

SEXUAL DIMORPHISM IN FOSSIL AND EXTANT SPECIES OF *CALLIANOPSIS* DE SAINT LAURENT

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A B S T R A C T

A large collection of fossil callianassid mud shrimp collected from the Olympic Peninsula, Washington, contains extremely well-preserved material that permits their reassignment from *Callianassa clallamensis* Withers and *Callianassa twinensis* Rathbun to the ctenochelid genus *Callianopsis* de Saint Laurent. In addition, examination of the Recent species *Callianopsis goniophthalma* Rathbun indicates that this species exhibits sexual dimorphism in the morphology of the major cheliped. The same pattern of dimorphism is also observable in the fossil material. Therefore, the fossil species *Callianopsis clallamensis* (Withers, 1924), and *Callianopsis twinensis* (Rathbun, 1926), are synonymized. Specimens originally referable to *Callianopsis clallamensis* represent males, and those originally referable to *Callianopsis twinensis* represent females. This may be the first observation of sexual dimorphism in the morphology of the major chelipeds within the family Ctenochelidae Manning and Felder, 1991.

Identification and interpretation of fossil callianassid mud shrimp, within the Callianassidae Dana, 1852, and the Ctenochelidae Manning and Felder, 1991, has historically been hindered by the nature of preservation of fossil material. Because of the delicate nature of most of the cuticular surfaces, fossil callianassids are largely represented by isolated claws and fingers. Unfortunately, the diagnostic characters of extant taxa, which include the nature of the pleopods, details of carapace architecture, and form of the abdomen, are not usually available for study in fossil specimens. The recent revision of the callianassids by Manning and Felder (1991), however, provided several morphological characters of the first pereopods which, for the first time, permit recognition of more realistic relationships between fossil and Recent taxa. Their clarification of the key characters necessary for recognition of genera has stimulated reassessment of several fossil taxa.

The purpose of this work is to describe the pattern of sexual dimorphism exhibited by specimens of *Callianopsis goniophthalma* (Rathbun, 1902) and to describe similar morphological variants within fossils from Cenozoic deposits in the state of Washington. On this basis, the two fossil species known from Washington, *Callianassa clallamensis* Withers, 1924, and *Callianassa twinensis* Rathbun, 1926, are considered synonymous.

The genus *Callianopsis* was erected in 1973 by de Saint Laurent to accommodate the sole Recent species, *Callianopsis goniophthalma* (Rathbun, 1902), known from the northeastern Pacific at slope depths of 480–650 m (Manning and Felder, 1991). Subsequently, several fossil species have been named. Karasawa (1993) reassigned *Callianassa titaensis* Nagao, 1941, from the early to early middle Miocene of Japan, to *Callianopsis*. Kato and Karasawa (1994) assigned *Callianassa muratai* Nagao and *Callianassa elongatodigitata* Nagao, 1941, from the upper Eocene-lower Oligocene of Japan, to the genus *Callianopsis*.

In the course of study of Cenozoic decapods from the state of Washington, two species of callianassids, *Callianassa clallamensis* Withers, 1924, and *Callianassa twinensis* Rathbun, 1926, have been restudied. Based upon well-preserved and more complete material than was available to Withers and Rathbun, it is now possible to suggest that these species can be referred confidently to *Callianopsis*. Furthermore, examination of males and females of the sole extant species, *Callianopsis goniophthalma*, reveals that sexual dimorphism can be recognized in the form of the major cheliped of this species. The same pattern of dimorphic characters can be recognized in fossil specimens of *Callianassa clallamensis* and *Callianassa twinensis*. Because the two fossil species occur in the same

rock units and because they exhibit very similar morphological variation to that seen in *Callianopsis goniophthalma*, it is concluded that they also represent sexual dimorphs, all of which can be assigned to *Callianopsis clallamensis*.

Sexual dimorphism in the first and often second pleopods is widely observed within the Callianassidae and the Ctenochelidae. Secondary sexual characters have been reported in several genera of the Callianassidae, including, but not necessarily limited to, *Callichirus* Stimpson, *Eucalliax* Manning and Felder, *Lepidophthalmus* Holmes, and *Sergio* Manning and Lemaitre. The genus *Callichirus* has been reported to possess sexually dimorphic major chelipeds; in adult males, the major chelipeds are strongly unequal (Manning and Felder, 1991). Males of species of the genus *Eucalliax* have more heavily calcified and differently sculptured major chelae than do females (Felder and Manning, 1994). Minor differences also occur in the minor cheliped of males and females of species of *Eucalliax* (see Felder and Manning, 1994). In addition, males of species of the genus *Lepidophthalmus* have more heavily armed major chelipeds and smaller teeth of the fixed finger and the dactylus of the major cheliped than do females (Felder and Rodrigues, 1993). Felder and Lovett (1989) speculated that more massive chelae in males may be related to adaptations in the male for combative behavior, including competition for females, access to burrows, and defending against other males. Interestingly, the chelae of males of species of *Callianopsis* are heavier and more massive than those of females, the same pattern as seen in species of *Lepidophthalmus* and *Eucalliax*. Species of the genus *Sergio* exhibit differences in eye pigmentation between males and females (Manning and Felder, 1995). Males of one species of callianassid, *Biffarius biformis* (Biffar, 1971), were reported to possess two different forms of the major cheliped (Biffar, 1971). Females of this species did not possess a "large" cheliped (Biffar, 1971: 229). The reason for the existence of the two forms of the major cheliped in males only of *B. biformis* was determined not to be related to age, size, hermaphroditism, or parasites, and no reasonable explanation for the two forms was offered by Biffar (1971). No reports of secondary sexual di-

morphic characters have been made for the Ctenochelidae.

SYSTEMATICS

Infraorder Anomura H. Milne
Edwards, 1832

Superfamily Thalassinoidea
Latreille, 1831

Family Ctenochelidae Manning
and Felder, 1991

Diagnosis.—Carapace with cardiac prominence; strong antennal scale on antenna; pediform third maxilliped usually with distal meral spine; male pleopod with appendix masculina; longitudinally carinate uropodal exopods, lacking dorsal plate and not possessing lateral notch or incision (Manning and Felder, 1991).

Subfamily Callianopsinae de
Saint Laurent, 1973

Diagnosis.—Carapace with dorsal oval; third maxilliped with ovate propodus and dactylus, and fingerlike appendices internae on pleopods (Manning and Felder, 1991). First and second pleopods sexually dimorphic, third through fifth pleopods similar.

Remarks.—Both de Saint Laurent (1973) and Manning and Felder (1991) reported that the second through fifth pleopods were similar in *Callianopsis*, the only genus in the subfamily Callianopsinae. The second through fifth pairs of pleopods are all foliaceous, and the third through fifth pairs are almost identical. The second pleopods differ from the third through fifth in the shape of both the endopods and exopods, as discussed below, and the second pleopods are also sexually dimorphic. The second pleopod in the male possesses an appendix masculina, while that of the female possesses a smaller appendix interna.

Genus *Callianopsis* de
Saint Laurent, 1973

Diagnosis.—Carapace with dorsal oval, cardiac prominence on dorsal carapace, low rostral carina, rostral spine, major cheliped with proximal meral hook, acute lateral projections on sixth abdominal somite, and uropodal ex-

Table 1. Measurements (in mm) taken on sixth somite (excluding lateral spine) of *Callianopsis goniophthalma* (Rathbun).

USNM Number	Length	Width	Sex
28354	8.8	8.8	Male
31864	6.5	6.2	Female
31862	3.1	3.0	Female
31867	5.2	5.2	Female

opod lacking lateral notch or incision (Manning and Felder, 1991).

Callianopsis goniophthalma
(Rathbun, 1902) (Figs. 1–4)

Callianassa goniophthalma Rathbun, 1902, p. 886; Rathbun, 1904, p. 154, pl. 8.

