COMPARISON OF SOME GENERA AND SPECIES OF BOX CRABS (BRACHYURA: CALAPPIDAE), SOUTHWESTERN NORTH ATLANTIC, WITH DESCRIPTION OF A NEW GENUS AND SPECIES

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ABSTRACT

Five species of calappid crabs from the southwestern Atlantic that belong to the genera Calappa, Cyclozodion new genus, and Paracyclois are analyzed on the basis of morphology, morphometries, geographic, and bathymetric range. Calappa tortugae, new rank, known in the past as C. angusta in the broad sense, is restricted and compared with its eastern Pacific twin species, C. saussurei. Two small species placed in Cyclozodion were until now unrecognized and partly included in Calappa angusta, broad sense. Cyclozodion angustum, a relatively smooth form, is the type species of the new genus, and C. tuberatum, a rough form superficially resembling Calappa tortugae, is described as new. Species of both Paracyclois and the Early Tertiary genus Calappilia in which it was subsumed are reviewed, the former is revalidated, and its only two species, western Atlantic P. atlantis and western Indo-Pacific P. milneedwardsii, are rediagnosed. Diagnoses and discriminations are accompanied by illustrations. Keys to calappid genera in the Western Atlantic, and for identification of Cyclozodion and Paracyclois species are given.

Holthuis (1958) revised five species of West Indian box crabs, Calappa cinerea Holthuis 1958, C. flammea (Herbst 1794), C. nitida Holthuis 1958, C. ocellata Holthuis 1958, and C. sulcata Rathbun 1898, but a species from that region known until now as C. angusta A. Milne Edwards 1880 was not included in his paper because the collection he studied included no representatives of that form. We find that this latter species is not at all well defined, and the purpose of this paper is to clarify its status and that of similar species in related genera.

Samples of decapod crustaceans from exploratory trawling by the Bureau of Commercial Fisheries RV Pelican, U.S. Fish and Wildlife Service RV Combat, National Marine Fisheries Service RV Silver Bay, RV Oregon, and RV Oregon II deposited in the crustacean collection of the National Museum of Natural History (USNM), Smithsonian Institution, contain specimens of a seldom reported calappid crab, Paracyclois atlantis Chace 1939, 1940 from the Caribbean region of the western North Atlantic, and representatives of a genus not previously recognized. Two small calappid species in the catalogued USNM crustacean collection have been attributed to Calappa angusta A. Milne Edwards 1880 by Rathbun (1937) and other authors (see Williams 1984) on the basis of what were thought to be juvenile characters exhibited by the carapace of that species. Review of the material in the USNM shows this concept to be in error. Moreover, representatives of the extant type series of C. angusta in the Museum of Comparative Zoology (MCZ), Harvard University, consist of very small juveniles, a holotype and four paratypes in which definitive characters are poorly developed, that surprisingly belong not to one but three calappid species. “Calappa angusta” as presently understood is in reality a complex of species belonging in Calappa Weber 1895 and the previously unrecognized genus.

Only two species of Paracyclois Miers 1886 have been described, the above mentioned, and the type species, P. milneedwardsii Miers 1886, from the western Indo-Pacific. Glaessner (1969) synonymized Paracyclois with Calappilia A. Milne Edwards 1873, considered until that time to include only species of Middle Eocene to Upper Oligocene ages in North America, Europe, and the East Indian region, but did not discuss reasons for his action. Because our determinations involved generic placement of material from trawl samples, we reviewed literature concerned with both of these genera and studied specimens of selected species of Calappilia in the fossil crustacean collection of the USNM. Austin B. Williams developed the text, C. Allan Child rendered the drawings, and both of us identified and cross-checked material.

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Key to Recent genera of Calappidae in the western Atlantic Ocean

1. Chelae essentially symmetrical, no unusually enlarged teeth or protuberances, Subfamily Matutinae ........................................... 2
2. Chelae dissimilar, major chela with large tooth on dactyl and pair of protuberances on propodus, Subfamily Calappinae .............. 3

2. Carapace considerably broader than long, regularly convex above ................................... Hepatus Latreille 1802
Carapace nearly as long as broad, dorsal surface uneven .................. Osachila Stimpson 1871

3. Posterolateral region of carapace not expanded into dentate, winglike projection .... 4
Posterolateral region of carapace expanded into dentate, winglike projection 5

4. Merus of cheliped bispinous on distal outer surface, with lower spine strong and greatly extended laterally ........................................ Acanthocarpus Stimpson 1871
Merus of cheliped not bispinous on distal outer surface, carapace subcircular, small spine at lateral angle .................. Cycloes De Haan 1837

5. Pereopod 5 with articles spineless .......... 6
Pereopod 5 with row of spines on flexor surface of ischium-merus ........................................ Paracyclois Miers 1886

6. Greatest span of winglike posterolateral projections less than maximal span between anterolateral margins; outer proximolateral corner of palm bearing short, flattened, smoothly crested ridge ........................................ Cyclozodion new genus
Greatest span of winglike posterolateral projections exceeding maximal span between anterolateral margins; outer proximolateral corner of palm bearing flattened acute spine or subrectangular ridge .................. Calappa Weber 1795

Calappa tortugae Rathbun 1933, new rank

Figures 1, 2
Calappa saussurei tortugae Rathbun 1933:183.
Calappa angusta.—(Part, not selected juveniles.) A.


Material studied.—Specimen lots in USNM recorded by Rathbun (1937) under C. angusta and C. saussurei tortugae (catalog numbers only) plus material added since that time.

