REVISI0N OF THE GENUS XIPHOCEPHALUS AND DESCRIPTION OF XIPHOCEPHALUS ELLISI N. SP. (APICOMPLEXA: EUGREGARINIDA: STYLOCEPHALIDAE) FROM ELEODES OPACUS (COLEOPTERA: TENEBRIONIDAE) IN THE WESTERN NEBRASKA SANDHILLS

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ABSTRACT: Xiphocephalus is revised, clarifying diagnosis of the epimerite complex, gametocyst, and oocyst. Xiphocephalus ellisi n. sp. (Apicomplexa: Eugregarinida) is described from Eleodes opacus (Coleoptera: Tenebrionidae) collected from Keith County in the Sandhills of western Nebraska. Measurements are means in micrometers. Developing trophozoites solitary; epimerite a complex of terminal epimerite and intercalating dimerite; epimerite elongate, ensiform, with transverse basal turbid, length 2–3 times width of basal turbid; width approximately half that of basal turbid; turbid toroidal, concavoconcave in anterio-posterior axis; dimerite roughly cylindrical, no longitudinal fold apparent, length approximately twice width. Association late, frontal, isogametotic. Protonemertes depressed ovoid, length 84.1, width 114.9, anterior distance to widest point 50.8. Protonemertes–deutonemertes septum clearly marked and constricted, width 99.3. Deutonemertes narrowly ovoid, length 1,094.0, maximum width 197.0, anterior distance to widest point 137.8, equatorial width 163.3. Total length 1,204.4. Nucleus ellipsoid, length 64.9, width 42.2; typically with 2–3 polysomal endosomes. Gametocytes roughly spherical, length 376.1, width 348.2, wall paperlike, papillated, dehiscing by simple rupture, releasing oocysts in coiled chains, epispore packet absent, gametocyst residuum present. Oocysts brown to black, broadly deltoid, gibbous in lateral aspect, slightly keeled in dorsal aspect, length 9.7, height 8.5; with terminal protruberances and a single, central, spherical residuum.

The family Stylocephalidae comprises 15 genera and 90 species united by the form and color of the oocyst and the structure and development of the gametocyst. Known species are described primarily from tenebrionid beetles. The genera Lepismatophila Adams and Travis, 1935, and Colepismatophila Adams and Travis, 1935, are reported only from Thysanura and their oocysts are aberrant, thus it is not clear that their placement among Stylocephalidae is correct. Stylocephalus Ellis, 1912, and Xiphocephalus Théodoridès, 1963, are among the most speciose genera in the family, encompassing over half of the family’s known diversity. At least 2 generic definitions of Xiphocephalus are currently in use, and although Xiphocephalus have been reported in Old World tenebrionid beetles from Europe (Blanchard, 1905; Théodoridès, 1954; Tuzet and Ormières, 1955, 1956), Africa (Théodoridès et al., 1965), and India (Devdhar and Amoji, 1977; Patil and Amoji, 1985), no type or voucher specimen is available to support a named species. No species is reported from the Nearctic, but little survey activity among Nearctic Stylocephalidae has been reported since Xiphocephalus was erected.

During an on-going biotic survey of the gregarine parasites of North American insects, a hereofore unknown gregarine species was discovered in populations of Eleodes opacus (Say, 1824) (Insecta: Coleoptera: Tenebrionidae: Eleodiini) in the Sandhills region of western Nebraska. The gregarine populations recovered are taxonomically distinct from known gregarine species and represent a new species of Xiphocephalus Théodoridès, 1963.

The taxonomy of Stylocephalidae is confused and chaotic but exemplifies the fundamental, generalized problem of gregarine taxonomy. Gregarine taxonomic diagnosis usually depends upon comparative morphometric analysis. The utility of such a comparison depends upon the developmental stability of the measurements chosen and the degree to which such measurements actually reflect the complex shape of the organism. The current system of gregarine morphometric analysis utilizes a rudimentary character set that inadequately describes gregarine shape. Additionally, ontogenetic stages (trophozoites, sporonts, and gamonts) are not always readily discriminated. Measurements can be taken from all 3 stages separately, but usually measurements are reported from mixed populations, accentuating developmental variation and exacerbating an already difficult task.