Callianopsis goniophthalma (Rathbun) de Saint Laurent, 1973, p. 515; Hart, 1982, p. 54, fig. 13; Manning and Felder, 1991, p. 789, figs. 7, 18.

Material examined.—Holotype ♂ (USNM 25238), collected off Point Conception, California, depth 278 fathoms (508 m); 1 ♂ (USNM 28354), collected at Clarence Strait, Alaska, depth 322 fathoms (589 m); 2 ♂♂ (USNM 31864), North Pacific Ocean, depth 300–313 fathoms (549–572 m); 1 ♀ (USNM 123363), collected at San Pablo Point, San Cristobal Bay, Baja California, Mexico (27°07'08"N, 114°33'10"W), depth 284 fathoms (519 m); 1 ♀ (USNM 31867), Yes Bay, Cleveland Peninsula, west side of Behm Canal, northwest of Ketchikan, Alaska, depth 229–234 fathoms (419–508 m); 1 ♀ (USNM 31862), Yes Bay, Behm Canal, depth 192–198 fathoms (351–362 m).

Remarks.—Rathbun (1902: 886) named *Callianassa goniophthalma*, now assigned to *Callianopsis*, based on specimens collected off Point Conception, California, and Clarence Strait, Alaska. At that time, she provided a very brief description of *C. goniophthalma* (Rathbun, 1902). In 1904, Rathbun provided a more complete description and noted differences in the first and second pleopods in males and females of the species. The first pleopod in the male of the species (Fig. 1J) is scythe-shaped and the second pleopod (Fig. 1K) possesses an ovate exopod that is longer than wide and a longer than wide obovate endopod that possesses a bifurcate appendix interna. One of the portions of the appendix interna is very long with short terminal hairs, while the other portion is short and stubby; presumably the long, narrow portion of the appendix interna of the second pleopod is the appendix masculina. The first

Table 2. Measurements (in mm) taken on the telson of *Callianopsis goniophthalma* (Rathbun).

USNM Number	Length	Width	Sex
28354	7.7	8.2	Male
31862	3.0	2.6	Female
31864	6.5	6.0	Female
31867	5.8	5.3	Female

pleopod of the female (Fig. 2M) has an oblong base with a long, thin, curled or hooked setose projection that extends distally from near the tip of the base of the pleopod. The tip of the pleopod bears long setal hairs. The second pleopod (Fig. 2N) possesses an obovate exopod. The endopod is broadly obovate and possesses a flap at the base that projects proximally and narrows distally. The appendix interna is located at the distalmost end of this flap. The base of the second pleopod is setose.

Rathbun (1904) did not, however, discuss morphological differences between males and females in the morphology of the major cheliped, the shape of the abdominal somites, and the overall size of the animals (Figs. 3A, B, 4A, B). Hart (1982) noted that the major chela of the male had a gap between the fingers that was not present in the female. The first abdominal somite in both sexes is nearly equidimensional and wider anteriorly than posteriorly. The second somite is about twice as long as wide and widens distally; the second somites are comparable in both sexes. The shapes of the third, fourth, and fifth somites differ slightly between the sexes. Each somite is wider than long and widens into rounded projections at the distal corners that overlap the next somite; however, in the male, the projections curve distally more sharply and the lateral margins of the somites curve distally more sharply than in the female. The projections are also somewhat longer and narrower in the male than in the female. The sixth somite of the male (Fig. 1M) and that of the female (Fig. 2P) are similar; they are approximately equidimensional in both sexes, and both bear lateral spinelike projections (Table 1). The telson in the male (Fig. 1M) is slightly wider than long, while in the female (Fig. 2P) it is slightly longer than wide (Table 2). The shape and size of the uropods appear to be similar in both the male and female (Figs. 1M, 2P).

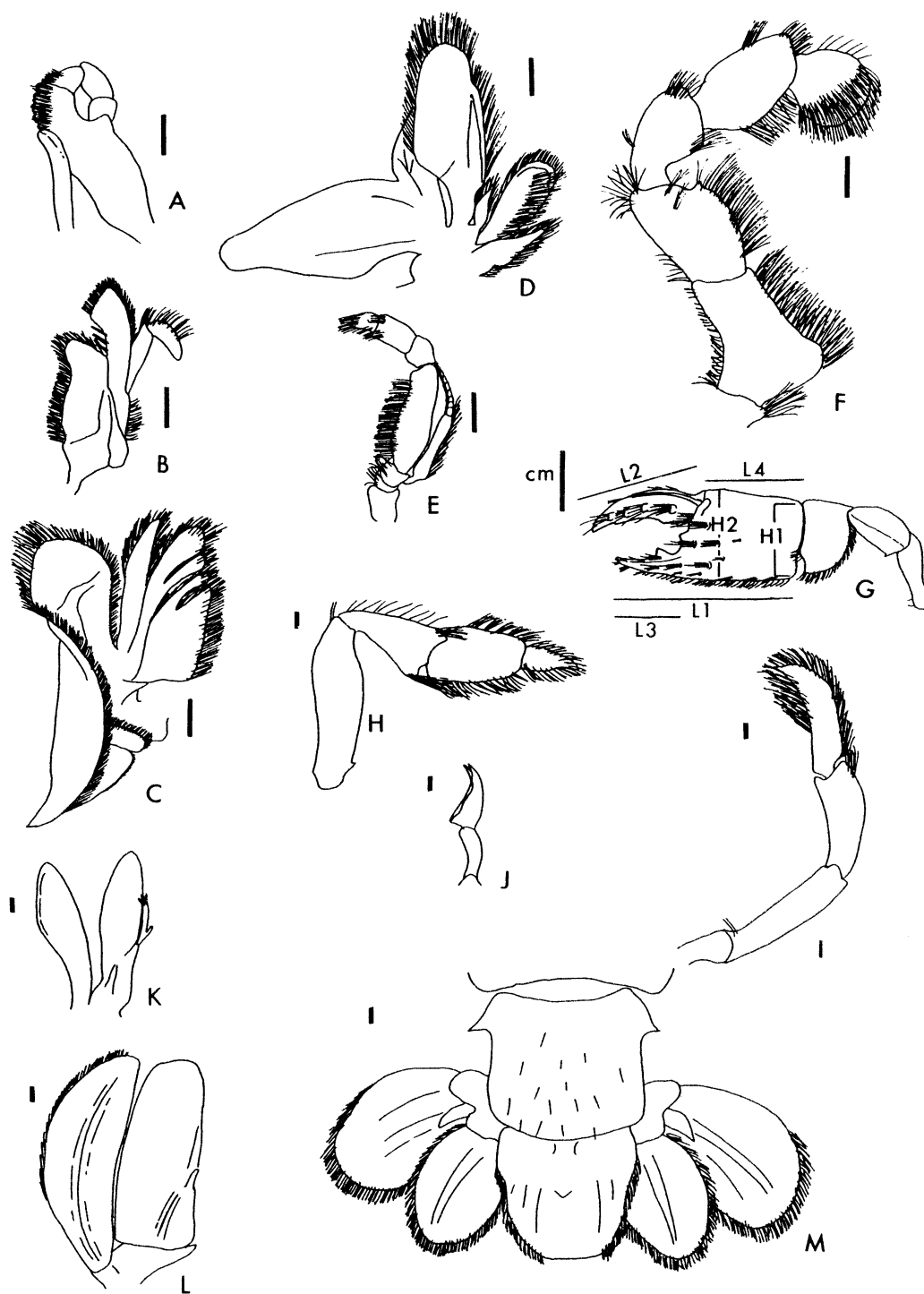


Fig. 1. *Callianopsis goniophthalma* (Rathbun). A, mandible, outer surface; B, maxilla 1, outer surface; C, maxilla 2, outer surface; D, maxilliped 1, outer surface; E, maxilliped 2, outer surface; F, maxilliped 3, outer surface; G, major cheliped; H, pereiopod 3, outer surface; I, pereiopod 5, outer surface; J, pleopod 1, outer surface; K, pleopod 2, outer surface; L, pleopods 3-5, outer surface; M, abdominal somite 6, telson, and uropods, dorsal view. Male, USNM 28354. Axes along which linear measurements on chelae were taken are indicated in G. Scale bars = 1 mm, except that for G.