North Carolina: USNM 68550.—101676. 1 σ, 1 Φ (juv.), 34°18'N, 75°58'W, SE off Cape Lookout, 137 m; Combat stn. 405, 21 June 1957.—101675. 1 σ; 34°19'N, 75°54'W, SE off Cape Lookout, 183 m; Combat stn. 402, 21 June 1957.—202745. 1 σ, 2 Φ; 33°48'48"N, 76°34'24"W, 46 m; BLM, 4 Mar. 1981.—202746. 1 Φ; 33°48'12"N, 76°34'24"W, 116 m; Duke Univ. for BLM, 14 May 1981.—202747. 1 Φ (ovig.); 33°47'36"N, 76°34'24"W, 116 m; Duke Univ. for BLM, 14 May 1981.—220962. 1 σ, 3 Φ; 33°48'36"N, 76°34'06"W, 69 m; Duke Univ. for MMS, 4 Mar. 1981.

South Carolina: 188682. 2 σ, 1 Φ; 32°18'30"N, 79°00'30"W, 84 m; Dolphin 577096, 3/4 Yankee trawl, MARMAP, 9 Mar. 1977.—188677. 1 Φ; 33°17'N, 77°08'42"W, 155 m; Dolphin 573426, 3/4 Yankee trawl, MARMAP, 15 Nov. 1973.—Silver Bay stn. 2263. 2 Φ; E of Charleston, 33°04'N, 78°12'W, 29 m; trawl, 28 July 1960.

Georgia: 155583. 1 σ; 30°50'30"N, 80°01'W, 93 m; M. Gray 209, 7 May 1963.—155582. 3 Φ; 30°55'30"N, 79°57'W, 91-119 m; M. Gray, 12 June 1963.—188680. 1 Φ; 31°43'30"N, 76°38'30"W, 64 m; Dolphin 576078, 3/4 Yankee trawl, MARMAP, 5 May 1976.

Florida: 66382. C. saussurei tortugae holotype, σ; Tortugas, about 12 mi S Red no 2 Buoy, 110 m; W. L. Schmitt, stn. 33–31, 22 July 1931.—66381. 1 Φ; same.—234461. 1 σ, 5 Φ; same.—68506, 68507, 68508, 68509, 68515, 71369.—101413. 6 σ, 3 Φ; off Jacksonville, 30°11'N, 80°17'W, 59 m; Combat stn. 72, 31 Aug. 1956.—101414. 2 σ, 1 Φ; SE Cape Canaveral, 28°32'N, 80°05'W, 119 m; Combat stn. 90, 3 Sept. 1956.—91137. 1 σ, 1 Φ; W Cape Romano, 25°35'N, 83°42'W, 110 m; Oregon stn. 35, 26 June 1950.—97487. 1 σ; SW Sarasota, 27°07'N, 83°19'W, 42 m; Oregon stn. 963, 4 Apr. 1954.—101678. 1 σ; S Cape San Blas, 29°10'N, 85°48'W, 101–130 m; Silver Bay stn. 100, 26 July 1957.—Silver Bay
FIGURE 1.—Calappa tortugae Rathbun, ♂ holotype, USNM 66382: a, carapace, eyes, and part of left cheliped; b, orbital region in frontal view; c, right chela and part of carpus; d, abdomen; e–f, first and second pleopods. ♂, USNM 202747: g, abdomen.
**Diagnosis.**—Carapace convex longitudinally and from side to side; mean length 0.9 times mean width \((N = 66)\); surface elevated in median tract and branchial regions, separated by well-marked furrow at each side running from orbit to level of cardiac region but thereafter becoming obsolescent; covered by prominent, densely and minutely granular protuberances of varied size more or less symmetricaly arranged, with more widely scattered and larger granules between them; arcuate anterolateral margins finely granulate, with larger granules at intervals; winglike extension with teeth largest at posterolateral angle preceded by up to 4 teeth progressively diminishing in size anteriorly, and followed posteriorly by 2 or 3 smaller teeth successively diminishing in size, all with beaded edges; mean maximal span between tips of posterolateral teeth slightly greater \((1.02)\) than mean maximal span between anterolateral margins; axis of largest tooth on winglike protuberance diverging from midsagittal line at angle of 20–25°.

Front trilobed, downturned, slightly broader than orbits; large central lobe with rather narrowly rounded tip barely visible in dorsal view, smaller lateral lobes directed anteriorly to accommodate narrowly oblique folded antennular peduncles; orbits noticeably raised above surrounding surface; interorbital width relatively narrow, its span relative to maximal span between posterolateral winglike extention rather narrow (see Figures 1 and 2).

Palms of chelipeds with external surface bearing irregular ornamentation moderately reminiscent of that on carapace; a lower zone of closely crowded coarse granules adjacent to beaded ventral margin, larger widely scattered irregular protuberances in central region becoming stronger and more closely arranged near base of dorsal “cockscomb” (crest of teeth), widely spaced irregular granules between these varying from obsolescent to well formed; short obliquely curved ridge rising from proximolateral corner to end anteriorly in subrectangular angle, crest minutely crenulate and in line with subdistal crest of 4 similar, narrowly separated broad teeth on merus.

Abdomen of each sex broadest at segment 3; latter fused with narrower segments 4 and 5 in male, segments in female relatively broader but essentially linear and free; segment 2 somewhat trilobed and bearing sparsely scattered low granules clustered laterally, segment 3 with much lower relief and low
juvenile to adult indicates that the winglike posterolateral projections. That is confirmed by measurements of young individuals noted above, but measurement of a series ranging from juvenile to adult indicates that the winglike posterolateral projections quickly become the widest part of the carapace as growth progresses, as is true of *Calappa* in general. Another way of expressing this width is to compare it with the interorbital distance. Interorbital distance expressed as a percent of maximum span across the posterolateral winglike projections is plotted for measured samples in Figure 2A (N = 71, \( \bar{x} = 0.347, SD = 0.039 \)). The eyes of *C. tortugae* are relatively smaller and the orbits more elevated than are those of species belonging to either *Paracyclois* or *Cyclozodion* new genus, and it is clear that the indicated ratio lies largely beyond that for these species, although it is comparable to that computed for a sample of *C. saussurei* Rathbun 1898 available in the USNM (Fig. 2B, N = 14, \( \bar{x} = 0.297, SD = 0.030 \), juveniles excluded). That sample contains a disproportionate number of very small juveniles; therefore it is useful to compute two ratios for that species, one that excludes the juveniles and one that includes them (Fig. 2C, N = 21, \( \bar{x} = 0.297, SD = 0.131 \)). These two species of *Calappa* are similar enough to be regarded as a geminate pair from either side of the Central American land mass, as implied by Rathbun’s descriptions. The chief difference is that *C. saussurei* has a much more coarse-granules clustered laterally; telson subtriangular. Male pleopod 1 rather stout, slightly curved and conically elongate, tapering to narrow distal opening with nearby cluster of minute horny spinules; pleopod 2 with slender stylet divided into 2 parts, gently curved proximal part stronger than distal part curved mesially upon itself as a crook, distal half of crook extending beyond tip of pleopod 1.