The developmental stability of morphometric characters is a critical issue for gregarine taxonomy. Measurements taken from sporonts and gamonts are relatively stable because these are mature specimens. Measurements taken from trophozoites or mixed populations are inherently nondiscriminating because they are based on a changing population; the resulting morphometrics are confounded by continuous developmental variation within a single gregarine taxon (see Watwood et al., 1997). These problems have led to a gregarine systematic that is at best in a state of chaotic flux, e.g., Stylocephalus, and at worst impenetrable and untenable, e.g., Gregarina. The description presented herein alleviates these problems by utilizing an extended morphometric character set for gamonts of Stenophoriaceae, restricting analysis of continuous morphometric characters to mature or invariant stages, and standardizing discontinuous epimerite characters. In addition to introducing a more rigorous gregarine taxonomic protocol, this work revises the generic definition of Xiphocephalus and proposes a new species within the genus.

MATERIALS AND METHODS

Eleodes opacus (Say, 1824) adults (n = 34) were collected from beneath cattle dung pats surrounding the stock tank at Beckius’ Windmill, approximately 2 km north of Roscoe, Keith County, Nebraska, between 15 June and 28 July 1997. Locality coordinates were determined with an Eagle Explorer Global Positioning Satellite locator. Beetles were transported to the laboratory at Cedar Point Biological Station, divided into lots of 4–6 individuals each, and held in 250-ml glass culture dishes (Carolina Culture Dishes, Carolina Biological Supply Company, Burlington, North Carolina) with damp filter paper. All beetles were held for at least 6 hr for gametocyst shedding and then either preserved as permanent specimens or examined for gregarine infection within 48 hr of collection. Beetles were eviscerated and their alimentary canals dissected in insect muscle saline (Belton and Grundfest, 1962).

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Table I. Described Xiphcephalus species, synonyms, and host records.

<table>
<thead>
<tr>
<th>Species</th>
<th>Year</th>
<th>Location</th>
<th>Host</th>
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<tr>
<td>X. africanaus</td>
<td>1965</td>
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<tr>
<td>X. gladiator</td>
<td>1905</td>
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**DESCRIPTION**