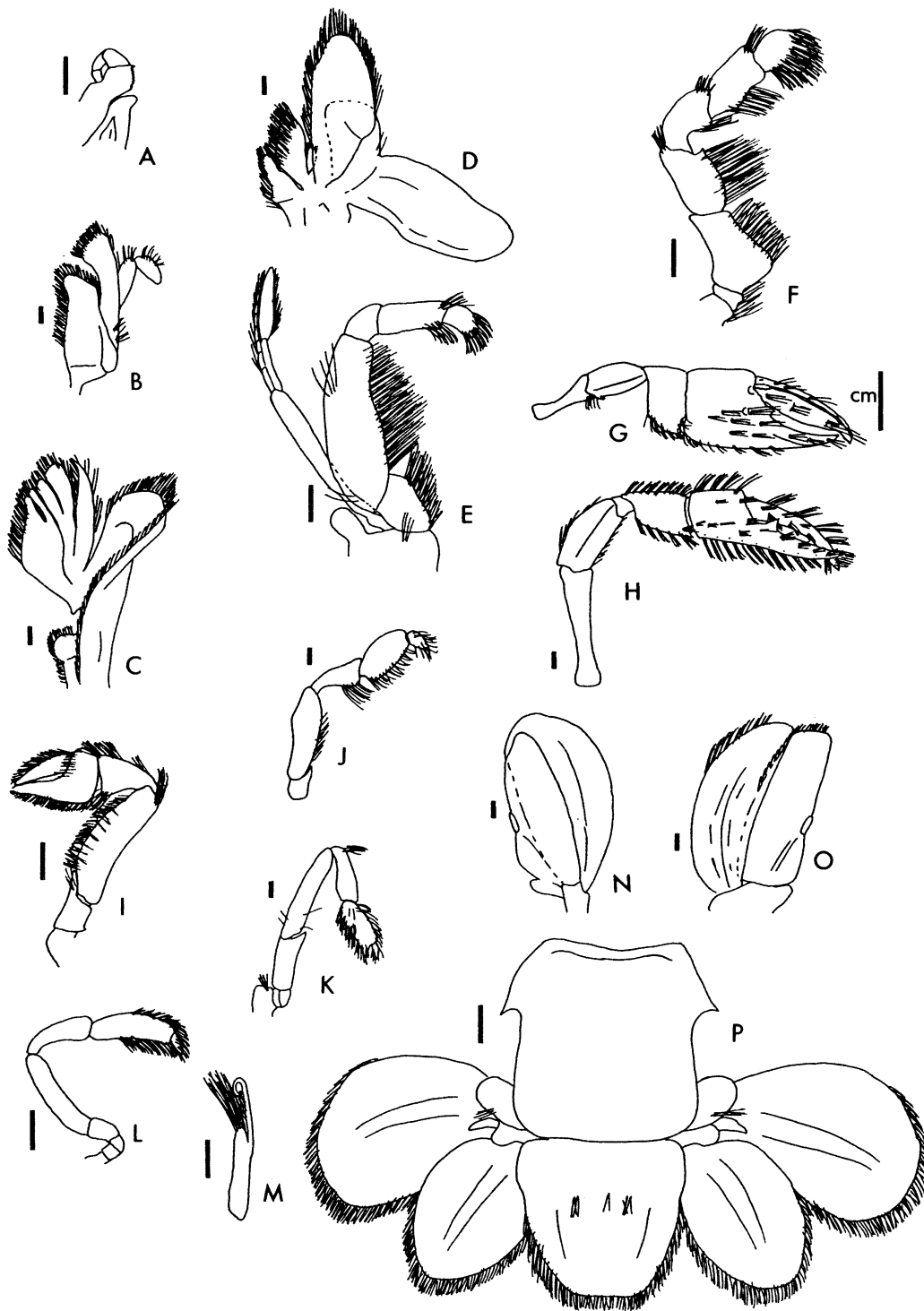


Fig. 2. *Callianopsis goniophthalma* (Rathbun). A, mandible, outer surface; B, maxilla 1, outer surface; C, maxilla 2, outer surface; D, maxilliped 1, outer surface; E, maxilliped 2, outer surface; F, maxilliped 3, outer surface; G, major cheliped; H, minor cheliped; I, pereiopod 2, outer surface; J, pereiopod 3, outer surface; K, pereiopod 4, outer surface; L, pereiopod 5, outer surface; M, pleopod 1, outer surface; N, pleopod 2, outer surface; O, pleopods 3-5, outer surface; P, abdominal somite 6, telson, and uropods, dorsal view. A, F, H, I, J, K, M, P, female, USNM 31867. B, C, D, E, N, O, female, USNM 31864. G, female, USNM 123363. L, female, USNM 31862. Scale bars = 1 mm, except that for G.



Fig. 3. *Callianopsis goniophthalma* (Rathbun). A, adult male (USNM 28354), dorsal view; B, adult female (USNM 31867), dorsal view. Scale bar = 1 cm.

