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Evaluation of extinct members of Asthenognathinae (Decapoda: Brachyura: Varunidae) based on new specimens from the Astoria Formation (Miocene), Oregon, USA

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Abstract

Only two genera are currently referred to Asthenognathinae, one extinct, *Globihexapus* Schweitzer and Feldmann, 2001, and the other ranging from Oligocene to Holocene, *Asthenognathus* Stimpson, 1858. Asthenognathinae is currently recognized as a member of Varunidae. New specimens of *Globihexapus* from the Miocene Astoria Formation, Newport, Oregon, are more complete than the original material and permit more detailed description of the type species. *Globihexapus* shares many features with *Asthenognathus* and is confirmed as member of that subfamily. A detailed diagnosis for the Asthenognathinae is provided, possibly for the first time. Latitudinal range for members of Asthenognathinae have broadened in the Holocene to include tropical occurrences, whereas southern hemisphere occurrences are not recorded today. No evidence of commensal lifestyle is reported for fossil occurrences.

Key words: Thoracotremata, Oregon, USA, Miocene, cuticle

1. Introduction

Globihexapus paxillus Schweitzer and Feldmann, 2001, was originally described from five specimens collected from the Miocene Astoria Formation. Originally assigned to Hexapodidae, it was later moved to the Asthenognathinae of Pinnotheridae (Kato, 2005; Feldmann et al., 2011). Asthenognathinae is now referred to Varunidae (De Grave et al., 2009; Schweitzer et al., 2010; Emmerson, 2017). New material collected from the Astoria Formation permits a more complete description of the type species of *Globihexapus*, *G. paxillus* Schweitzer and Feldmann, 2001 (Figs. 1, 2, 6), and evaluation of its family and subfamily placement. *Globihexapus* is confirmed as a member of Asthenognathinae.

The Astoria Formation was originally described by Howe (1926) and subdivided into three main units: lower sandstone, shale, and upper sandstone. The formation is comprised of volcaniclastic sand and silt, and it is well known for its fossiliferous content including marine mammals, bryozoans, corals, crabs, fish, and plants (Prothero et al., 2001). Both biostratigraphic and paleomagnetic studies place the age of the Astoria Formation as early to early middle Miocene (Prothero et al., 2001).

2. Systematic Paleontology

Institutional abbreviations: CM, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA; KSU D, Kent State University decapod collection, Kent, Ohio, USA; F, OU, Museum of Natural and Cultural History, Condon Fossil Collection, University of Oregon, Eugene, Oregon, USA.

Order Decapoda Latreille, 1802
Infraorder Brachyura Latreille, 1802
Section Thoracotremata Guinot, 1977
Superfamily Grapsoidea MacLeay, 1838

Family Varunidae Miers, 1886

Diagnosis: Davie et al. (2015, p. 1119).

Discussion: According to Davie et al. (2015) and WoRMS (2021), Varunidae embraces five subfamilies, including the Asthenognathinae Stimpson, 1858. Historically, *Asthenognathus* and the superficially similar genus *Tritodynamia* Ortmann, 1894, had been placed within Pinnotheridae De Haan, 1833 (Tesch, 1918) (Figs. 3–5). Some authors synonymized the two genera (Balss, 1922), but later authors retained the two as separate genera (Ng et al., 2008). Ng et al. (2008, p. 252) placed *Asthenognathus* and Asthenognathinae in the Varunidae, based upon features of the pleon, sternum, gonopods, and pereiopods. They also noted that *Tritodynamia horvathi* Nobili, 1905, was potentially different from *Tritodynamia* sensu stricto and more like varunids in morphology and behavior as compared to the other species of *Tritodynamia*. They placed *Tritodynamia* s. s. within the monotypic Tritodynamiinae Števčić, 2005, within Macrophthalmidae Dana, 1851. Palacios-Theil et al. (2009) recovered *Asthenognathus atlanticus* Monod, 1933, nested within the Varunidae and sister to *Tritodynamia horvathi*. They confirmed removal of those two species and genera from Pinnotheroidea De Haan, 1833. Anker and Ng (2014) reiterated the similarity of *T. horvathi* with varunids. Thus, the affinities between *Asthenognathus* spp. and at least one species of *Tritodynamia*, *T. horvathi*, have been confirmed by molecular phylogenetic (Palacios-Theil et al., 2009) and morphological analysis, and they are regarded as members of Varunidae and Asthenognathinae here.

Several extinct species have been referred to *Asthenognathus* over the past few decades. Because the extant species of the genus are regarded as members of Varunidae, we examined some of the fossil members of *Asthenognathus* to confirm their placement in the family, subfamily, and genus. An extinct genus has been referred to Asthenognathinae, *Globihexapus* Schweitzer and Feldmann, 2001, and its placement was also verified.

One extinct species in particular, *Asthenognathus urretae* Schweitzer and Feldmann, 2001, is well represented by dozens of specimens. The morphological features of these specimens fit the diagnosis of Varunidae, including a quadrate to subquadrate carapace with a smooth surface and poorly defined regions, a bilobed front and orbits without fissures, confluent anterolateral and posterolateral margins, robust and swollen chelae which are more or less isochelous, possession of a wide thoracic sternum, sternal sutures 1/2 and 2/3 distinct, and sternal suture 3/4 indistinct. *Globihexapus* belongs to Varunidae based upon possession of these same features. Because the other fossil species of *Asthenognathus* are quite similar to *A. urretae*, we retain these species in the genus at this time.

The Oligocene age of some species of *Asthenognathus* make the genus one of the earlier occurring within Varunidae, and it ranges into the Holocene (Table 1). *Globihexapus* is restricted to the Miocene.

Subfamily Asthenognathinae Stimpson, 1858

Included genera: *Asthenognathus* Stimpson, 1858; *Globihexapus* Schweitzer and Feldmann, 2001; *Tritodynamia* Ortmann, 1894 (part).

Diagnosis: Carapace trapezoidal, wider than long; regions not well-defined; front narrowing distally, axially sulcate, strongly deflexed, not extending or extending slightly beyond orbits; straight frontal margin entirely or nearly entirely occupied by orbits; orbits shallow, orbital margin sinuous, usually rimmed; fronto-orbital width 40–50% maximum carapace width; anterolateral and posterolateral margins confluent, lateral flank flaring out posteriorly; posterolateral reentrant large; posterior margin nearly straight, posterior width about two-thirds maximum carapace width; branchial regions sometimes with crest extending posteriomesially from midpoint of lateral margin; sternite 4 typically without anterior projections, sternite 8 barely visible in postero-ventral view; pleonal somites 1 and 2 very short in males; ischium of maxilliped three about as long as or slightly shorter than merus; pereiopod 5 much shorter than pereiopods 2–4.

Material examined: *Asthenognathus urretae* Schweitzer and Feldmann, 2001, CM 54591-54628; *Globihexapus paxillus*, F-35796, F-35807, F-35793, F-81922–F-81935; *Tritodynamia horvathi*, KSU D 319, Holocene, Fukuoka, Japan.