X. africanaus (Théodore, Desportes, and Jolivet, 1965)

*Stylocephalus* africanaus Théodore, Desportes, and Jolivet, 1965

*Erodus granipennis* Fairmaire; Kénitra, Morocco

*Pimelia grandis* Klug; Tutti Island, Shemba, Khartoum, Sudan

*Pimelia platynota* Fairmaire; Kénitra, Morocco

*Pimelia ronduripennis* Kraatz; Kénitra, Morocco

*Pogonobasis raffrayi* Haag; Burri, Khartoum, Sudan

*Prionothea coronata* Olivier; Tutti Island, Shemba, Khartoum, Sudan

*Thriptera crinita* Klug; Shemba, Khartoum, Sudan

*Zophosis trilineata* Olivier; Saint Louis, Senegal

**X. ellisi** n. sp.

ex. *Eleodes opacus* (Say); Keith County, Nebraska, USA

**X. gladiator** (Blanchard, 1905) Corbel, 1971

*Stylocephalus* gladiator Blanchard, 1905

*Stylocephalus* gladiator Watson, 1916

ex. *Elenophorus collaris* Linnaeus; Nîmes, France

*Gonocephalus* gonocephali Patil and Amoiji, 1985

*Eleodes opacus* (Say); Keith County, Lincolnshire, USA

**X. karnatakaensis** (Devdh and Amoiji, 1977) Levine, 1984

*Stylocephalus* karnatakaensis Devdh and Amoiji, 1977

*Gonocephalus* hoffmannseggi Stevens; Dharwar, Karnataka, India

**X. latipes** Patil and Amoiji, 1985

ex. *Sclero* latipes (Guérin-Meneville); Dharwar, Karnataka, India

**X. phaleriae** (Tuzet and Ormières, 1955) Corbel, 1971

*Stylocephalus* phaleriae Tuzet and Ormières, 1955

*Phaleria cadaverina* Fabricius; Sète, France

**X. reiterae** Patil and Amoiji, 1985

*Schlumbergera* reitteri Gebien; Dharwar, Karnataka, India

**X. serpentina** (Devdh and Amoiji, 1977) Levine, 1984

*Stylocephalus* serpentina Devdh and Amoiji, 1977

*Gonocephalus* hoffmannseggi Stevens; Dharwar, Karnataka, India

Permanent parasite preparations were made with wet smears of gregarines and host gut tissues (Clapton, 1996). Wet smears were fixed for 3 min in APA (ethanol, formalin, and acetic acid [Galigher and Kozlof, 1971]), washed in 70% ethanol, stained with either either Semichon's acetocarmine (Semichon, 1924) or Heidenhain's hematoxylin (Galigher and Kozlof, 1971), dehydrated in ethanol, cleared with xylene, and mounted in Damar balsam (Galigher and Kozlof, 1971). Gametocytes were stained with acridine orange and counterstained with DAPI (4',6-diamidino-2-phenylindole). Water was added to the margins of the culture plate to provide humidity, and the gametocytes were held for maturation and dehiscence. Oocyst structure and dimensions were taken from fresh preparations of oocysts in agar monolayer mounts prepared as follows. Molten agar (1.5% solution) was pipetted onto a clean glass slide and allowed to drain, and the slide was quickly chilled on a cold aluminum block to produce a thin, uniform layer of agar. Oocysts were placed in a small (ca. 5 µl) drop of water on a 12-mm-round cover glass (#0 thickness), and the agar slide was inverted to pick up the cover glass. The resulting preparation produced a monolayer of oocysts trapped between the agar layer and the cover glass. The monolayer technique provides a uniform object plane well suited for light microscopy with dry or oil-immersion objectives.

Observations were made with an Olympus B-Max 50 compound microscope with 20X, 40X, and 100X universal planapochromatic objectives and either phase contrast condensers or differential interference contrast prisms. Digital photographs were taken with an AGFA ActionCam digital camera through the aforementioned microscope with either a green density filter (phase contrast condensers) or a neutral density filter (differential interference contrast prisms and condenser). Measurements were taken from digitized images of live specimens with BioScan Optimas® v.4.1 image analysis software (BioScan Inc., Edmonds, Washington). Drawings were made with the use of digitized images of live and fixed specimens. Photographic plates were processed and assembled with Adobe Photoshop® 4.0 software (Adobe Systems, Inc., San Jose, California).

Morphometric measurements taken were those depicted in Figures 1 and 2. Measurements (in micrometers) are presented as range values followed by means, standard deviations, and sample sizes in parentheses. Terminology for parasite ontogenetic stages and anatomy largely follows that proposed by Levine (1971). Filippioni (1949) recognized 2 distinct components comprising an epimere complex in *Stylocephalus*: the terminal epimere or holfast proper and the diemeter, an intercalating neck or stalk between the epimere and the protomere. Filippioni's (1949) epimere complex terminology is adopted herein. Terminology for shapes of planes and solids is consistent with that suggested by the Systematics Association Committee for Descriptive Biological Terminology (Anonymous, 1962). Additional terminology is derived from Harris and Harris (1994).

**DESCRIPTION**

X. théodorei, 1963

*Stylocephalus* X. théodorei, 1963

*Stylocephalus* ellisi, 1912, pro parte

**Revised diagnosis**

Eugregarina Léger, 1892, sensu strictu Levine et al. (1980); Sepatina Lankester, 1885, sensu strictu Levine et al. (1980); Stenophoricae Levine, 1984, sensu Chakravarty, 1960; Stylocephalidae Ellis, 1912, with the characters of the genus *Xiphcephalus* Théodore, 1963, amended as follows: epimere complex elongated into a cylindrical, often filiform diemeter, expanding terminally to form the epimere proper; epimere elongated into a xiphoïd process (including deltoid, eniform, lanceolate, and gladiate forms), terminating in a sharp or rounded point; gametocytes papillate, with internal pseudocyst residuum; oocysts axially asymmetric, broadly deltoid, gibbous in lateral aspect, slightly keeled in dorsal aspect (including hat-, purse-, stone-, and seed-shaped of previous authors), emerging in chains.

**Taxonomic summary**

Type species: *Xiphcephalus* gladiator Blanchard, 1905

Corbel, 1971.

**Remarks**

Théodore (1963) defined 3 subgenera within *Stylocephalus*: *Stylocephalus* (Conicocephalus), *Stylocephalus* (Stylocephalus), and *Stylocephalus* (Xiphcephalus), using the specific form of the epimere proper to distinguish each of the 3 taxa. He also noted strong correlation between the shape of the epimere proper and the general form of the diemeter. *Stylocephalus* (Conicocephalus) is characterized by a broad, conical diemeter terminating in a distinctive nipple. *Stylocephalus* (Stylocephalus) is characterized by a cylindrical diemeter terminating in a simple sphere. *Stylocephalus* (Xiphcephalus) is characterized by a cylindrical, often filiform diemeter bearing a long, xiphoïd, or lanceolate epimere with a blunt or sharp apex. (Corbel, 1971) elevated *S. (Xiphcephalus)* to the generic level in his revision of the *Stylocephalidae* but failed to distinguish his diagnosis on the filiform nature of the diemeter. He did not alter the position of *S. (Conicocephalus)*. Subsequent authors
The authors have confirmed the *Xiphocephalus* sensu strictu hypothesis, describing 5 (Devi and Amo, 1977; Patil and Amo, 1985) of the genus' 6 species since Corbel (1971) elevated *Xiphocephalus*. In addition, gametocyst structure and developmental pattern and oocyst structures are consistent among known species of *Xiphocephalus*. The genus is amended here to clarify the diagnostic intent of Théodorides (1963) and to include known gametocyst and oocyst morphology. Described species of *Xiphocephalus* are presented in Table 1.