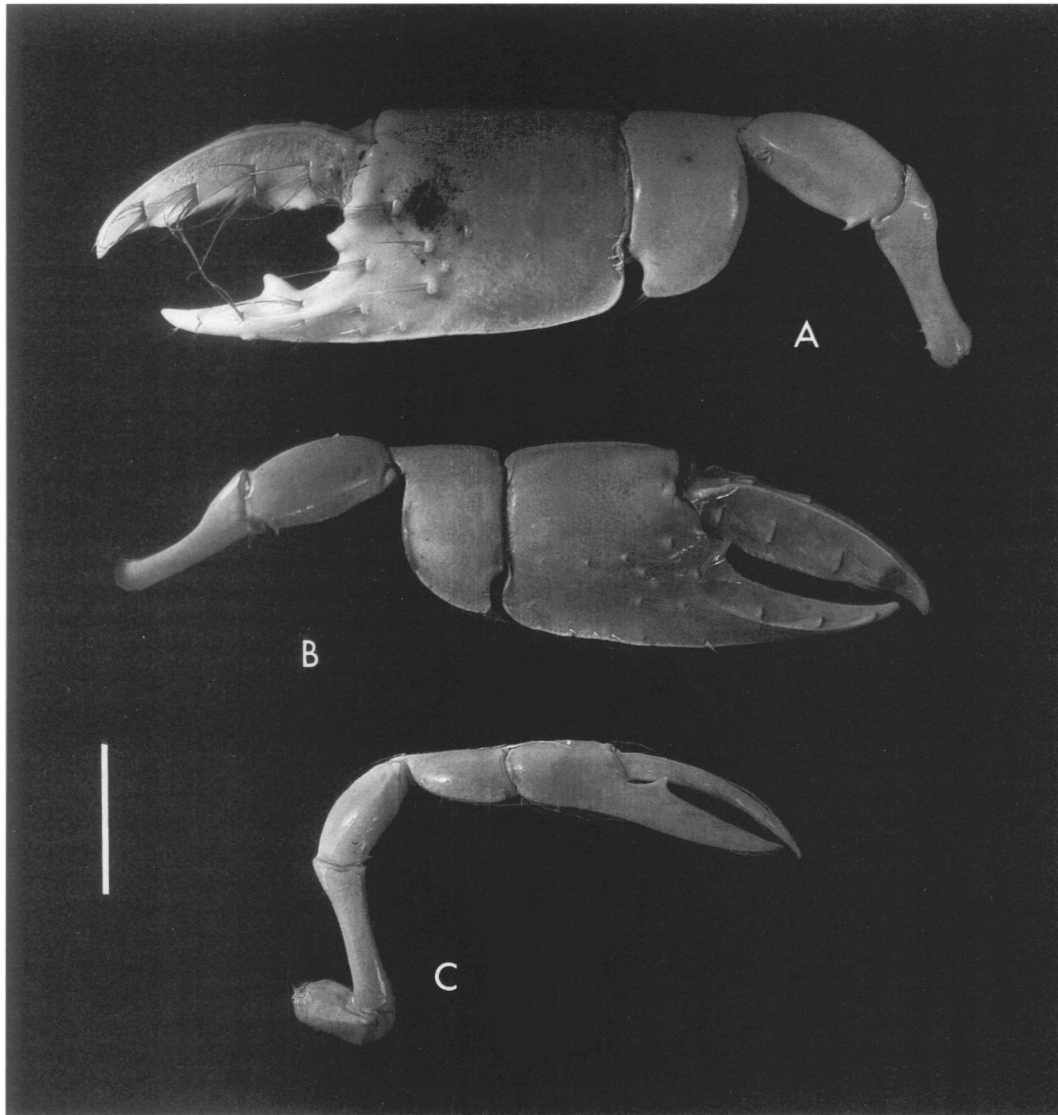


Fig. 4. *Callianopsis goniophthalma* (Rathbun). A, outer surface of major cheliped of male (USNM 28354); B, outer surface of major cheliped of female (USNM 31867); C, outer surface of minor cheliped of indeterminate sex (USNM 31864). Scale bar = 1 cm.

There may be an overall adult size difference between males and females. In four specimens studied, one was definitively identified as a male (USNM 28354) and one as a female (USNM 31867). One specimen was identified as a female based solely on the second pleopods (USNM 31864); it lacks the first pleopods. Another specimen was determined to be a juvenile female (USNM 31862). In the three females, the overall body

length, measured from the tip of the rostrum to the tip of the telson, is less than in the male specimen (Table 3).

The major differences between males and females lie in the nature of the major chelae. The two sexes are similar in other segments of the chelipeds; the ischium, carpus, and merus of each is similar, but the chelae are quite different (Table 4). In the male (Figs. 1G, 4A) the overall shape of the manus is

Table 3. Measurements (in mm) taken on the entire body length of *Callianopsis goniophthalma* (Rathbun), measured from the tip of the rostrum to the tip of the telson.

Specimen number	Sex	Length
28354	male	78.9
31862	female	±27
31867	female	53.2
31864	female	62.1

longer than high, while in the female (Figs. 2G, 4B) the manus is about equidimensional. The manus of the male is more stout than in the female. In the male, the upper margin is thick and rounded, and the lower margin is narrower and very thin on the edge. In the female, the upper and lower margins of the manus are thin, especially on the lower margin, and the lower margin of both sexes possesses a row of setal pits. The sexes differ in the nature of the distal margin of the manus. The male possesses a distal margin that extends slightly obliquely from the upper to lower margin. In the female, the distal margin initially extends nearly perpendicular to the upper margin and then continues at about a 45 degree angle to its articulation with the fixed finger. The distal margin of the male possesses an inflated ridge along the articulation with the base of the movable finger and a sharp tooth below the inflated ridge. The female lacks the inflated ridge and possesses a sharp triangular tooth in the notch between the two fingers. The female possesses a few more tubercles than the male on the outer surface of the manus, but this also varies between individuals and may not be a useful character in differentiating the two sexes. The inner surface of the manus of the male has an inflated ridge paralleling the distal margin, extending along the articulation with the movable finger. The bulbous area contains a scattering of small tubercles. In the female, the inflated ridge is less pronounced and possesses a linear arrangement of very small tubercles paralleling the distal margin.

The two sexes differ in several aspects of the fixed finger. The fixed finger of the female is widely triangular from upper to lower margin with a peaked ridge extending along the length of the finger. Three tubercles are situated on the upper portion of the ridge, and the finger is thin from inner to outer surface. The fixed finger of the male is narrower from upper to lower margin and possesses a rounded

Table 4. Measurements (in mm) taken on the major chela of *Callianopsis goniophthalma* (Rathbun).

USNM Number	Sex	H2	L1	L2	L3	Handedness
31864A	Male	16.6	31.0	22.6	13.5	Left
31864B	Male	12.1	22.6	16.3	9.3	Left
28354	Male	14.7	29.5	19.7	11.8	Left
123363	Female	12.3	25.5	18.9	12.0	Right
31867	Female	8.3	16.0	11.2	7.7	Left
31862	Female	3.5	6.9	4.5	3.0	Left

tooth positioned just proximal to the center of the finger. The finger possesses a ridge extending along its length and a row of setose tubercles along the upper and lower edge of the ridge. The finger of the male is wider than the fixed finger of the female. The inner surface of the fixed finger of the male possesses a ridge extending from the base of the finger and terminating just under the position of the central tooth. In the female that ridge extends from the base to the tip of the finger.

The male and female differ in the nature of the movable finger as well. In the male, the finger is markedly arched from proximal to distal end, while in the female it is straighter. Each possesses a ridge that begins in a row of tubercles at the proximal end and extends to the tip of the finger. The tubercles at the beginning of the ridge are much larger and more pronounced in the male. Each possesses a row of setal pits below the ridge. The lower margin of the movable finger differs between the male and the female. In the male, there is a minutely toothed projection near the base of the movable finger, and another small toothed ridge about three-fourths of the distance to the tip of the finger. In the female, a serrated ridge extends from near the base of the movable finger to about three-quarters of the length of the finger. The movable finger of the male is more stout than that of the female. The upper surface of the movable finger is similar in both sexes. Each possesses a short ridge with two setose pits paralleling the outer edge of the upper surface, and each possesses a row of about five setose tubercles paralleling the inner edge. The inner surface of the movable finger differs between the male and female. The female possesses a sharp ridge extending from the base of the finger to about the midlength of the finger; the ridge becomes progressively weaker along its length until it disappears at the midlength. A

few small tubercles are situated at the base of the finger where the ridge originates. In the male, the ridge is much more pronounced and extends almost to the tip of the finger; it possesses about six large tubercles at the base of the ridge. In addition, the ridge itself is composed of numerous small tubercles for about one-third of its length.

Remarks on Habitat.—Little is known about the habitat of *Callianopsis goniophthalma*. As mentioned, it has been collected from slope depths of 480–650 m (Manning and Felder, 1991). Hart (1982) reported that it inhabits deep waters, probably in burrows.

Callianopsis clallamensis
(Withers, 1924), new combination
(Figs. 5–7)

Callianassa clallamensis Withers, 1924, p. 122, pl. 4, figs. 4–7; Rathbun, 1926, p. 114, pl. 26, figs. 6–12; Berglund and Goedert, 1992, pp. 2–3.

Callianassa twinensis Rathbun, 1926, p. 115, pl. 27, figs. 1–4; Berglund and Goedert, 1992, pp. 2–3.

Material Examined.—Fifty-seven ♂♂, including USNM 490197–490212, collected from site RB18, West Twin Shale Quarry, located in W, Sec. 23, T31N, R10W of Twin Rivers Quadrangle, 7.5' series, Clallam County, Washington. Two ♂♂ (USNM 490226, 490227) collected from site RB38, mouth of Joe Creek, located in NE, SE, Sec. 13, T31N R11W of Pysht Quadrangle, 7.5' series, Clallam County, Washington. Thirty ♀♀, including USNM 490213–490223, collected from RB18 locality. Two ♀♀ (USNM 490228, 490229) collected from site RB19, mouth of Jansen Creek, located in SE, SE, Sec. 26, T33N, R14W of Clallam Bay Quadrangle, 15' series, Clallam County, Washington. Two individuals of indeterminate sex (USNM 490224, 490225) collected from RB18 locality.

