64 pp.
- RAJABAI, K.G. 1961. Studies on the early development of Brachyura. VII. Early development of Metopograpsus messor (Forskal), Plagusia depressa squamosa (Herbst), Metasesarma rousseauxii A, Milne-Edwards, and Sesarma tetragonum (Fabricius) on the family Grapsidae. J. Zool. Soc. India. 13: 154-165.
- RICE, A.L. 1979. A plea for improved standards in crab zoeal descriptions. Crustaceana. 37: 213-218.
- RICE, A.L. 1980. Crab zoeal morphology and its bearing on the classification of Brachyura. Trans. Zool. Soc. London. 35: 271-424.

- SCHLOTTERBECK, R.E. 1976. The larval development of the lined shore crab Pachygrapsus crassipes Randall, 1840 (Decapoda, Brachyura, Grapsidae) reared in the laboratory. Crustaceana. 3: 184-200.
- SERENE, R. & SOH, C.L. 1970. New Indo-Pacific genera allied to Sesarma Say (Brachyura, Decapoda, Crustacea). Treubia. 27: 387-408.
- SOH, C.L. 1969. Abbreviated development of a non-marine crab, Sesarma (Geosesarma) perracae (Brachyura, Grapsidae), from Singapore. J. Zool. London. 158: 357-370.
- WARNER, G.F. 1968. The larval development of the mangrove tree crab Aratus pisonii (H. Milne-Edwards) reared in the laboratory (Brachyura, Grapsidae). Crustaceana. Suppl. II, pp. 249-258.
- WEAR, R.G. 1970. Life-history of New Zealand Brachyura. IV. Zoea larvae hatched from crabs of the family Grapsidae. N.Z.J. Mar. Freshw. Res. 4: 3-35.
- WEBBER, W.E. & WEAR, R.G. 1981. Life-history studies on New Zealand Brachyura. V. Larvac of the family Majidae. N.Z.J. Mar. Freshw. Res. 15: 331-383.