**Measurements in mm.**—Carapace: smallest \( \sigma \) length 14.4, maximum anterior width 15.8, maximum width across winglike projections 15.4; largest \( \sigma \), same 35.1, 42.3, 44.8; smallest \( \varphi \), same 10.7, 11.5, 11.4; largest \( \varphi \), same 29.7, 34.5, 35.7.

**Known range.**—North Carolina to Florida, around Gulf of Mexico, Leeward Islands to off Venezuela, 13–238 m (see Powers 1977 in part).

**Remarks.**—Milne Edwards’s *Calappa angusta* 1880 has been generically misplaced. The next available name for the species is *Calappa saussurei tortugae* Rathbun 1933, raised to full specific rank.

The young of *C. tortugae* have long been regarded as having the greatest carapace width anterior to the winglike posterolateral projections. That is confirmed by measurements of young individuals noted above, but measurement of a series ranging from juvenile to adult indicates that the winglike posterolateral projections quickly become the widest part of the carapace as growth progresses, as is true of *Calappa* in general. Another way of expressing this width is to compare it with the interorbital distance. Interorbital distance expressed as a percent of maximum span across the posterolateral winglike projections is plotted for measured samples in Figure 2A (N = 71, \( \bar{x} = 0.347, SD = 0.039 \)). The eyes of *C. tortugae* are relatively smaller and the orbits more elevated than are those of species belonging to either *Paracyclois* or *Cyclozodion* new genus, and it is clear that the indicated ratio lies largely beyond that for these species, although it is comparable to that computed for a sample of *C. saussurei* Rathbun 1898 available in the USNM (Fig. 2B, N = 14, \( \bar{x} = 0.297, SD = 0.030 \), juveniles excluded). That sample contains a disproportionate number of very small juveniles; therefore it is useful to compute two ratios for that species, one that excludes the juveniles and one that includes them (Fig. 2C, N = 21, \( \bar{x} = 0.297, SD = 0.131 \)). These two species of *Calappa* are similar enough to be regarded as a geminate pair from either side of the Central American land mass, as implied by Rathbun’s descriptions. The chief difference is that *C. saussurei* has a much more coarse-

**Cyclozodion new genus**

**Diagnosis.**—Carapace slightly wider than long and moderately convex; front narrow and trilobate; median lobe rounded and much much broader than lateral lobes; without lateral epibranchial spine or tooth; anterolateral margins regularly arcuate and entire or lightly crenulate, broadest span anterior to junction with posterolateral margin; each posterolateral margin bearing strongly spiniferous winglike projection, width between principal spines on latter less than greatest width of carapace, axis of principal spine on lobe diverging from midsagittal line at angle of about 40°.

Eyes large, peduncles short, robust, closely encased in oval orbits scarcely raised above surrounding area; interorbital distance 0.40–0.70 (0.80 in smallest juveniles) of span between tips of principal spines on posterolateral margin. Antennules folding obliquely; antennae with quadrate basal article not reaching frontal margin, flagellum very short. Outer maxillipeds with ischium longer than broad, longer than distally truncate merus with its anterointernal angle distinctly notched. Pereopods 2–5 spineless.

**Type species.**—*Cyclozodion angustum* (A. Milne Edwards 1880).

**Etymology.**—From the Greek “cyclo”, round, and “zodion”, a small carved figure, for the shape of the carapace. The gender is neuter.

**Remarks.**—Two small species fit between *Calappa* and *Paracyclois*. These species have the orbital characteristics of *Paracyclois*. They have posterolateral spines that cover a narrower span than do those of *Calappa*, but in general shape they resemble some juveniles of that genus. The two small species could almost be cited as examples of brachyuran neoteny, for they seemingly maintain a juvenile *Calappa*-like carapace facies while attaining sexual maturity. We are faced with the prospect of further splitting the family by introducing a new genus to contain these two species, or broadening the concept of *Paracyclois* to contain them. However, lack of any spines on the pereopods and shape of the proximolateral ridge on the extensor face of the cheliped palms, to point out only two features, clearly set them apart from *Paracyclois*. Rathbun (1937) and others perhaps unconsciously took the alternate route of accommodating them in...
what she called Calappa angusta, saying that the narrow span across the posterolateral winglike projections of the young of that species broadened with age into a full Calappa-like form. Analysis of measurements on a large series of specimens does not support this viewpoint (see Figure 2), and we therefore choose to erect the new genus for reception of these two small species.

Key to species of Cyclozodion

1. Carapace smooth to slightly tuberculate; front with central lobe shallowly concave, margin smooth; chelipeds with upper surface of carpus smooth

C. angustum

Carapace definitely tuberculate; front with broadly concave central lobe sharply granular near tip and on margins continuous with mesial margin of lateral lobe; chelipeds with upper surface of carpus tuberculate

C. tuberatum

Cyclozodion angustum (A. Milne Edwards 1880)

Figures 2, 3

Calappa angusta A. Milne Edwards 1880:18 (part).—A. Milne Edwards and Bouvier 1902:123, pl. 24, figs. 5–8; pl. 25, figs. 1–3; p. 125, fixed type locality.—Rathbun 1937:210 (part, selected juveniles).—Williams 1965:154; 1984:273 (part, selected juveniles).