Discussion: Asthenognathinae was originally named as a family and described in the same paper with members of Grapsidae MacLeay, 1838, and Ocypodidae Rafinesque, 1815, although no specific relationship between or among the taxa was indicated (Stimpson, 1858). There does not appear to have ever been a detailed diagnosis of Asthenognathinae published until now. Currently, the extant members of the subfamily include only three species of *Asthenognathus*, with the possible addition of *Tritodynamia horvathi*. The fossil species of *Asthenognathus* and species of the extinct *Globihexapus* are similar to extant *Asthenognathus* spp. in possession of a trapezoidal carapace; small, forward directed, rimmed orbits; confluent anterolateral and posterolateral margins; a strongly flared posterolateral corner of carapace; a posterolateral reentrant; third maxillipeds with the ischium and merus similar in size; short first pereiopods; longer pereiopods 2–4; very reduced fifth pereiopods; and sternite 8 not visible in ventral view. Thus, placement of the fossil species of *Asthenognathus* and *Globihexapus* within Asthenognathinae seems confirmed.

One discrepancy appears to be in the nature of the male pleon for some extinct species of *Asthenognathus*. In extant *Asthenognathus* spp., the male pleon is reported as having all somites free. However, somites 1 and 2 appear to be very short (*A. atlanticus*: Monod, 1933, fig. 8F; *A. hexagonum*: Yang & Tang, 2008, fig. 1E; *A. inaequipes*: Lee et al., 2010, fig. 1H) or sometimes not even illustrated (*A. atlanticus*: Monod, 1956, fig. 541c). The extinct species of *Asthenognathus* have been reported as having male pleonal somites 3–5 fused (Schweitzer and Feldmann, 2001). Examination of specimens of *A. urretae* indicates that males appear to have 5 elements including the telson (Fig. 3.2), except one specimen that may show a tiny bit of an additional somite (Fig. 3.3). The tiny nature of the male pleonal somites 1 and 2 in extant species of *Asthenognathus* makes this issue difficult to resolve, as they could be obscured in fossil specimens. Specimens of *Globihexapus paxillus* have free male pleonal somites (Fig. 2.3).

A feature historically considered very important for *Asthenognathus* and related taxa is the size and shape of the ischium and merus of the third maxillipeds (Tesch, 1918). Tesch (1918) diagnosed *Asthenognathus* as having the merus slightly shorter than the ischium, and *Tritodynamia* as having the merus as long as the ischium. The fossils described here have the merus slightly longer than the ischium of the third maxillipeds (Fig. 2.3).

Examination of a photograph of *Asthenognathus atlanticus* (accessed from WoRMS, 2021, photo by H. Hillewaert), multiple specimens of *A. urretae*, and a specimen of *T. horvathi* (KSU D 319) indicates that sternite 8 is reduced. It is barely visible in fossils of *A. urretae* when the specimens are rotated posterodorsally (Fig. 3.4), and it is much reduced in *T. horvathi* (Fig. 5.4). It is not visible in specimens of *Globihexapus paxillus* in ventral view (Fig. 2.3). The photograph of *A. atlanticus* shows that sternite 8 is not visible in ventral view but whether it can be seen in posterior view is not known. Thus, it seems reasonable to suggest that sternite 8 is reduced in Asthenognathinae. *Tritodynamia horvathi* possesses a dual press-button mechanism, including one on sternite 5 (Guinot, 1976). Sternites 5 of examined individuals of *T. horvathi*, *A. urretae*, and *G. paxillus* clearly possess a press-button sternal locking mechanism axially (Figs. 2.4, 3.5, 5.3).

Tritodynamia horvathi has a male gonopore located very close to the suture between sternites 7 and 8 and positioned axially (Fig. 5.4). A possible preserved male gonopore in *A. urretae* is in a similar position (Fig. 4). This male gonopore position is more like that reported for ocypodoids as compared to varunids, in which the male gonopore is separated from the pereiopod 5 coxa by the episternite (Davie et al., 2015). We can find no description of the position of the male gonopore in extant *Asthenognathus*; thus, this discrepancy remains unresolved.

Therefore, the extinct fossil species of *Asthenognathus* and *Globihexapus* are similar to both extant *Asthenognathus* and *Tritodynamia horvathi* in most regards. *Tritodynamia horvathi* has been suggested to be a varunid, the family embracing Asthenognathinae, and has been recovered as sister to a species of *Asthenognathus* in a phylogeny. Thus, because the fossil species are similar to species recovered as asthenognathines, we suggest that they remain in Asthenognathinae.

Genus *Asthenognathus* Stimpson, 1858

Type species: *Asthenognathus inaequipes* Stimpson, 1858, by monotypy (extant).

Other species: *Asthenognathus alleronensis* Pasini et al., 2017 (extinct); *A. atlanticus* Monod, 1933 (extant); *A. australensis* Feldmann et al., 2011 (extinct); *A. cornishorum* Schweitzer and Feldmann, 1999 (extinct); *A. globosus* (Karasawa, 1990) (extinct); *A. hexagonum* Rathbun, 1909 (extant); *A. laverdensis* De Angeli and Garassino, 2006 (extinct); *A. microspinus* Casadío et al., 2004 (extinct); *A. rakosensis* Müller, 2006 (extinct); *A. sakumotoi* Karasawa, 2018 (extinct); *A. urretae* Schweitzer and Feldmann, 2001 (extinct).

Diagnosis: Carapace trapezoidal, length about 75% width; small, forward directed, rimmed orbits; fronto-orbital width 40–50% carapace width; anterolateral and posterolateral margins confluent, posterolateral corner strongly flared; posterolateral reentrant well-developed; third maxillipeds with the ischium and merus similar in size; short first pereiopods; longer pereiopods 2–4; strongly reduced fifth pereiopods; sternite 8 not visible in ventral view; male pleonal somites possibly with somites 3–5 fused.

Discussion: We elect to retain the referred fossil species of *Asthenognathus* in the genus, as they share similar carapace features, and where present, sternal and pleonal features with one another and the extant species. Examination of material referred to each of the fossil species will be necessary to confirm their generic placement.

***Asthenognathus urretae* Schweitzer and Feldmann, 2001**

(Figs. 3, 4)

Asthenognathus urretae Schweitzer and Feldmann, 2001, p. 342, fig. 5; Casadío et al., 2004, p. 100; Feldmann et al., 2011, p. 122; Emmerson, 2017, p. 28; Karasawa, 2018, p. 32; Maguire et al., 2018, p. 36.