Emended Description.—Dorsal carapace longer than wide; rostral spine broken, antennules fairly stout at base, rest of front not well known; dorsal oval extending about half length of carapace; low ridge beginning at center of distal half of carapace and extending posteriorly, ridge terminating in cardiac prominence; lateral margin rimmed, slightly convex; distal margin slightly concave. Abdominal somite 1 short, proximal edge rounded, convex, concave and widening posteriorly, extending relatively straight along distal margin. Somite 2 very long; proximal margin convex; lateral margin slightly sinuous, concave centrally, rimmed; distal margin rounded and convex, rounded projection on

each corner, slightly concave centrally. Somite 3 short; proximal margin convex; lateral margin straight; distal margin slightly concave and slightly sinuous. Somite 4 short; proximal margin somewhat convex; lateral margin straight, rounded corners; distal margin slightly concave with rounded projections on each corner. Somite 5 wider than 4; margins not well known. Somite 6 not well known, narrowest of all somites. Telson not well known.

Meri of pereopods much longer than wide, upper and lower margins sinuous, upper margin convex proximally and concave distally; lower margin concave proximally and convex distally, in some with row of tubercles along lower margin; ischia short, rectangular, proximal margin extending obliquely, upper margin straight, distal margin with narrow, spine-like projection at lower corner, spine extending along lower margin of merus for short distance.

Ischium of major cheliped much longer than high, widest at articulation with merus, thinning proximally, proximal margin unknown.

Merus of major cheliped longer than high, subelliptical, narrowest at distal end, outer surface extremely convex; bearing prominent longitudinal keel positioned just below mid-width, sharper and more pronounced near distal end; proximal margin strongly convex at articulation with ischium, point of maximum convexity at intersection with keel margin; upper margin convex proximally and flattening distally; lower margin convex, very small spine on proximal lower corner directed obliquely from margin; distal margin poorly known.

Carpus of major cheliped higher than long, outer surface convex; proximal margin sinuous, bearing triangular, toothlike projection at articulation with merus, concave just below projection, convex to lower corner; upper margin relatively straight; lower margin convex forward and downward, terminating in sharp corner at intersection with distal margin; distal margin concave, bearing small toothlike projection at lower articulation with manus, margin concave below toothlike articulation, intersecting lower margin at sharp corner; 2 or 3 tubercles along lower portion of distal margin.

Manus of major cheliped of female ranging from somewhat longer than high to some-

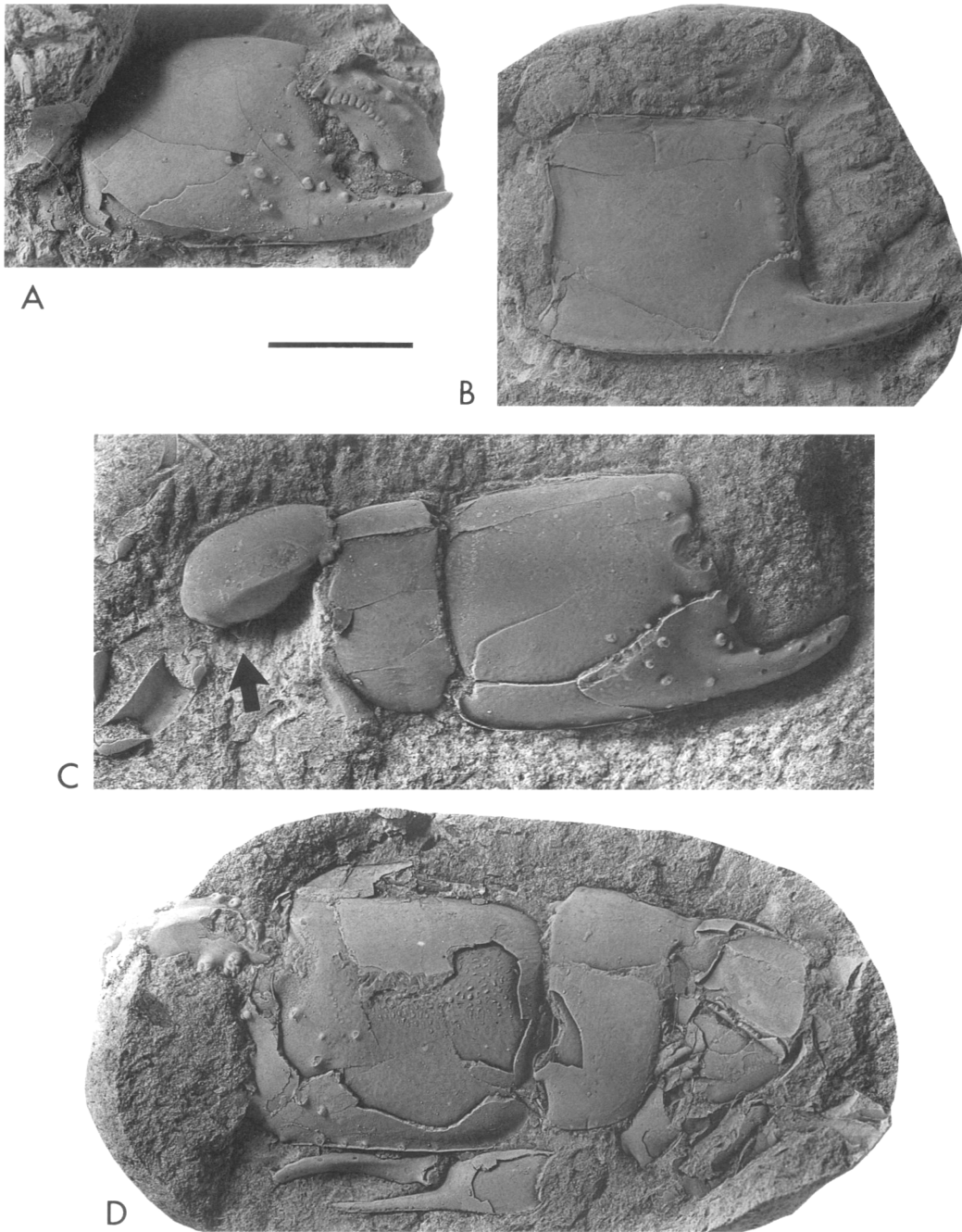


Fig. 5. *Callianopsis clallamensis* (Withers), male specimens. A, outer surface of major chela, USNM 490209; B, inner surface of major cheliped, USNM 490204; C, outer surface of merus, carpus, and chela of major cheliped, USNM 490197, arrow indicating meral spine; D, outer surface of carpus and chela of major cheliped and inner surface of minor chela, USNM 490198. Scale bar = 1 cm.