Material studied.—MCZ 6653. Juvenile holotype; off Barbados, 183 m; Hassler, 27–30 Dec. 1871.—MCZ 2702. 1 σ (juv.) paratype; off Barbados, 188 m; Blake stn. 273, 1878–79.—MCZ 2917. 1 juv. paratype; N Yucatan, Mexico, 23°13'N, 89°16'W, 154 m; Blake stn. 86, 1877–78.

Florida: USNM 101419. 1 φ; off Cape Canaveral, 27°30'N, 78°52'W, 421 m; Combat stn. 238, 3 Feb. 1957.—Silver Bay stn. 2480. 1 σ, 2 φ; 26°06'N, 79°10'W, 223–229 m; dredge, 9 Nov. 1960.—2445. 1 σ (juv.); Straits of Florida, 24°08'N, 80°08'W, 252 m; dredge, 3 Nov. 1960.—2452. 4 σ, 4 φ, 3 φ ovig.; same, 28°30'N, 79°04'W, 228–238 m; dredge, 5 Nov. 1960.

Silver Bay stn. 3467. 1 juv.; off Great Bahama Bank, 27°27'N, 78°00'W, 229–274 m; dredge, 25 Oct. 1961.—3502. 1 juv.; S Great Inagua I., 20°54'N, 73°37'W, 137–183 m; dredge, 5 Nov. 1961.—3496. 1 φ; same, 20°58'N, 73°42'W, 183 m; dredge, 4 Nov. 1961.—5193. 1 σ, 1 φ (ovig.); Puerto Rico, W Mayaguez, 18°16'N, 67°22'W, 274 m; trawl, 18 Oct. 1963.—Oregon stn. 2643. 1 juv.; off Virgin Gorda, B.W.I., 18°03'N, 64°27'W, 274–329 m; trawl, 5 Oct. 1959.—6715. 2 σ, 1 φ; W Anguilla I., 18°36'N, 63°27'W, 201–238 m; dredge, 30 May 1967.—5015. 2 φ (juv.); off Barbados, 13°02'N, 59°34'W, 201–247 m; dredge, 20 Sept. 1964.—USNM 110230. 1 φ; same, 91–336 m; J. B. Lewis, NR4-2, date unknown.—USNM 110231. 1 juv.; same, NR8-2.—USNM 110232. 1 σ (juv.); same, NR12-4.—Oregon stn. 4982. 1 φ; Honduras Banks off Thunder Knoll, 16°06'N, 81°10'W, 165 m; dredge, 9 June 1964.—4928. 1 σ, 1 φ (jvs.); Colombia off Isla Providencia, 14°05'N, 81°21'W, 188 m; dredge, 8 June 1964.—Oregon II stn. 10190. 1 φ; Nicaragua, off Mosquito Coast, 14°42'N, 81°38'W, 141 m; dredge, 19 Nov. 1968.—10515. 1 φ (ovig.); Guyana, N New Amsterdam, 07°47'N, 57°12'W, 95 m; trawl, 28 Apr. 1969.

Description.—Carapace convex, slightly more arched in longitudinal than in transverse profile, length 0.94 width; surface densely but smoothly and uniformly covered with closely crowded granules; obsolescent raised tubercles in median longitudinal row on gastric and cardiac regions and in more or less concentric arcs on branchial regions; raised median tract separated from branchial regions by well-defined longitudinal depression at either side extending from protogastric to intestinal region; anterolateral margin regularly convex, minutely granulate; posterolateral margin extended into winglike prolongation bearing 1 large spine preceded by 3 or 4 much smaller spines, and succeeded by a single obsolescent spine and imperceptibly curved sector converging toward obscurely trilobed posterior margin.

Front trilobed, broader than orbits; broad central lobe concave in dorsal view, downturned, rounded tip not visible; narrower lateral lobes slightly divergent, partly enveloping curved antennular peduncles folded obliquely at slightly less than 45° angle to each other; orbits raised above surrounding region but not markedly so, a single obscure dorsal fissure; mean maximal interorbital distance 0.60 mean maximal span between principal spines on posterolateral winglike extensions.

Chelipeds with ornamentation on extensor surface not well divided into horizontal zones typical of many calappid species; lower margin with almost uniformly crowded obsolescent granules merging into a field of similar granules extending over lower 1/2 of surface; horizontal row of 3–5 low tubercles subparallel to lower margin; 4 or 5 similar scattered tubercles tending to arrangement in diagonal rows in central
FIGURE 3.—*Cyclozodion angustum* (A. Milne Edwards), ♀ ovigerous, Silver Bay stn. 5193: a, carapace, eyes, and part of left cheliped; b, orbital region in frontal view; c, right chela and part of carpus; d, fifth pereopod; h, abdomen. ♀, Silver Bay stn. 2452: e, abdomen; f-g, first and second pleopods.
area, and 6–10 more obscure tubercles dorsally near "cockscomb"; a low flattened smooth ridge proximolaterally in line with tubercles subparallel to lower margin and with subdistal crest of broad flattened teeth on merus, anterior tooth of latter with subrectangular tip, second biconcave acute, third and fourth obsolete and slightly crenulate. Pereopods 2–5 spineless.

Abdomen of each sex broadest at segment 3; latter fused with narrower segments 4 and 5 in male, segments in female relatively broader but essentially linear and free; segment 2 of male somewhat trilobed, that of female less strongly so, each with scattering of obsolete granules on these members; telson subtriangular. Male pleopod 1 stout, slightly curved and conically elongate, tapering to narrow distal opening with nearby cluster of minute horny spinules; pleopod 2 with slender stylet divided into 2 parts, gently curved proximal part stronger than distal part diverging obliquely mesad, tip only slightly exceeding that of pleopod 1.