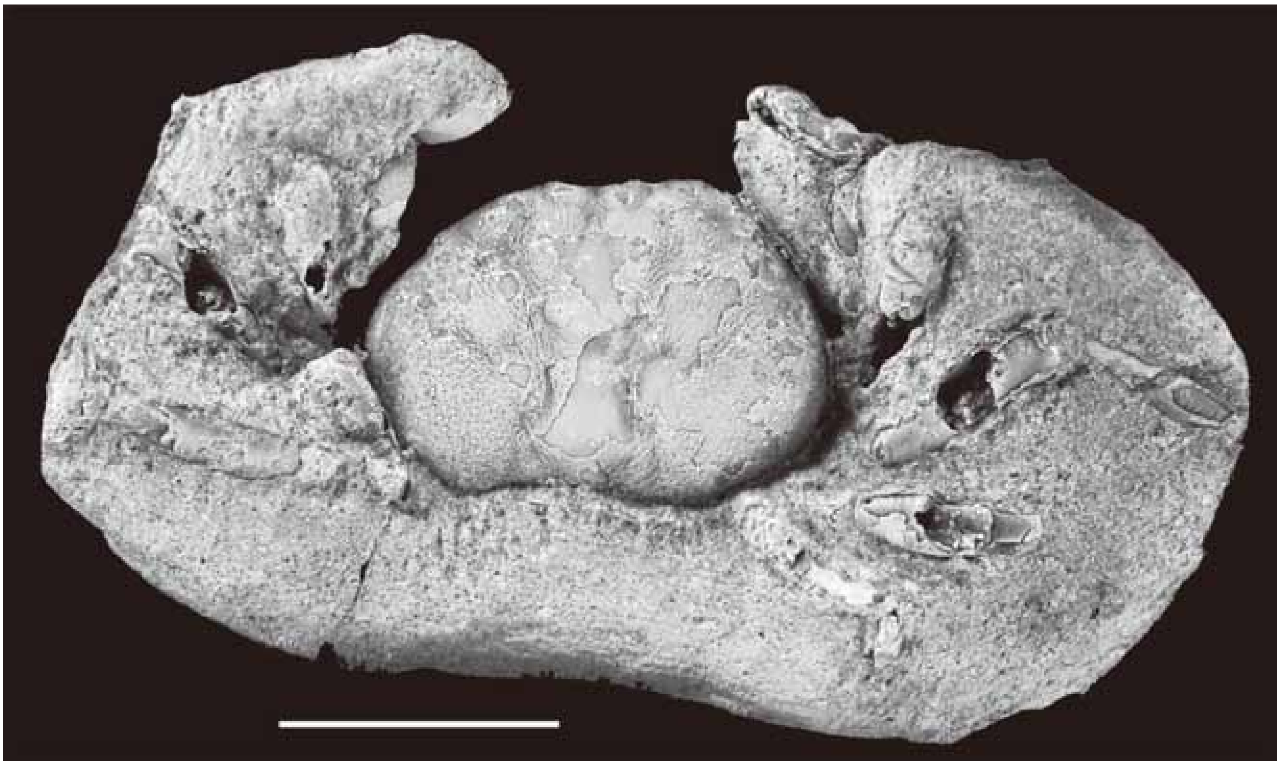

Fig. 1. *Globihexapus paxillus* Schweitzer and Feldmann, 2001. Specimen F-81922, dorsal carapace and portions of all five right pereiopods. Scale bar = 1 cm.

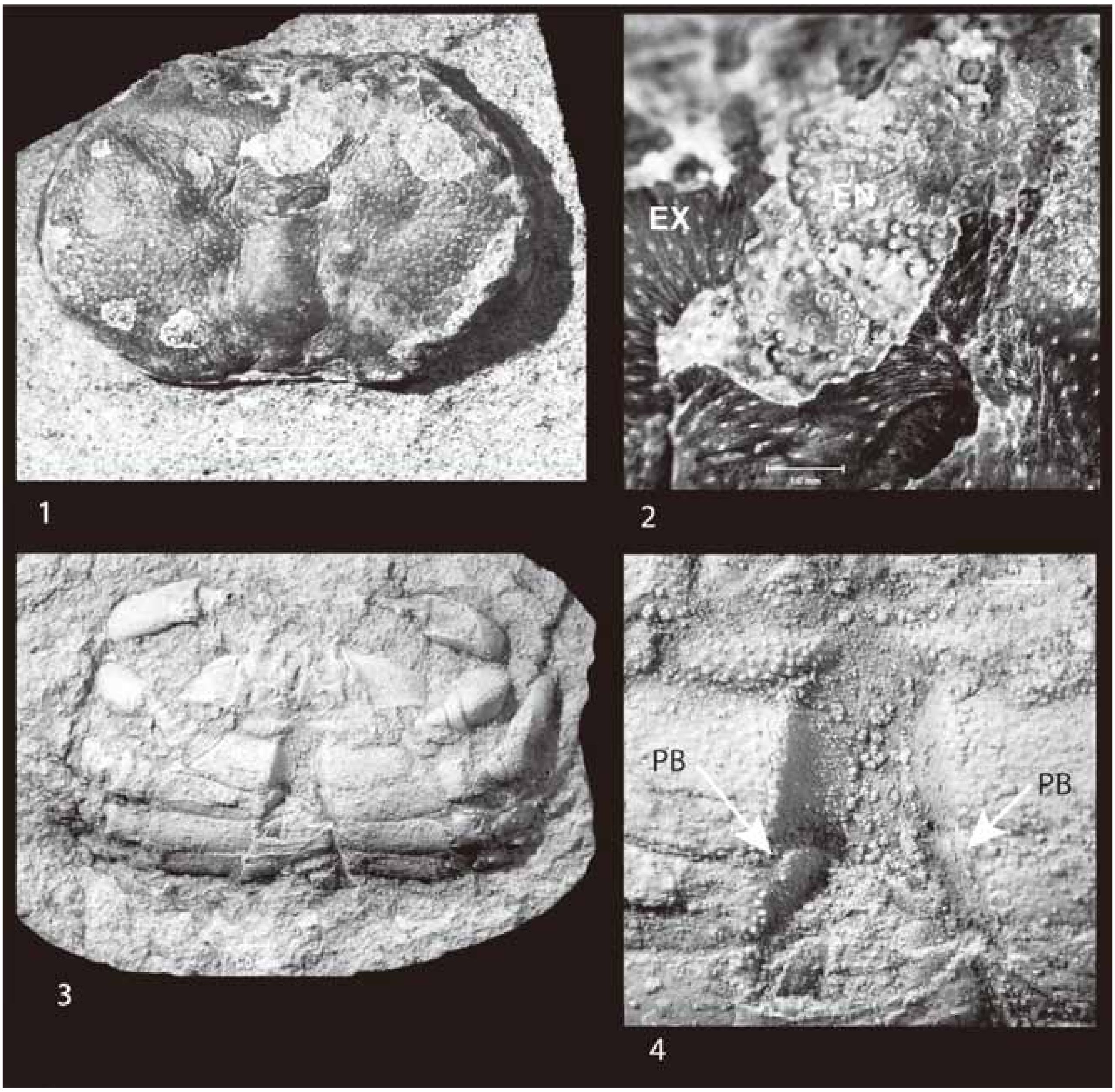

Fig. 2. ***Globixexapus paxillus*** **Schweitzer and Feldmann, 2001**. ***1–2***, F-81923, carapace with well preserved exocuticle surface (***1***) and enlargement of axial region with exfoliated exocuticle (EX) and exposed endocuticle (EN) (***2***). ***3–4***, F-35807, male ventral view showing third maxillipeds, sternum, and portion of pleon (***3***) and enlargement of pleonal cavity with press-button pleonal locking mechanism (PB) indicated (***4***). Scale bar 1 = 5 mm; scale bars 2–4 = 1 mm.

Diagnosis: Carapace subquadrate, length about 75% width; carapace often wrinkled; front narrow, fronto-orbital width about 40% carapace width; beaded rim on anterolateral margin; sternal sutures one and two distinct, complete; sternal suture three/four a groove; female pleonal somites free; male pleonal somites appearing fused but somites one and two may be reduced in size; sternite five with press-button locking mechanism; possible male gonopore between sternal sutures seven and eight; male fifth pereiopod coxae without gonopore; ischium slightly shorter than merus of third maxilliped; fifth pereiopod much smaller than pereiopods 2–4.