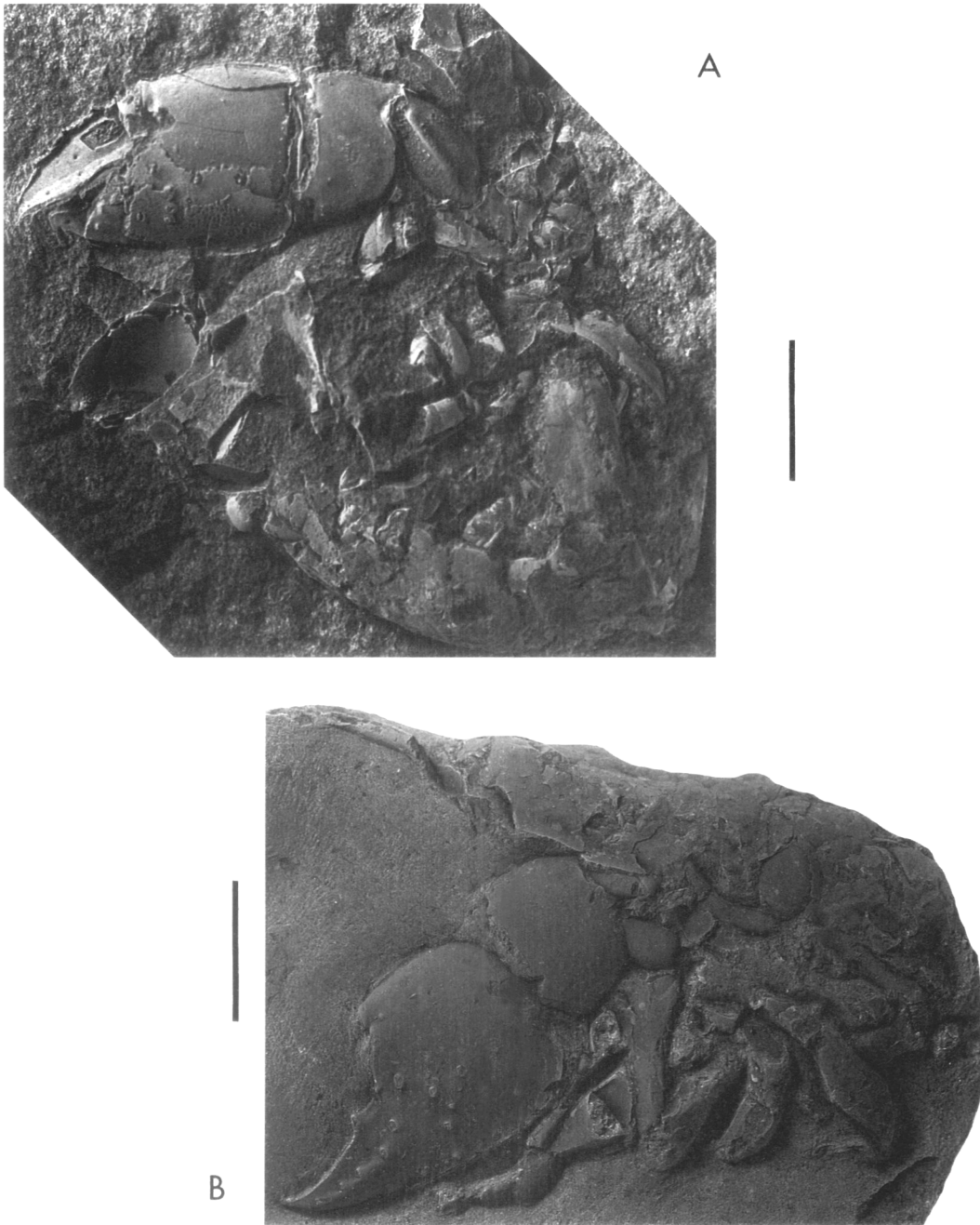


Fig. 6. *Callianopsis clallamensis* (Withers), female specimens. A, outer surface of merus, carpus, and chela of major cheliped and portions of abdomen, USNM 490228; B, dorsal carapace, appendage segments, and outer surface of major chela, USNM 490213. Scale bars = 1 cm.

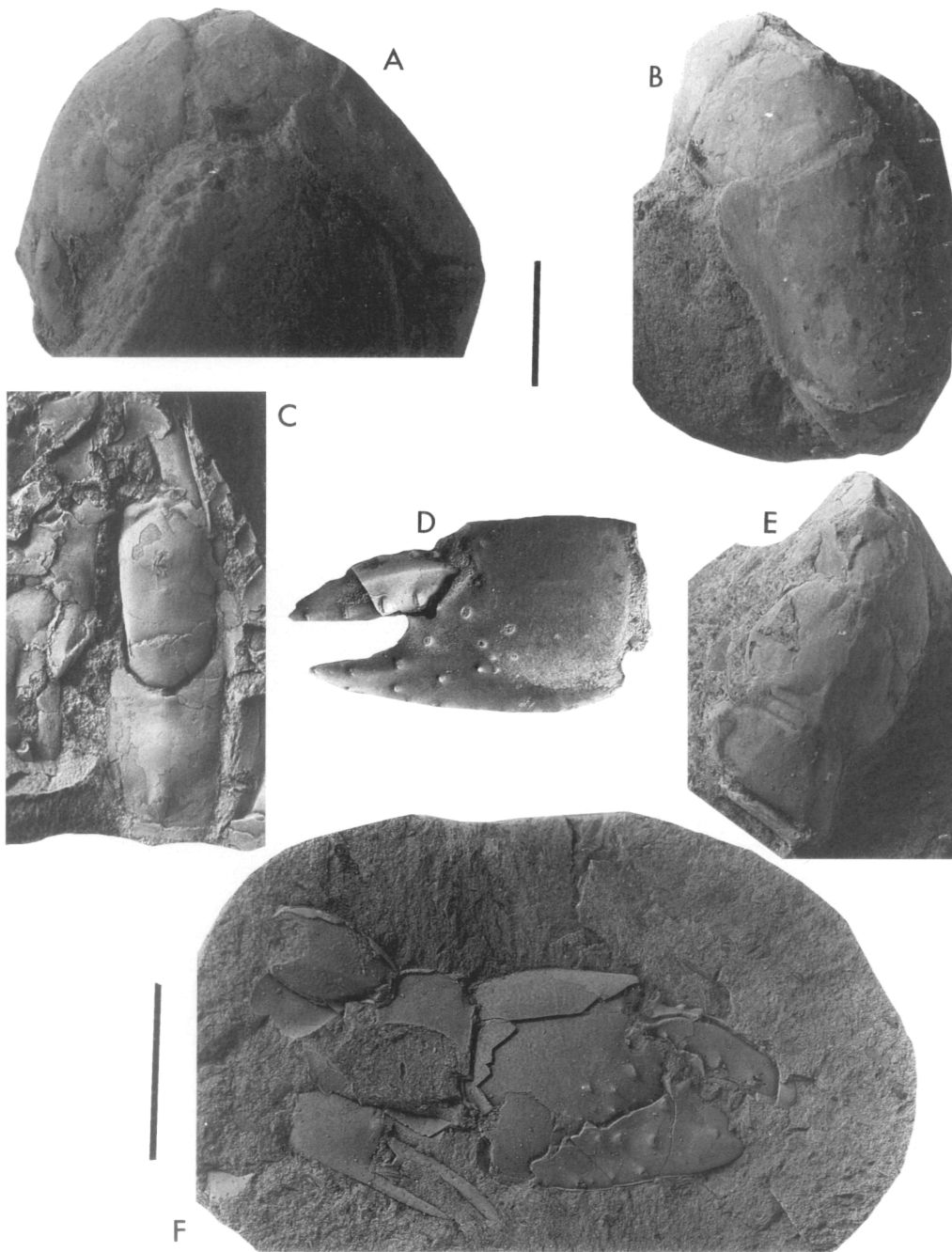


Fig. 7. *Callianopsis clallamensis* (Withers). A, lateral view of abdominal somites 1–6, unknown sex, USNM 490225; B, oblique proximal view of abdominal somites 1–3, unknown sex, USNM 490225; C, dorsal carapace showing dorsal oval and cardiac prominence, unknown sex, USNM 490224; D, outer surface of major chela of female, USNM 490220; E, oblique distal view of abdominal somites 4–6, unknown sex, USNM 490225; F, outer surface of major chela and inner surface of minor chela of female, USNM 490217. Scale bars = 1 cm. Upper scale bar for 7A–E. Lower scale bar for 7F.

what higher than long, narrowing slightly posteriorly; proximal margin slightly sinuous, rimmed, rounded articulations with carpus on upper and lower corners of margin; outer surface of manus convex but flattening near fixed finger; 6–9 tubercles located near propodus with setal pits directed distally; distal margin oblique to lower margin, originating perpendicular to upper margin near articulation with dactylus and curving to meet fixed finger at about 45 degree angle, tooth and notch located just above propodus; upper margin rounded, rimmed; lower margin thinner, rimmed, row of 5 or 6 setal tubercles paralleling lower margin and extending onto fixed finger; inner surface relatively smooth with few tubercles near articulation with dactylus.