Measurements in mm.—Carapace: holotype \( \sigma \) length 7.3, maximum anterior width 7.9, maximum span across winglike posterolateral projections 6.5; nontypes, same, smallest \( \sigma \) 17.3, 19.0, 15.1; largest \( \sigma \) 21.5, 22.9, 18.2; smallest \( \varphi \) 19.8, 18.5, 16.1; ovigerous \( \varphi \) 26.4, 24.5, 20.8.

Color.—Preserved specimens display a sprinkling of tiny pale orange spots on posterior 2/3 of carapace and upper exposed parts of chelipeds.

Known range.—Florida off Cape Canaveral to Colombia, off Isla Providencia, and Guayana, 95–421 m.

Remarks.—Cyclozodion angustum was originally based on juvenile specimens of quite small size and placed in the genus Calappa. Subsequent authors have followed this lead, attributing the narrowed span across the posterolateral winglike projections in all stages from juvenile to adult to youthful allometric phases seen in Calappa. Broadening of the winglike span in C. tortugae actually becomes established at very early stages, as pointed out above in the discussion of that species.

The eyes are relatively larger than in C. tortugae, the orbits less protuberant, and in frontal view the orbits are less elevated above the plane of the beaded anterolateral margin than in that species. Interorbital width expressed as a percent of maximum span across the posterolateral winglike projections is significantly higher in Cyclozodion angustum than in Calappa tortugae, another indication of the differential in size of orbits and carapace shape in these two species (Fig. 2A, D), although there is minimal overlap in this ratio for a few specimens. Two versions of this ratio are given for Cyclozodion angustum: one for the bulk of material measured and analyzed (Fig. 2D, \( N = 27, \bar{x} = 0.581, SD = 0.040 \)) and one that includes the very small individuals in the type series (Fig. 2E, \( N = 30, \bar{x} = 0.595, SD = 0.060 \)). Except for the range of percentages, indicating the relatively larger eyes of the types, there is no difference between the two sets of data.

Other features that distinguish C. angustum and Calappa tortugae are found on the chelipeds. The exposed carpal surface is smooth in the former, rough in the latter, and the procoxal ventral corner of the extensor surface on the palm bears a low rounded crest in the former but an anteriorly subrectangular crest in the latter.

**Cyclozodion tuberatum new species**

Figures 2, 4


Material studied.—Specimen lots in USNM recorded by Rathbun (1937) under Calappa angusta (catalog numbers only) plus material added since that time.


North Carolina: USNM 51070.—101676.1 \( \varphi \); off Cape Lookout, 137 m.—Silver Bay stn. 3333. 1 \( \sigma \); off Cape Fear, 33°48’N, 76°34’W, 73 m; trawl, 14 Aug. 1961.

Florida: USNM 20028, 68505, 68515, 71370, 71371.—169921. 2 unsexed; off Sebastian Inlet, 80 m.—101415. 1 \( \sigma \), 1 \( \varphi \) (juv.); Florida Straits, 119 m.—77291. 2 \( \varphi \); off Key West.—101420. 1 \( \varphi \); same, 73–91 m.—101677. 1 \( \sigma \); Gulf off W Fla., 31–35 m.—91140. 2 \( \sigma \), 1 juv.; same 113 m.

Oregon stn. 6040. 1 \( \varphi \); off St. Augustine, 29°47’N, 80°33.5’W, 35 m; dredge, 24 Apr. 1966.—Silver Bay stn. 3704. 1 \( \varphi \); off Cape Canaveral, 28°30’N,
FIGURE 4.—*Cyclozodion tuberatum* new species, ♂ holotype, USNM 234462: a, carapace, eyes, and part of left cheliped; b, orbital region in frontal view; c, right chela and part of carpus; d, fifth pereopod; e, abdomen; f–g, first and second pleopods. ♀ allotype, USNM 234463: h, abdomen.
Description.—Carapace convex, slightly more arched in longitudinal than in transverse profile, length 0.92 width; low tubercles of varied sizes scattered more or less symmetrically, much broader on gastric, cardiac, and anterior branchial regions than on posterior 1/3 and tract within perimeter, similar raised ornamentation on extensor surfaces of chelipeds; tubercles covered with low, smooth, tightly packed granules, but surface between elevations more coarsely and less thickly granular; raised median tract on gastric and cardiac region separated from branchial regions by well-defined but shallow depression to either side extending from postorbital to intestinal regions; anterolateral margins regularly divided into anterior rectangulo-acute tooth, all slightly crenulate on margins; field above this crest coarsely granulate; exposed surface of carpus tubercululate and granulate like palm.

Abdomen of each sex broadest at segment 3; latter fused with narrower segments 4 and 5 in male, segments in female relatively broader but essentially linear and free; segment 2 somewhat trilobed and bearing scattered obsolete granules, segment 3 with much lower relief and low granules scattered laterally; telson subtriangular. Pleopod 1 stout, slightly curved and conically elongate, tapering to narrow distal opening with nearby cluster of minute horny spines; pleopod 2 with slender stylet divided into 2 parts, gently curved proximal part stronger than distal part diverging obliquely mesad, tip only slightly exceeding that of pleopod 1.

Measurements in mm.—Carapace: holotype 9 20.6, 23.2, 21.7, 22.0; nontypes, same, smallest 9 16.0, 16.1, 14.9; smallest 9 12.0, 12.6, 10.9; allotype 9 21.1, 23.1, 21.7.

Color.—No evidence of persistent minute spots of color as on preserved specimens of Calappa angusta.

Known range.—North Carolina off Cape Lookout through Bahamas, eastern Gulf of Mexico, Surinam; 31-188, rarely 640 m.

Etymology.—The name is from the Latin "tubera-" because of the similarly tuberculate and granulate like palm.

Remarks.—Cyclozodion tuberatum has been confused with Calappa tortugae because of the similar-
ity in ornamentation. However, body proportions of the two species differ, as exemplified by the relationship of interorbital width to maximum span between posterolateral projections of the carapace (Fig. 2A, F, N = 40, $\bar{x} = 0.519$, SD = 0.057).