Description (modified from Schweitzer and Feldmann, 2001, p. 342): Carapace subquadrate to trapezoidal in outline, length about 75% width, more variable in females (ranging from 0.63–0.87, n = 6) than males (ranging from 0.73–0.77, n = 4); moderately vaulted longitudinally; nearly flat transversely; lateral margins well defined, nearly vertical to dorsal carapace

Table 1. Paleolatitudes of extinct and latitudes of extant occurrences of Asthenognathinae. Paleolatitudes for each locality calculated in Paleobiology Database (November, 2021). Locations for extant *Asthenognathus* taken from Yang and Tang (2008), Lee et al. (2010), and Faasse et al. (2021). Extant species with modern locations in bold.

Species	Age	Location	Paleolatitude/Latitude
A. laverdensis	Oligocene	Italy	47°N, 18.8°E
A. microspinus	Oligocene	Argentina	43.4°S, 63.7°W
A. cornishorum	Oligocene–Miocene	Washington, USA	47.8°N, 115°W
A. urretae	Oligocene–Miocene	Argentina	51°S, 67.6°W
A. australensis	Miocene	Argentina	54.3°S, 63°W
A. globosa	Miocene	Japan	38°N, 134°E
A. rakosensis	Miocene	Hungary	47°N, 18.8°E
A. sakumotoi	Miocene	Japan	37.5°N, 130.4°E
A. alleronensis	Pleistocene	Italy	42.7°N, 10.8°E
A. atlanticus	**Holocene**	**Eastern Atlantic, Mediterranean Sea, North Sea**	**Farthest North: 52.366°N, 3.46°E** **Farthest South: 5.613°N, -0.166°W**
A. hexagonum	**Holocene**	**Indo-Pacific Ocean China, Thailand**	**Farthest North: 23.4°N, 116.77°E** **Farthest South: 11.58°N, 102.97°E**
A. inaequipes	**Holocene**	**China, Japan, Korea**	**East China Sea: 30.88°N, 125.87°W** **Korea: 34.87°N, 127.90°W**
G. paxillus	Miocene	Oregon, USA	44.5°N, 119.4°W
G. kosekii	Miocene	Japan	40.7°N, 137.4°E

anteriorly and laterally flared posteriorly. Carapace often wrinkled as though very thin and delicate. Front narrow, about 13% maximum carapace width measured at posterolateral corners, projected forward and downward with sulcate axis. Orbits complete above and laterally, partly closed below, open ventromesially; rimmed by narrow, distinct, thickened border which thickens to small protuberance near midlength, upper orbital margin sinuous. Fronto-orbital margin about 40% maximum carapace width and narrower than posterior margin. Anterolateral margins diverging posteriorly in smooth curve, defined by narrow, beaded rim extending from lateral corner of orbit to posterolateral corner; rim defines nearly vertical lateral margin along anterolateral margin and curves posteroventrally across posterolateral area to intercept posterolateral corner. Posterolateral corner biconcave, rimmed, with prominent protuberance situated 65% the distance from posterolateral corner to posterior corner defining anterior point of insertion of pereiopod 5; defined anteriorly and posteriorly by sharp angle. Posterior margin wide, about 59% total width, weakly rimmed.

Dorsal surface smooth to weakly areolated with mesogastric and cardiac regions poorly defined by shallow grooves, cardiac region with three nodes on molds of interior; extremely subtle ridge extends from cardiac region anterolaterally to intercept lateral margin at point where marginal rim curves posteroventrally. Surface ornamented by uniformly spaced, tiny setal pits.

Sternum broadening posteriorly, widest at sixth sternite; anterior and posterior margins sinuous; sutures 1/2 and 2/3 complete and distinct; suture 3/4 developed as a ridge; sternite 3 granular; sternite 4 longest; sternites 5–7 wide, sternite 8 very reduced, short and narrow, visible in postero-ventral view; sternites 4–6 with posterolaterally projecting episternal processes defining sinuous margin. Buccal frame trapezoidal, narrowing slightly anteriorly; third maxilliped quadrate, longer than wide, with longitudinal groove extending length of merus, merus appearing slightly longer than ischium.

Female pleon not fused, widest at somites 4 and 5, narrowing anteriorly and posteriorly, laterally convex, with subtle axial ridge transversely, sutures between somites sinuous, with a concave forward indentation axially (Fig. 3.1); immature female pleon about 54% total sternal width measured at level of sixth sternite;