Fixed finger thin, triangular in shape, bearing row of about 4 tubercles on low ridge on outer surface with setal pits directed forward, 2 or 3 tubercles situated beneath ridge of tubercles; inner surface with few tubercles with setal pits directed forward, small ridge paralleling occlusal surface situated about three-fourths distance from lower margin.

Dactylus stouter than fixed finger, bearing row of 3 or 4 tubercles with setal pits directed distally paralleling occlusal surface, smooth ridge paralleling these extending along mid-width, 2 rows of tubercles with setal pits directed forward on upper margin, inner surface with smooth ridges paralleling lower and upper margins, sometimes with short row of tubercles between 2 ridges.

Manus of major cheliped of male nearly square, longer than high, outer surface convex; proximal margin fairly straight with slight protuberances near lower margin at articulation with carpus; upper margin straight; lower margin rimmed, slightly convex, row of small tubercles paralleling it extending onto fixed finger; 7–9 large tubercles on manus near fixed finger with setal pits directed distally; 1 tubercle sometimes present near articulation with dactylus; distal margin extending slightly obliquely from upper to lower margin, bearing bulbous elongate protuberance near articulation with dactylus, 2 tubercles or denticles positioned just below elongate protuberance; inner surface smooth, flattened, few tubercles near base of both fingers, several closely spaced tubercles positioned longitudinally on bulbous area paralleling inner distal margin, row of small tubercles paralleling lower inner margin.

Table 5. Measurements (in mm) taken on the major chela of female *Callianopsis clallamensis* (Withers).

USNM Number	L1	L2	L3	L4	H1	H2
490229	>21.5	>10.8	8.4	12.7	13.5	14.7
490213	22.0	—	9.8	>8.6	—	9.6
490219	16.3	—	5.7	—	—	>9.6
490218	21.5	>11.5	9.4	10.6	11.5	>12.0
490220	22.8	>12.3	9.0	12.3	13.1	14.3
490215	22.6	—	8.9	—	—	>13.9
490228	>16.6	>11.3	>5.3	11.8	11.3	13.3
490223	25.0	—	10.6	14.3	15.3	>17.0
490222	>21.3	15.3	—	13.4	14.4	15.7
490216	20.0	11.4	9.0	—	—	12.2
490221	—	—	—	11.3	12.1	14.4

Fixed finger with row of 3 or 4 small tubercles with setal pits directed forward paralleling upper margin; blunt tooth midway on occlusal surface; inner surface with row of setal pits paralleling lower margin; several setal pits scattered on inner surface.

Dactylus stout, triangular in cross section, heavily ornamented; bearing ridge on outer margin with 4–12 closely spaced tubercles, tubercles ending about halfway down length of ridge; 2 rows of widely spaced tubercles situated on upper margin with setal pits directed distally; occlusal surface ornamented with several large tubercles containing setal pits directed distally; inner surface with several tubercles near base of dactylus.

Minor chela much smaller than major chela; manus longer than high; fixed finger long, narrow; dactylus long, narrow, incurved; significant gape centrally, fingers meeting distally; fixed finger with row of setal pits on inner surface extending onto manus; dactylus with row of setal pits on inner surface; outer surface unknown.

Measurements.—Measurements taken on the major chela of female specimens are presented in Table 5, and of male specimens in Table 6. Measurements taken on the minor chelae of female and male specimens are presented in Tables 7, 8, respectively. Measurements taken on the meri and carpi of the major cheliped of females and males are presented in Tables 9, 10, respectively. Measurements taken on the meri of pereopods of a male specimen are presented in Table 11.

Localities and Stratigraphic Position.—The RB19 locality is located in the Jansen Creek Member of the late Eocene to Oligocene

Table 6. Measurements (in mm) taken on the major chelae of male *Callianopsis clallamensis* (Withers).

USNM Number	L1	L2	L3	L4	H1	H2
490203	27.9	>12.4	>6.9	20.6	18.8	20.0
490210	>32.3	>18.4	>7.6	25.0	18.8	22.7
490211	>27.1	>14.0	>4.8	17.8	—	17.2
490202	23.2	—	—	16.2	14.7	16.2
490201	34.6	—	12.0	21.8	17.1	19.4
490197	27.7	—	8.7	17.0	15.6	17.3
490209	25.1	13.3	8.1	—	—	14.5
490198	—	—	—	18.8	17.4	19.0
490208	29.6	—	9.7	17.7	—	17.2
490206	29.4	—	—	17.7	15.4	18.0
490199	—	16.3	9.4	—	—	—
490205	>30.3	9.3	15.8	19.4	16.0	18.4
490212	>24.6	—	—	—	—	—
490204	27.3	—	—	16.6	—	16.3
490227	13.0	—	3.7	8.7	7.2	8.3
490226	>31.3	—	10.3	>17.2	—	15.8
490207	33.5	—	—	21.9	17.1	19.2

Table 7. Measurements (in mm) taken on the minor chelae of female *Callianopsis clallamensis* (Withers).

USNM Number	L1	L2	L3	L4	H2
490217	>12.0	5.7	5.6	9.3	5.0
490214	>9.7	5.5	5.6	8.5	>4.4

Table 8. Measurements (in mm) taken on the minor chelae of male *Callianopsis clallamensis* (Withers).

USNM Number	L1	L2	L3	L4	H2
490198	16.5	7.0	7.5	11.9	4.9
490207	18.4	—	8.4	11.1	5.7

Table 9. Measurements (in mm) taken on the merus and carpus of the major cheliped of female *Callianopsis clallamensis* (Withers). H = maximum height; L = maximum length.

USNM Number	L-carpus	H-carpus	L-merus	H-merus
490213	>11.6	>7.5	—	—
490218	11.0	6.4	—	—
490228	11.0	6.6	9.4	5.1
490214	12.6	6.2	—	—
490217	—	—	9.4	5.9

Table 10. Measurements (in mm) taken on the merus and carpus of the major cheliped of male *Callianopsis clallamensis* (Withers). H = maximum height; L = maximum length.

USNM Number	H-carpus	L-carpus	H-merus	L-merus
490200	12.8	8.5	—	10.5
490211	10.5	17.8	—	—
490202	14.3	7.3	—	10.2
490198	17.7	10.6	—	—
490197	14.9	>7.5	7.5	12.4
490199	—	—	8.5	13.4
490207	18.1	10.3	6.9	12.1

Table 11. Measurements taken on the meri of pereopods of *Callianopsis clallamensis* (Withers). L = maximum length; W = maximum width.

USNM 490206	L	W
Third pereopod	13.5	4.8
Second pereopod	>11.9	3.9

Makah Formation. The Makah Formation is believed to have been deposited in a deep marginal basin (Snaveley *et al.*, 1980), at depths from 300–1,830 m (Rau, 1964). The Jansen Creek Member lies near the middle of the Makah Formation and is believed to be late Eocene in age based upon mollusc and foraminifera assemblages (Snaveley *et al.*, 1980). It is overlain by beds that are Oligocene in age (Snaveley *et al.*, 1978). The Jansen Creek Member is believed to be an allochthonous unit resulting from erosion of uplifted, older rocks that bordered the deep marginal basin where the Makah Formation was being deposited (Snaveley *et al.*, 1980). Most of the decapods of the Makah Formation have been collected from the Jansen Creek Member (Feldmann *et al.*, 1991).

Both the RB18 and RB38 localities are located in the upper Oligocene to lower Miocene Pysht Formation, which is estimated to be 1,100–1,400 m thick (Snaveley *et al.*, 1978). Age estimates for the Pysht Formation have been determined using foraminifera (Rau, 1964; Snaveley, 1983) and molluscs (Addicott, 1976). The Pysht Formation overlies the Makah Formation, and has been interpreted to have been initially deposited in a deep marginal basin, 300–1,830 m, that subsequently shallowed near the top of the formation (Rau, 1964; Addicott, 1976).