Other differences include shape of the proximo-ventral crest on the extensor face of the cheliped palm, rounded in the former, ending anteriorly in a subrectangular point in the latter, and in shape of the male pleopod 1 (see Figures 1 and 4). Cyclozodion tuberatum most closely resembles Calappa angustum, although there are superficial similarities to fossil Calappitia scopuli Quayle and Collins as pointed out below.

**Paracyclois Miers 1886**


*Diagnosis paraphrased and emended.*—Carapace about as long as broad, and moderately convex; front narrow and trilobate; median lobe rounded and much broader than lateral lobes; without lateral epibranchial spine or tooth; anterolateral margins regularly arcuate, broadest span anterior to juncture with posterolateral margin; each posterolateral margin bearing strongly spiniferous lobe or wing-like projection, width between principal spines on lobes less than greatest width of carapace (posterolateral winglike prolongations more fully developed in *Calappa*); axis of principal spine on winglike projection diverging from midsagittal line at angle of 25-40°. Subhepatic regions of carapace concave; channel thus formed communicating with antennary region (and thereby with buccal cavity) by a notch situated between it and inferior wall of orbit. Posterior abdominal segments distinct.

Eyes large, peduncles short, robust, closely encased in oval orbits scarcely raised above surrounding area; interorbital distance at least 0.40 and usually 0.45-0.60 or more of span between tips of principal spines on posterolateral margin. Antennules folding obliquely; antennae with quadrate basal article not reaching frontal margin, flagellum very short. Outer maxillipeds with ischium longer than broad, longer than distally truncate merus with its anterointernal angle distinctly notched. Pereopods 2–5 with row of spines on flexor surface of ischium-merus.

*Remarks.*—Miers (1886, emended) considered Paracyclois to be an apparent connecting link between *Calappa, Cycloes* De Haan 1837, and *Platyzodion* H. Milne Edwards 1837 in which the merus of the outer maxillipeds is distally truncate and bears the next article at its anterointernal angle, which is prolonged in the form of a lobe or tooth; but *Paracyclois* is distinguished from the first two of the above-mentioned genera by the absence of any lateral spine on the margin of the carapace and the broader basal antennal article, and from *Calappa* by both the reduced winglike prolongations of the carapace which bear strong spines, and by presence of spines on the flexor margin of the ischium and merus of pereopods 2–5.

**Key to species of Paracyclois**

1. Carapace with 3 obviously projecting lobulate spines on posterior margin ............... *P. milne-edwardsii* Carapace with posterior margin only faintly trilobed .................. *P. atlantis*  

**Paracyclois atlantis Chace 1939**

Figures 2, 5

Paracyclois atlantis Chace 1939:51.—1940:27, figs. 11, 12.

*Material studied.*—*Silver Bay* stn.—3467. 1 σ; off Grand Bahama Bank, 27°27'N, 79°00'W, 228–274 m; dredge, 25 Oct. 1961.—3510. 2 σ; Santaren Channel, 22°55'N, 78°36'W, 273 m; dredge, 7 Nov. 1961.—USNM 81986. 1 φ; off Punta Alegre, Cuba, 22°46.5’N, 79°W, 326 m; *Atlantis* stn. 3419, 30 Apr. 1939.—*Oregon* stn. 2603. 3 σ, 1 φ (ovig.); Puerto Rico, E San Juan, 18°30'N, 65°55'W, 258–292 m; trawl, 25 Sept. 1959.—5914. 1 σ; W Anguilla Is., 18°18'N, 63°19'W, 201 m; dredge, 25 Feb. 1966.—6700. 3a; S Barbuda Is., 17°27'N, 62°04'W, 248–285 m; trawl, 19 May 1967.—3636. 1 o-; Belize, 17°17'N, 87°59'W, 228 m; trawl, 10 June 1962.—4445. 1 juv.; *Netherlands Antilles, S Bonaire, 10°50'N, 68°00'W, 183 m; trawl, 10 Oct. 1963.—4856. 1 o*; Colombia, off Barranquilla Is., 11°08'N, 74°23.8’W, 183 m; trawl, 19 May 1964.—*Oregon* stn. 3585. 1 o; Panama, Gulf of Mosquitos, 09°12'N, 81°30'W, 247–256 m; trawl, 25 May 1962.—3587. 1 o; Panama, Canal Zone, 09°18’N, 80°25’W, 137 m; trawl, 29 May 1962.—1983. 1 o; Venezuela off Orinoco R. mouths, 09°53'N, 59°53'W, 228 m; trawl, 3 Nov. 1957.—2294. 1 o; Surinam E of Paramaribo, 07°25’N, 54°08’W, 192–210 m; trawl, 9 Sept. 1958.
Figure 5.—Paracyclois atlantis Chace, ♂ Silver Bay stn. 3510: a, carapace, eyes, and part of right cheliped; b, orbital region in frontal view; c, right chela and part of carpus; d, fifth pereopod; e, abdomen; f–g, first and second pleopods. ♀, Oregon stn. 5914: h, abdomen.
Diagnosis.—Carapace convex longitudinally and from side to side except where posterolateral winglike extensions occur; surface uneven, elevations roughly falling into 5 longitudinal rows, pair of furrows bordering median elevation deepest by far; minutely granular and coarsely punctate except on extreme posterior part where punctations disappear and granules become larger; small posterolateral winglike projections bearing 4 large and 1 or 2 rudimentary spines, 1 rudimentary spine often present between 2 anterior larger ones, spine next to posteriormost always largest and very much so in juveniles, somewhat curved anteriorly, with tendency for anterior curvature in others as well; posterior margin trilobate in dorsal view, lateral lobes prolonged ventrally on either side of abdomen.

Front deflexed, tip invisible in dorsal view, very slightly wider than greatest diameter of orbit and trilobate, median lobe rounded triangular and lateral lobes very narrow and traversed by notch separating front from orbits; orbital margin very slightly raised above surrounding region; mean maximal interorbital distance 0.50 mean maximal span between major posterolateral spines (see Figure 2G).