*Xiphocephalus ellisi n. sp.*

(Figs. 3–12)

**Wrotezoite** (Figs. 3, 4, 8): Developing trophozoite solitary (Figs. 3, 8), attached to host ventricular epithelium. Holmental an epimerite complex of terminal epimerite and intercalating diamerite. Epimerite elongate, xiphid (Figs. 3, 4, 8), eisnotref ormally obese, with transverse basal tami, narrowing anterior, length 2–3 times width of basal tami, approximately equal that of diamerite; width essentially half that of basal tami, less than that of diamerite; enlarging posteriorly at fusion with diamerite to form a basal tami; tami toroid, concavo-concave in anterioposterior axis, width approximately twice length; diamerite roughly cylindrical, tapering anterior with distinct constriction at junction with epimerite, little or no evidence of longitudinal folds, length approximately twice width; without visible septum at junction with protomerite but clearly differentiated by decreased density of cytoplasm. Protomerite broadly ovoid to very broadly ovoid. Protomerite–deutomerite septum clearly marked and constricted. Deutomerite obovoid to narrowly obovoid, Nucleus ellipsoid to broadly ellipsoid; with 2–3 distinct polysomal endosomes.

**Gamont** (Fig. 5): Protomerite depressed ovoid to very broadly ovoid, length (PL) 60.3–118.6 (84.1 ± 15.0, 30), width (PW) 85.3–168.7 (114.9 ± 21.2, 30), PL/PW 0.6–0.9 (0.7 ± 0.1, 30), anterior distance to widest point (PLA) 33.0–71.9 (50.8 ± 9.8, 30), posterior distance to widest point (PLP) 19.7–52.0 (33.2 ± 9.0, 30), PL/PL 0.7–2.9 (1.6 ± 0.5, 30), PLA/PLP 0.3–0.4 (0.3 ± 0.4, 30), PL/PW 0.2–0.4 (0.3 ± 0.1, 30). Protomerite–deutomerite septum equally marked and constricted, width (SW) 67.8–139.4 (99.3 ± 16.3, 30), PW/SW 0.9–1.3 (1.2 ± 0.1, 30). Deutomerite obovoid to very narrowly obovoid, length (DL) 150.6–1,638.3 (1,094.0 ± 313.4, 30), maximum width (DWM) 101.3–240.0 μm.

**Figures 1, 2.** Morphometric measurements for Stylocephalidae. 1. Trophozoite. 2. Oocyst. DL, deutomerite length; DLA, deutomerite length anterior greatest width; DLE, deutomerite length at equator (~ DL); DLP, deutomerite length posteriad greatest width; DWE, deutomerite width at equator; DLM, deutomerite greatest width; KD, karyosome diameter; NL, nucleus length; NW, nucleus width; OH, oocyst height; OL, oocyst length; PL, protomerite length; PLP, protomerite length anterior greatest width; PPL, protomerite length posteriad greatest width; PW, protomerite width; RD, residuum diameter; SH, oocyst shoulder height; SW, width at protomerite–deutomerite septum; TL, total length.