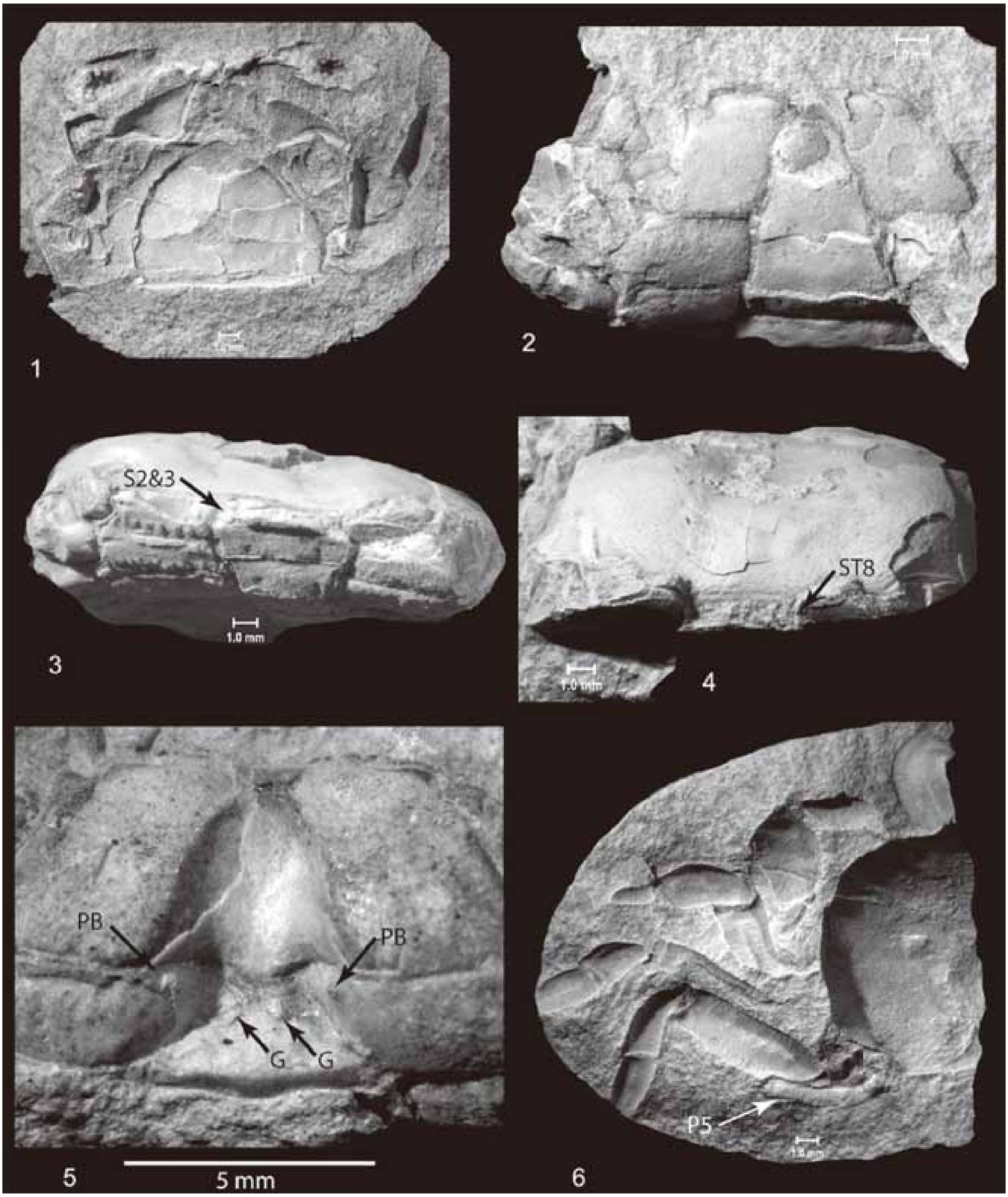

Fig. 3. *Asthenognathus urretae* Schweitzer and Feldmann, 2001. ***1***, CM 54594, female pleon. ***2***, CM 54597, male pleon showing telson and three somites. ***3–4***, CM 54596, male, possible pleonal somites 2 and 3 (S2 & 3) shown in posterior view (***3***) and sternite 8 (ST8) (***4***). ***5***, CM 54598, male, press-button pleonal holding mechanism (PB) and cross sections of gonopods one (G). ***6***, CM 54593, five pereiopods with small pereiopod 5 (P5) indicated. Scale bars 1–4, 6 = mm. Scale bar 5 = 5 mm.

mature female pleon about 73% maximum sternal width. Male pleon may exhibit fusion of two somites, at most 6 segments detectable, usually 5, straight sided, widening to 51% maximum sternal width measured at posteriormost end; press-button holding mechanism present on sternite 5 of males. Cross-section of male gonopods one visible (Fig. 3.5), possible male gonopore visible on sternite 8 near suture with sternite 7.

Table 2. Measurements (in mm) taken on specimens of *Asthenognathus urretae*. Sex indicated where determined.

Specimen Number	Maximum carapace length	Maximum carapace width	Fronto-orbital width	Frontal width	Sex
CM 54591	11.3	14.8	7.0	2.8	—
CM 54592	5.4	7.1	—	—	—
CM 54600	10.0	13.0	9.8	2.8	—
CM 54599	14.0	18.2	8.0	3.0	M
CM 54602	11.6	16.0	—	—	M
CM 54596	14.4	19.6	7.8	—	M
CM 54598	13.1	17.6	7.8	3.1	M
CM 54622	8.5	11.3	5.2	2.2	F
CM 54623	11.1	13.2	5.6	2.3	F
CM 54624	11.7	13.3	6.0	2.3	F
CM 54625	11.7	16.9	7.0	—	F
CM 54626	12.0	18.9	7.4	3.0	F
CM 54606	14.2	19.1	—	—	—
CM 54609	11.9	16.1	—	—	—
CM 54593	13.2	18.9	—	—	—
CM 54608	13.9	14.4	6.6	—	—
CM 54603	13.5	18.7	7.2	2.4	—
CM 54617	12.7	16.3	6.8	2.8	—
CM 54615	10.5	13.3	—	—	—
CM 54607	15.0	20.4	8.2	3.0	—
CM 54613	11.2	13.9	—	—	—
CM 54618	10.8	15.7	—	—	—
CM 54619	11.4	15.7	6.8	2.9	—
CM 54611	14.3	18.6	8.0	3.8	—
CM 54616	11.2	14.9	6.8	2.2	—
CM 54604	12.1	16.8	6.5	2.7	—
CM 54614	10.4	12.3	—	—	—
CM 54612	9.0	13.0	—	—	—
CM 54621	8.4	10.6	—	—	—
CM 54610	9.9	13.6	5.9	2.5	—

First pereiopod with globose carpus and manus; each slightly longer than high; manus ornamented by one or more subtle longitudinal rows of tiny nodes. Fixed finger slender, slightly curved, with tiny denticles on occlusal surface. Pereiopods 2–4 similar in size, with flattened, elongate meri, 5.9 times as long as wide and 59% of maximum carapace width. Pereiopod 5 reduced in size, much smaller and shorter than P2–P4, no evidence of male gonopore on coxa of P5.

Measurements: Measurements (in mm) taken on specimens of *Asthenognathus urretae* are presented in Table 2.

Material Examined: KSU D 2845, consisting of 50+ specimens, and CM 54591–54628, collected from the type locality near El Calafate, Santa Cruz Province, Argentina (Schweitzer and Feldmann, 2001).

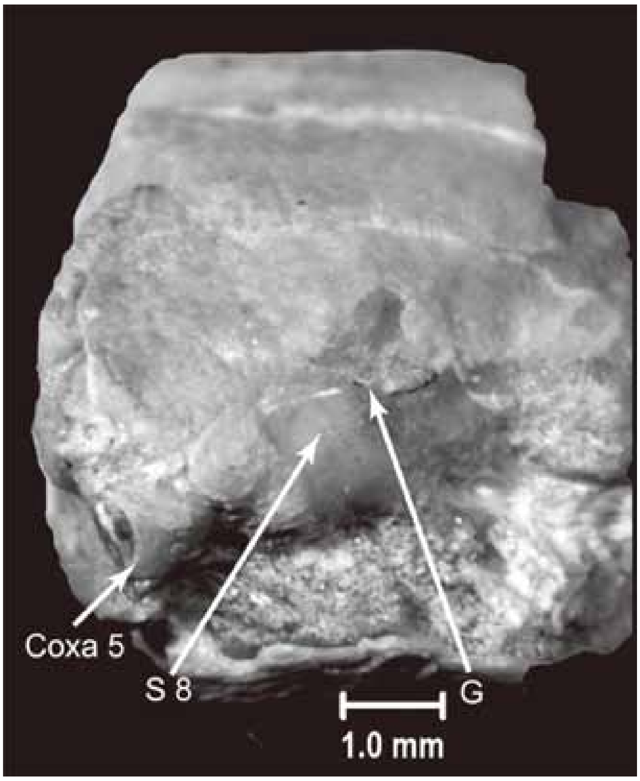

Fig. 4. *Asthenognathus urretae* Schweitzer and Feldmann, 2001. CM 54595. Oblique posterior view of male gonopore (G), coxa of pereiopod 5 (coxa 5), and sternite 8 (S 8) indicated. Scale bar = 1 mm.

Discussion: Detailed examination of more than ninety specimens of *Asthenognathus urretae*, collected from the type locality, yielded new observations. A possible male gonopore was exposed by careful preparation, as well as most of a male coxa 5 indicating no evidence of a male gonopore (Fig. 4). This strongly suggests placement in Thoracotremata. One specimen exhibits two cross sections of male gonopods (Fig. 3.5); this is supported by the length of the gonopod in an extant specimen of *A. hexagonum*, reported as 9 mm long (Yang and Tang, 2008) and thus long enough to be exposed at the position of the fifth sternite. Tesch (1918) diagnosed *Asthenognathus* as having the merus slightly shorter than the ischium of the third maxilliped. *Asthenognathus urretae* has a merus slightly longer than the ischium, but the maxilliped articles may not be fully exposed from the sediment.