Palm of chelipeds with extensor surface ornamented in horizontal zones, well defined in lower 1/4 but obscure in upper 3/4; lower margin beaded with sharp granules, progressively raised, spiniform and remote proximally, flanked by narrow band of moderately crowded granules; lower half bearing low scattered protuberances, partly interspersed in granular zone and tending to horizontal arrangement, but becoming more widely and somewhat diagonally scattered in upper 1/2; proximolateral corner bearing short oblique obsolescent ridge surmounted by 3 or more acute to crenulate spines, most prominent distally; in line with subdistal crest of larger, uneven, ragged spines on merus. Pleopods 2-5 with row of almost uniform spines on flexor surface of merus, extensor surface of carpus entire.

Abdomen of each sex broadest at segment 3, latter fused with narrower segments 4 and 5 in male though nonfunctional articulations sometimes apparent, segments in female relatively broader but essentially linear and free; segment 2 trilobed and rather sharply granular, segment 3 with lower relief and bearing obsolescent granules clustered laterally; telson subtriangular. Male pleopod 1 rather stout, slightly curved and conically elongate, tapering to distal opening; pleopod 2 with slender stylet divided into 2 parts, gently curved proximal part stronger than distal part curved mesially upon itself as a crook, distal half of crook extending beyond tip of pleopod 1 and recurved near tip.

Known range.—Grand Bahama Bank to Panama and Surinam, 187-365 m.

Measurements in mm.—Carapace: smallest $\varnothing$ length 19.8, maximum anterior width 20.7, maximum span across posterolateral winglike projections 17.2; same, largest $\varnothing$, 57.1, 62.2, 50.5; smallest $\varphi$, 20.6, 22.2, 18.3; largest $\varphi$, 53.2, 58.5, 48.7.

Remarks.—See next species.

Paracyclois milneedwardsii Miers 1886

Figures 2, 6

Paracyclois milneedwardsii Miers 1886:289, pl. 24, fig. 1.—Sakai 1976:134 (Engl. text), 85 (Jpn. text), pl. 41, fig. 2.


Material studied.—USNM 233655. 2 $\varnothing$, 2 $\varphi$; Japan, Shikoku I., Tosa Bay; K. Sakai.—233654. 1 $\varphi$; Philippines, Balayan Bay, southern Luzon, 13° 47'20"N, 120°48'30"E, 329 m; Albatross stn. 536, trawl, 20 Feb. 1909.—Same. 1 $\varphi$; S Balayan Town, 141-195 m; trawl, 21 June 1966.—Same. 1$c$; S Sapating, 270-305 m; trawl, 29 July 1966.—Albatross stn. 5453. 2 $\varphi$; E coast Luzon, San Bernardino Str., NE Legaspi Light, 13°12'N, 123°49'18"E, 267 m; trawl, 7 June 1909.—5242. 2 $\varnothing$ (juv.). Mindanao near Vanivan Is., 06°51'53"N, 126°14'10"E, 349 m; trawl, 14 May 1908.

Diagnosis.—Carapace irregularly orbiculate, broadest at a point anterior to midlength of anterolateral margins, latter sweeping in regular curve to winglike protuberance of posterolateral margins bearing 4 unequal spines, anterior one longest; posterior margin bearing 3 strong flattened lobular spines ornamented with coarse tubercles extending onto adjacent intestinal region; margins behind anterior 1/4 of length tending to be rimmed by narrowly upturned, granular lip; median tract separated from branchial regions by rather prominent groove at either side extending from gastric to intestinal regions; surface granular and ornamented with low, smooth rounded tubercles tending to arrangement in concentric arcs diminishing in size toward lateral, posterolateral, and intestinal areas.

Front slightly narrower than orbit, trilobed, broadly rounded central lobe with downturned tip not visible in dorsal view, 3 low peripheral lobes on its upper surface; lateral lobes much narrower and slightly divergent to accommodate folded anten-
FIGURE 6.—*Paracyclois milneedwardsii* Miers, σ, USNM 233655: a, carapace, eyes, and part of right cheliped; b, orbital region in frontal view; c, right chela and part of carpus; d, fifth pereopod; e, abdomen; f-g, first and second pleopods. ♀, USNM 233654: h, abdomen.
nlar peduncles; ocular peduncles short and thick, granulated above; orbital margins slightly raised above surrounding region, mean maximal interorbital distance 0.50 mean maximal span between major posterolateral spines (Fig. 2H, N = 7, SD = 0.051).

Palm of chelipeds with ornamentation on extensor surface obscurely arranged in horizontal zones; lower margin granulate, sharply so in proximal 3/4; lower 1/3 of surface coarsely granular, becoming less sharply so as it merges into central zone; upper 2/3 bearing obscure diagonal rows of obsolescent tubercles in central portion, but stronger and less regularly arranged tubercles near base of dorsal “cocks-comb”; a spine near proximoventral corner in line with subdistal row of ragged, forward trending spines on merus. Pereopods with flexor surface of ischium and merus strongly but irregularly spinose; carpus bearing biserial row of smaller spines on extensor surface.

Abdomen of each sex broadest at segment 3; latter fused with narrower segments 4 and 5 in male, segments in female relatively broader but essentially linear and free; segment 2 trilobed, less so in female than in male and bearing obsolescent granules closely clustered or fused on lobes, segment 3 with much lower relief and obsolescent granules clustered mainly on lobes; telson subtriangular. Male pleopod 1 rather stout, slightly curved and conically elongate, tapering to narrow distal opening; pleopod 2 with slender stylet divided into 2 parts, gently curved proximal part stronger than distal part curved mesially upon itself as a rather closed crook, distal half of crook extending beyond tip of pleopod and recurved near tip.

Known range.—Japan, Philippines, the type locality north of Admiralty Islands (Sakai 1976), 141–349 m for specimens studied.