Remarks.—The fossil material may be referred to *Callianopsis* based on several criteria. The overall shape of the abdominal somites is similar in the fossil specimens to those of extant *Callianopsis*; unfortunately, the sixth somite is poorly preserved in the fossils, so that the sharp lateral spine on that somite could not be observed. The dorsal carapace of the fossil material exhibits a dorsal oval and cardiac prominence that are diagnostic of the genus *Callianopsis* (Manning and Felder, 1991). In addition, Karasawa (1993) reported fossil specimens of *Callianopsis* that possessed a dorsal oval; these specimens displayed major cheliped mor-

phology very similar to the fossil specimens recovered from Washington.

The major chelipeds possess several characteristics that permit referral of the fossil specimens to the genus *Callianopsis*. The merus of the major cheliped of *Callianopsis* possesses a small distal spine located on the lower margin (Figs. 1G, 2G); this spine was observed in male specimens of *Callianopsis clallamensis* (Fig. 5C). In addition, the merus possesses a longitudinal ridge extending from the distal margin approximately three-quarters of the distance along the length of the merus (Figs. 5C, 6A). The carpus of *Callianopsis* possesses a paddle-like flange on the lower margin, and this flange is seen in specimens of both sexes of *Callianopsis clallamensis*. The carpus of *Callianopsis* also possesses a blunt triangular extension on the upper proximal margin, where it articulates with the merus. This character is seen in the fossil specimens.

Several aspects of the chelae of the fossil specimens are comparable to characters ascribed to the genus *Callianopsis*. In addition, these characters exhibit obvious dimorphism that parallels the differences between males and females in the sole extant species of *Callianopsis*. In male specimens of *Callianopsis goniophthalma* (Figs. 1G, 4A) and fossil specimens originally attributed to *Callianassa clallamensis* (Fig. 5), the major chela is nearly square and wide, especially on the upper margin. Both species possess a triangular tooth on the distal margin in the notch between the two fingers and another positioned about one-half of the way along the fixed finger. Each possesses large setal tubercles on the outer surface of the manus and an inflated ridge paralleling the distal margin at the articulation of the movable finger with the manus. Each possesses a row of small setal pits paralleling the lower margin and a similar arrangement of setal tubercles on the fixed finger. The distal margin of each extends slightly obliquely from the upper to lower margin. The inner margin of the manus in both possesses an inflated ridge extending along the distal margin that possesses a scattering of small tubercles. The movable finger of each exhibits a ridge extending along the upper part of the outer surface; the ridges are initially composed of closely spaced tubercles. The movable finger of each is arcuate, and possesses a row of setal pits along

Table 12. Tabulation of handedness in both sexes of *Callianopsis clallamensis* (Rathbun). The sex of approximately 98 individuals could not be determined.

Sex	Right	Left	R/L ratio	Handedness undetermined
Male	30	28	1.07	0
Female	22	9	2.44	1

the outer surface and two rows of setal pits on the upper surface. Minor differences include a stronger ridge on the fixed finger in the Recent male specimens, and larger tubercles on the manus and movable finger in the fossil specimens.

In female specimens of *Callianopsis goniophthalma* (Figs. 2G, 4B) and fossil specimens originally referred to *Callianassa twinensis* (Figs. 6, 7), the manus is nearly equidimensional and is thin, especially along the lower margin. Both species possess a distal margin that first extends perpendicular to the upper margin and then extends at about a 45 degree angle until it meets the movable finger; the distal margin also has a sharp, triangular tooth positioned between the two fingers. The fossil specimens possess a shallow sulcus just proximal to the sharp tooth. Each exhibits a sharp ridge extending along the fixed finger that also possesses a row of setal tubercles positioned above and paralleling it. Each has a row of small setal tubercles paralleling the lower margin and an arrangement of tubercles on the manus. The movable finger of each possesses a ridge extending along the entire length of the finger, and in both the Recent and fossil species, the ridge initiates in several closely spaced tubercles. Both have a similar arrangement of setal pits on the movable finger, but the fossil specimens appear to lack the serrate ridge evident in the Recent specimens. Female specimens of *Callianopsis clallamensis* exhibit a definite tendency for the major chela to be on the right first pereiopod (Table 12). This tendency is not seen in Recent specimens; however, it should be noted that there are many more fossil specimens than Recent specimens, and that the fossils may represent a more accurate sample of handedness in the females of *Callianopsis*.

Because the fossil specimens possess a wide range of characters attributable to the Recent genus *Callianopsis*, they are referred to that genus with confidence. Analysis of

many genera in the families Callianassidae and Ctenochelidae shows that the combination of characters including a small, distal meral spine and a central meral keel, a carpus with a paddle-like flange, major chelae with a tooth on the distal margin and on the fixed finger (in the males only), and unequal major chelipeds is unique to the genus *Callianopsis*. The numerous similarities between the male specimens of *Callianopsis goniophthalma* and fossil specimens originally referable to *Callianassa clallamensis* and, in addition, similarities between the female specimens of *Callianopsis goniophthalma* and fossil specimens originally referable to *Callianassa twinensis* clearly suggest that the two fossil species should be referred to a single species and that they represent sexual dimorphs of that species, *Callianopsis clallamensis* (Withers).

This new material extends the record of the genus *Callianopsis* in North America at least into the Oligocene and perhaps into the late Eocene, with the discovery of female specimens of *Callianopsis clallamensis* in the late Eocene Jansen Creek Member of the Makah Formation. Interestingly, the Oligocene-early Miocene specimens reported in this study are quite similar to the Recent specimens of *Callianopsis* found on the Pacific Coast of North America.

Because of the clear evidence that sexual dimorphs of the genus *Callianopsis* exist, it is possible that Japanese species referred to that genus could also be one of a pair of sexual dimorphs. Reexamination of the Japanese material seems warranted based upon these new findings. It would be interesting to determine exactly how many fossil Japanese species of *Callianopsis* exist, since some could represent sexual dimorphs, and, in addition, to determine whether extant Japanese species of *Callianopsis* exist. In fact, the Japanese species *Callianopsis muratai* (Nagao, 1941), originally assigned to *Callianassa*, was reported to exhibit two varieties (Nagao and Huzioka, 1938). Nagao and Huzioka (1938) figured several specimens, and plate VI (I) no. 7 appears to represent a female, and plate VI (I) no. 10 appears to represent a male of *Callianopsis muratai* (Nagao). Subsequently, in 1941 Nagao erected a new species, *Callianassa elongatodigitata*, for material collected from the same unit as *Callianopsis muratai*. Both of these species

have been reassigned from *Callianassa* to *Callianopsis* (see Kato and Karasawa, 1994). Upon examination of these two species, it appears that Nagao may have assigned males to *C. muratai* and females to *C. elongatodigitata*. In 1941, Nagao named another species, *Callianassa kusiroensis* that he described as being intermediate in form between *Callianopsis muratai* and *Callianopsis elongatodigitata*. It seems probable that *Callianassa kusiroensis* Nagao, 1941, is also referable to the genus *Callianopsis* and may be synonymous with either *C. muratai* or *C. elongatodigitata*. However, reexamination of the type material is necessary to confirm revision of these three taxa. Analysis of other Japanese species of *Callianopsis* could help determine the range of variation in the genus and the diversity of the genus in terms of numbers of species over geologic time.

ACKNOWLEDGEMENTS

We thank Ross E. and Marion Berglund for collecting much of the fossil material and donating it for our study. John and Gloria Cornish and J. Goedert also donated several specimens to the study. Annette B. Tucker and R. A. and Barbara J. Schweitzer assisted in the field. Raymond B. Manning provided specimens of *Callianopsis goniophthalma* from the National Museum of Natural History, Smithsonian Institution, for the study. Manning and Darryl L. Felder read the preliminary draft and made many useful suggestions. This is Contribution 584, Department of Geology, Kent State University, Kent, Ohio, 44242.

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RECEIVED: 20 June 1996.

ACCEPTED: 30 September 1996.

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