Females and males may be weakly sexually dimorphic. In males, the carapace width is on average 13.3 mm, with a range of 11.6 to 14.4 m (n = 4). In females, the average width is 11.2, with a range of 8.5 to 12.2 (n = 6). In females the mean L/W is 75.5% but is more variable (ranging from 0.63–0.87, n = 6) than in males, in which the mean L/W is 74.3% (ranging from 0.73–0.77, n = 4). These are not differences that would be apparent upon inspection of the carapace and are only noted once measurements are taken.

Genus *Globihexapus* Schweitzer and Feldmann, 2001

Type species: *Globihexapus paxillus* Schweitzer and Feldmann, 2001, by original designation.

Other species: *Globihexapus kosekii* Kato, 2005.

Diagnosis: Carapace wider than long, length about two-thirds carapace width, maximum width in posterior of carapace; fronto-orbital width about 40% carapace width; lower orbital margin with blunt tooth; suborbital region with transverse depression parallel to a blunt crest; carapace regions, moderately developed; peg-like ornamentation on rim of anterolateral margins; third maxilliped with merus slightly longer than ischium; first pereiopod shorter than pereiopods two and three; fifth pereiopod much reduced; chelae globose, distinct spine on occlusal surface of the movable finger of chelipeds; male pleon narrow, with all somites free; female pleon very wide, with all somites free; sternite 3 granular, sternite 5 with press-button locking mechanism axially, sternite 8 not visible in ventral view.

Discussion: *Globihexapus* was originally described based upon dorsal carapace and a few pereiopod characters. The genus was placed in Hexapodidae (Schweitzer and Feldmann, 2001), but reexamination of the type material of *Globihexapus paxillus* revealed a minute pair of fifth pereiopods seen in paratypes USNM 501843, USNM 501844, and USNM 501845

(Kato, 2005). No additional specimens of *G. paxillus* had been discovered to confirm the observation until now.

Kato (2005) transferred *Globihexapus* to Asthenognathinae, at that time placed in Pinnotheridae. As discussed above, that subfamily placement is retained herein. *Globihexapus* is well-differentiated from *Asthenognathus* in possessing relatively well-developed carapace regions, a wider carapace with respect to the length, and peg-like ornamentation on the anterolateral margins.

A diagnostic character for the genus appears to be a distinct spine on the occlusal surface of the movable finger of the chelipeds. *Globihexapus kosekii* was described as possessing this spine, and the new specimens of *G. paxillus* also do. In addition, the specimens herein described possess features of the pleon and sternum that were not observed in the type material, also similar to that of *G. kosekii*. Thus, the diagnosis for *Globihexapus* is here expanded and revised.

***Globihexapus paxillus* Schweitzer and Feldmann, 2001**

(Figs. 1, 2, 6)

Globihexapus paxillus Schweitzer and Feldmann, 2001, p. 333, figs. 1, 2; Kato, 2005, p. 74; Schweitzer et al., 2010, p. 143; Emmerson, 2017, p. 280.

Diagnosis: Carapace wider than long, length about two-thirds carapace width, maximum width in posterior of carapace; fronto-orbital width about 40% carapace width; lower orbital margin with blunt tooth; suborbital region with transverse depression parallel to a blunt crest; carapace regions, moderately developed; peg-like ornamentation on rim of anterolateral margins; third maxilliped with merus slightly longer than ischium; first pereiopod shorter than pereiopods two and three; fifth pereiopod much reduced; chelae globose, distinct spine on occlusal surface of the movable finger of chelipeds; male pleon narrow, with all somites free; female pleon very wide, with all somites free; sternite 3 granular, sternite 5 with press-button locking mechanism axially, sternite 8 not visible in ventral view.

Description: Carapace wider than long, length about one-third maximum carapace width, rounded-trapezoidal, widest in posterior one-third, flattened on dorsal surface both transversely and longitudinally; branchiostegal regions steep laterally, at about 90° to dorsal surface anteriorly, flaring out laterally posteriorly. Carapace surface wrinkled along and on axial regions and protogastric regions, pitted dorsally, with peg-like, widely spaced granules on branchial and branchiostegal regions.

Front narrow, about 14% maximum carapace width; axially depressed, sulcate, weakly concave on each side lateral to axis, with weak inner orbital projection. Orbits shallow, concave, with distinct beaded rim on upper margin, outer-orbital angle weakly projected, lower orbital margin with large blunt tooth; fronto-orbital width about 40% maximum carapace width. Suborbital region with transverse depression beginning at inner orbital position, extending laterally and dorsally to merge with anterolateral margin; blunt crest parallel and ventral to depression.

Anterolateral margin extending nearly straight initially, then becoming strongly convex and merging with posterolateral margin; anterolateral segment with beaded rim anteriorly, interrupted and notched at intersection with cervical groove, becoming a row of granules as it approaches the posterolateral margin. Branchiostegal region steep, nearly perpendicular to carapace dorsally, flaring out to a lower angle ventrally; lower margin with strong rim and posterolateral reentrant; posterior margin straight, rimmed.

Mesogastric region with narrow anterior projection, widening posteriorly, bounded anteriorly by quadrate epigastric regions; metagastric region poorly defined, long, wider than base of mesogastric region; urogastric region long, narrow; cardiac region strongly inflated, pentagonal; intestinal region narrow, moderately inflated, an extension of posterior angle of cardiac region. Protogastric regions flattened, longer than wide, hepatic regions quadrate, flattened; branchial regions very large, not differentiated, with a broad round swelling posterior to protogastric region and smaller swelling lateral to urogastric region.

Buccal frame quadrate, pterygostome granular. Third maxillipeds with quadrate merus and ischium, merus slightly longer than ischium. Sternum broad, sternite 3 granular, short; sternites 4–7 wide, sternite 4