Measurements in mm.—Carapace: smallest σ length 18.2, maximum anterior width 17.3, maximum span across posterolateral winglike projections 15.4; same, largest σ, 53.2, 53.3, 47.8; smallest φ, 21.3, 19.9, 17.7; largest φ, 45.6, 44.8, 40.4.

Remarks.—The two species of Paracyclois, basically similar in carapace outline, have relatively larger eyes and orbits than the two species of Calappa discussed above (Fig. 2), and the orbits in frontal view are less elevated above the plane of the anterolateral margin. Interorbital width expressed as percent of maximum span across the posterolateral projections is virtually the same in samples of the two species (P. atlantis, N = 20, x = 0.494, SD = 0.044, Fig. 2G; P. milneedwardsii, N = 10, x = 0.496, SD = 0.051, Fig. 2H). Spination of the posterolateral projections is much more slender and remote than in either Calappa or Cyclozodion, and well-developed spination on the chelipeds and ventral margin of the ischium-merus of the fifth legs clearly sets them apart from species of these genera. Distribution in two well-separated centers, western Indo-Pacific and Caribbean, seems to reflect an ancient Tethyan track.

Calappilia A. Milne Edwards 1873


Ross and Scolaro (1964) summarized scattered references to fossil species of Calappilia known up to that time, Glaessner (1929) compiled a listing and an overview (1969), and Quayle and Collins (1981) gave notes along with description of an additional species. We reviewed all references to these species, and examined selected species (*) in the paleontological crustacean collection of the USNM in order to compare features of Calappilia with those of other genera treated herein.

Five species of Calappilia are known from the western hemisphere: *C. hondoensis Rathbun 1930, Upper Eocene, Calif.; C. bonairensis Van Straelen 1933, Upper Eocene, Bonaire, Netherlands, West Indies; *C. diglypta Stenzel 1934, Middle Eocene, Tex.; C. sp.? Roberts 1956, Lower Eocene, N.J.; *C. brooksi Ross and Scolaro 1964, Upper Eocene, Fla.

Seven species and one variety are known from Europe: C. verrucosa A. Milne Edwards 1873, the type species, and C. sexdentata A. Milne Edwards 1876, Middle Oligocene, SW France; C. perlata Noelting 1885, Lower Oligocene, Germany; C. incisa Bittner 1886, Middle Eocene, Italy; C. dacica Bittner 1886, Middle-Upper Eocene, Hungary; C. dacica var. lyrata Lörenty and Beurlen 1929, Upper Eocene, Hungary; C. vicetina Fabiani 1910, Upper Eocene, Italy; C. scopuli Quayle and Collins 1981, Upper Eocene, England.

Two species are known from the East Indies: C. borneoensis Van Straelen 1923, Middle Eocene, Borneo; C. bohmi Glaessner 1929, Upper Eocene, Java.

Diagnosis.—For purposes of comparing Calappilia with Calappa, Cyclozodion, and Paracyclois,
we paraphrase essential features of A. Milne Edwards's original description.

Near *Calappa* and *Mursia*; distinguished from former because carapace not extended above ambulatory legs (Fig. 7) in manner of a shield, and from latter by absence of large spines laterally prolonged beyond cephalothoracic shield; front very narrow and ornamented with 2 small slightly divergent points very similar to those of *Calappa*; [orbital] border cut by two narrow fissures.

![Figure 7.—Calappilia brooksi Ross and Scolaro, carapace and left eyestalk; USNM 648599, Upper Eocene, Fla.](image)

Carapace very convex, recalling that of *Calappa* or certain representative Leucosiidae; gastric and cardiac regions separated in lateral portions by deep grooves; hepatic region not clearly delimited; branchial region very inflated in anterior part but much narrowed posteriorly, surface covered with coarse tubercles in anterior part; posterior branchial lobe extended, constituting a prominence directed laterally and a little posteriorly; posterior border bearing a tubercle much less developed than branchial prominence at level of branchiocardiaco groove.

Ambulatory legs missing; fragment of chela with very compressed dactyl bearing granular crest, armed at base with large tubercle recalling that developed in *Calappa*; palm covered with large tubercles analogous to those ornamenting carapace, and their size notable compared to those on body.

**Measurements of selected species in mm.—** Carapace: *C. brooksi* length 18.8, width 21.5; *C. dacica* length 32, width 37; *C. hondoensis* length 19, width 18.7.

**Remarks.**—The features of *Calappilia* mentioned by A. Milne Edwards suggest much closer similarity to *Calappa* than to *Paracyclois*, and the brief diagnosis by Rathbun (1930) confirms this in broad outline. All of the species of *Calappilia* are small, comparing favorably with the range of sizes shown by the two species of *Cyclozodion* described here. There is considerable diversity in ornamentation of the carapace among species of *Calappilia*, with a tendency to development of coarse tubercules dorsally and along the margins, especially posterolaterally, but minimal development of posterolateral winglike projections, with some exceptions. Lobular tubercles along this margin are usually similar in size, although in *C. scopuli* (Quayle and Collins 1981:740, pl. 104, fig. 8) there is a developed posterolateral spine and, except for the problematic frontoorbital region, a marked similarity to *Cyclozodion* in outline of the carapace. The holotype of *Calappilia hondoensis* (USNM 371094) has an obscure posterolateral spine rather wider than long. Rathbun (1930) pointed out that Milne Edwards's (1873) figure of *C. verrucosa* is longer than wide whereas the measurements given show it wider than long. The left eyestalk of *C. brooksi* (USNM 648599, Fig. 7), fossilized projecting forward in its orbit, seems relatively slender compared with eyestalks of both *Cyclozodion* and *Paracyclois*, although only a remnant of it may be preserved.

On the basis of size, shape, and ornamentation of the carapace, relative thickness of eyestalks, and age, we regard Early Tertiary *Calappilia* and Recent *Paracyclois* as distinct. *Calappilia scopuli* and perhaps *C. hondoensis* seem to form closer links with Recent *Cyclozodion* than with *Calappa*, emphasizing similarities among the latter three genera.

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