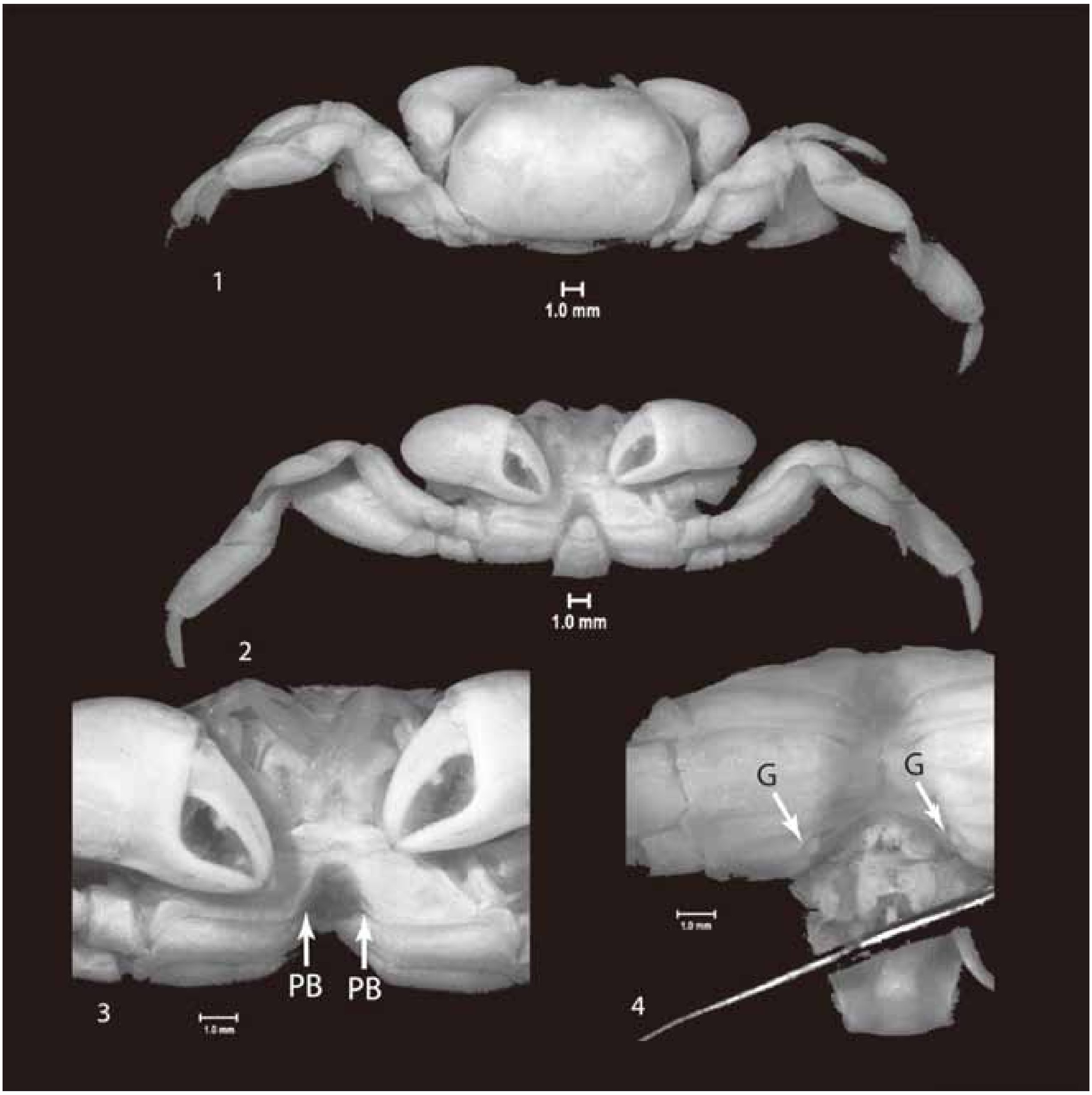

Fig. 5. *Tritodynamia horvathi* Nobili, 1905. KSU D319, male. ***1***, dorsal view. ***2***, ventral view. ***3***, ventral view of pleonal cavity with press-button sternal holding mechanism (PB). ***4***, posteroventral view of male gonopores (G). Scale bars = 1 mm.

longest, sternites 4–7 directed laterally, sternite 8 not generally visible, possibly rotated so as to be visible in posterior view, possible tiny portion of sternite 8 visible on F-35793. Pleonal cavity of male deep, narrow, extending onto sternite 4, sternite 5 with press-button locking mechanism. Male pleon with all somites appearing to be free. Female pleon very wide, all somites free, telson very short and wide.

Chelipeds short, weakly heterochelous, manus bulbous, slightly longer than high, carpus bulbous; movable finger of cheliped with narrow spine on occlusal surface, near base. Basal elements of pereiopods 2 and 4 only preserved; pereiopod 3 longest, ischium, merus, and carpus all longer than high. Pereiopod 5 shorter than pereiopods 3 and 4.

Measurements: Measurements (in mm) taken on the *Globihexapus paxillus* are presented in Table 3.

Material examined: F-81922–F-81935; KSU 279, cast of paratype USNM 501844; F-35796 (female), F-35807 (male); F-35793 (male).

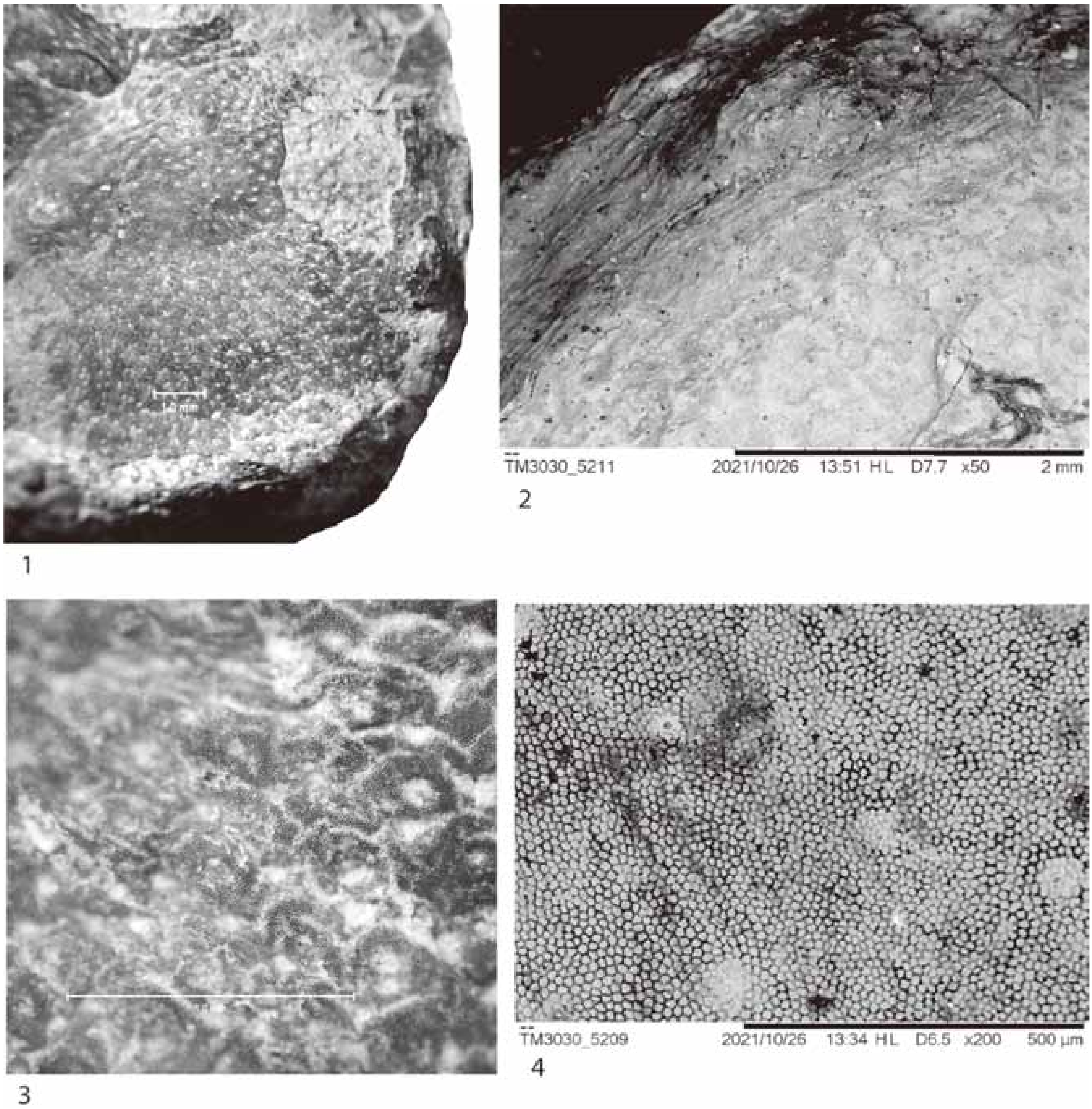

Fig. 6. *Globihexapus paxillus* Schweitzer and Feldmann, 2001. F-81923. ***1***, enlargement of the exfoliated region on the right branchial region, with exfoliated exocuticle (EX) and exposed endocuticle (EN). ***2***, SEM image of the exocuticle surface of the right branchial region and folded cuticle in the cervical groove. ***3***, enlargement of lower surface of the exocuticle showing pentagonal boundaries between nodes. ***4***, enlargement of exocuticle surface illustrating honeycomb structure on the surface reflecting the hexagonal prismatic structure (Dillaman et al., 2013) of the cuticle. Scale bars 1, 3 = 1 mm. Scale bar 2 = 2 mm. Scale bar 4 = 0.5 mm.

Discussion: *Globihexapus paxillus* was originally described based mainly on characters of the dorsal carapace. A few of the new specimens are preserved in ventral view. Those specimens retaining the ventral surface are preserved in concretions. The other specimens are preserved in matrix, possibly from concretions.

Many specimens of *Globihexapus paxillus* have asymmetrical branchial regions. These do not appear to be the result of a bopyrid isopod or other parasite because the asymmetry is not in the form of a bulbous swelling (Fig. 1). The specimen in Fig. 1 has a left branchial region that is projected somewhat further laterally than the right branchial region. Specimen F-

81924 is sheared slightly so that the point of maximum width is further posteriorly on the right side as compared to the left side. Comparison with the extant specimen of *Tritodynamia* confirms that the cuticle in that species is soft; thus, it is probable that the specimens of *G. paxillus* were deformed or crushed slightly when they were buried.

The carapace cuticle exhibits wrinkling which may also be the result of soft cuticle when buried (Fig. 2.1). The carapace exocuticle surface is finely punctate on the axial part of the branchial region and granular on the abaxial branchial region (Fig. 2.2). The mesogastric and urogastric surfaces are finely wrinkled with folds forming concave forward arcs. The surface of the cervical and branchiocardiac grooves are strongly folded with the fold axes parallel to the axis of the grooves (Figs. 2.1, 6.2). The granular surfaces in the branchial regions are punctate axially and each granule is set off by a polygonal boundary (Fig. 6.3). At higher magnification, the exocuticle surface is comprised of μm scale polygons (Fig. 6.4) (Dillaman et al., 2013) reflecting the outer surface of the vertical fibers of which the exocuticle is constructed. The endocuticle exhibits a granular outer surface (Fig. 6.3) with polygonal boundaries between granules. The endocuticle is populated by fine scale polygonal structures suggesting that the vertical fibers penetrate both the endocuticle and exocuticle.

3. Discussion

Fossil species of *Asthenognathus* are known from the Oligocene of Argentina; Italy; and Washington, USA. Miocene occurrences have been recorded from Argentina; Washington, USA; Hungary; and Japan. A Pleistocene occurrence has been reported from Italy. Extant species include *Asthenognathus hexagonum* and *A. inaequipes*, which are Indo-Pacific in distribution. *Asthenognathus atlanticus* has been identified from the eastern Atlantic Ocean ranging from Morocco to the English Channel, including in the Mediterranean Sea (Faasse et al., 2021). A recent occurrence of this species was reported from the North Sea, which suggests that the species may be expanding its geographic range (Faasse et al., 2021). Examination of the paleolatitude of the fossil occurrences of species of *Asthenognathus* indicates that during the Oligocene and

Table 3. Measurements (in mm) taken on specimens of *Globihexapus paxillus*.

Specimen Number	Maximum carapace length	Maximum carapace width	Fronto-orbital width	Posterior width	Frontal width
F-81933	11.8	19.4	8.7	6.7	2.7
F-81931	12.7	18.6	7.2	9.5	2.9
F-81927	10.0	17.7	8.3	6.0	2.0
F-81924	10.9	18.8	7.4	8.9	2.0
F-81925	11.0	18.0	7.7	9.2	2.4
F-81935	12.5	17.0	6.4	7.5	2.7
F-81928	12.7	18.2	7.9	9.2	2.6
F-81923	13.9	21.8	8.9	10.0	1.8
F-81930	12.6	18.5	—	—	—
F-81926	12.4	19.9	—	10.6	—
F-81932	14.2	18.4	—	—	—
F-81929	—	14.0	5.0	—	2.6
F-81934	—	17.9	—	—	—
F-81922	11.4	17.1	—	—	—

Miocene, species of *Asthenognathus* inhabited localities between 51° and 54° south latitude, similar to the 52°N latitude reported by Faasse et al. (2021). Species of Asthenognathinae appear to have changed in latitudinal range over time (Table 1). During the Oligocene, *Asthenognathus* inhabited a range of ±43°–47°. During the Miocene, that range expanded to ±37.5°–54.3°. Holocene latitudinal occurrences for *Asthenognathus* range from 5.6°–52.3°N, but with no southern hemisphere occurrences. There are no southern latitudinal occurrences after the Miocene. Thus, the lineage has been adapted to survive over a broad range of latitudes over the past 20 or so million years, more recently becoming restricted to the northern hemisphere but over a broader latitudinal range there.

In modern environments, individuals of species of *Asthenognathus* are usually found in commensal associations with axiidean shrimp, sea urchins, sipunculid worms, and polychaete worms (Faasse et al., 2021). *Asthenognathus atlanticus* inhabits intertidal regions to depths of about 200 m and usually is associated with burrows of another organism but not obligatorily (Glémarec and Hily, 1979). Modern collections of extant species indicate that they are rare, possibly due to living commensally in burrows (Faasse et al., 2021). Fossil occurrences are quite variable. *Asthenognathus urretae* is known from at least 90 specimens from the type locality (KSU and CM collections). Similarly, *A. microspinus* is known from more than 40 specimens. These abundant occurrences do not support a commensal, cryptic habitat and may be more similar to that exhibited by *Tritodynamia horvathi*, as well as other varunids, which are known to swarm (Takahashi et al., 1999; Ng et al., 2008). Most extinct species are described from 15 or fewer specimens, including *A. alleronensis*, *A. australensis*, *A. cornishorum*, *A. globosus*, *A. laverdensis*, and *A. sakumotoi*. *Asthenognathus rakosensis* is known from one fragmental specimen. *Globihexapus paxillus* was originally described from five specimens, and 17 more are reported here. Fossil occurrences of both *Asthenognathus* spp. and *Globihexapus* spp. include what appear to be molts and corpses. No specimens were recovered from burrows or were associated with another organisms. Thus, the extinct asthenognathines yield no evidence of a commensal lifestyle.

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