**Figures 3–7.** *Xiphocephalus ellisi* n. sp. 3. Solitary trophozoite. 4. Protomerite and epimerite complex of trophozoite, detail. 5. Gamont. 6. Oocyst chain. 7. Oocyst with central residuum and enfolding sporozoites.
303.8 (197.0 ± 45.4, 30), anterior distance to widest point (DLA) 49.8–419.0 (137.8 ± 67.6, 30), posterior distance to widest point (DLP) 27.1–1,425.7 (956.1 ± 281.7, 30), equatorial width (DWE) 113.1–255.6 (163.3 ± 34.3, 30), anterior distance to equatorial plane (DLH) 349.8–830.2 (559.5 ± 129.9, 30), DL/DWM 1.5–7.7 (5.5 ± 1.1, 30), DWM/DWE 0.9–1.3 (1.2 ± 0.1, 30), DLA/DWM 0.4–1.4 (0.7 ± 0.2, 30), DLP/DWM 0.3–7.0 (4.8 ± 1.2, 30), DLH/DWE 2.7–4.8 (3.5 ± 0.6, 30), DWM/SW 1.3–2.5 (2.0 ± 0.3, 30), DWE/SW 1.3–2.1 (1.6 ± 0.2, 30). Total length (TL) 737.4–1,736.8 (1,204.4 ± 272.8, 30). Indices: PL/TL 0.1–0.1 (0.1 ± 0.0, 30), PL/DL 0.1–0.5 (0.1 ± 0.1, 30), PW/DWM 0.5–0.9 (0.6 ± 0.1, 30), PW/DWE 0.6–0.9 (0.7 ± 0.1, 30), DL/TL 0.1–1.0 (0.9 ± 0.1, 30). Nucleus ellipsoid, typically abaxial; length (NL) 38.2–86.8 (64.9 ± 11.6, 30), width (NW) 21.1–66.8 (42.2 ± 10.5, 30), distance to protomerite–deuteromerite septum (NDS) 24.9–981.5 (201.9

± 220.0, 30, NL/NW 1.1–2.1 (1.6 ± 0.2, 30); typically with 2 but sometimes 3 polysomal endosomes, diameter (KD) 11.9–26.5 (17.2 ± 3.5, 30).

**Association** (Fig. 9): Frontal; isogamontic; late and ephemeral; leading directly to syzygy, associated pairs fusing laterally during syzygy; associations, syzygial pairs, and gametocytes located between host ventricular peritrophic membrane and posterior pericellular epithelium. Gamonts in association morphometrically similar to solitary gamonts; epimerite absent.

**Gametocytes** (Figs. 10, 11): White to opalescent in color, becoming tan to light brown with maturity; roughly spherical; length 285–480 (376.1 ± 63.4, 36), width 240–470 (348.2 ± 63.9, 36); no hyaline coat apparent, gametocyct wall desiccating to become paperlike, papillated (cf. Figs. 10, 11). Gametocytes mature within 48–72 hr and dehisce by simple rupture of the gametocyst walls (Figs. 10, 11). Oocysts are extruded in a coiled chain to form a single, tangled, sticky mass (Fig. 11); episporus pellet absent, gametocyct residuum present.

**Oocysts** (Figs. 6, 7, 12): Axially asymmetric, broadly deltoid, gibbow in lateral aspect, slightly keeled in dorsal aspect, very uniform in size and shape; length (OL) 8.9–10.3 (9.7 ± 0.3, 31), height (OH) 7.8–9.1 (8.5 ± 0.3, 31); with slight terminal protruberances or shoulders, height (SH) 1.6–2.5 (2.0 ± 0.2, 31); with a single, central, spherical residuum, diameter (RD) 1.2–2.0 (1.6 ± 0.2, 31); octozooic, sporozoites resting in tandem, folded around central residuum. Extruded in chains (Fig. 7). Oocysts dark brown under transmitted light, black under reflected light.

**Taxonomic summary**

**Host:** *Eleodes opacus* (Say, 1824) (Insecta: Coleoptera: Tenebrionidae: Eleodesini).

**Symbiotype:** One symbiotype specimen is deposited with the Division of Entomology, University of Nebraska State Museum (UNSM), Lincoln, Nebraska. The symbiotype is identified with 3 labels: a collection label, "NE: Keith Co.: Cedar Point Biol Stn, N41°12′25.8″W101°36′56.8″, July 20, 1997: R. E. Clpton, coll.""; a NFS deposition label, "Clpton: NSF DEB-9705179, NSF PROJECT VOUCHER, REC-9700143"; and a blue UNSM voucher label "RESEARCH PROJECT VOUCHER Specimen." Additional voucher specimens are retained by the author.

**Host records:** *Eleodes opacus* adults.

**Locality:** 41° 12′ 25.8″W, 101° 36′ 56.8″E, Beckius Windmill, 2 km north of Roscoe, Keith County, Nebraska.

**Infection site:** Trophozoites and gamonts were observed along the length of the ventriculus, anterior to the ileum and the attachment of the Malpighian tubules. Associations primarily located in the ileum. All endogenous life cycle stages were observed between host ventricular peritrophic membrane and ventricular epithelium. Gametocytes collected from host feces.

**Prevalence:** 90.3% (28 of 31 beetles examined postmortem).

**Specimens deposited:** The holotype slide is deposited in the Harold W. Manter Laboratory for Parasitology (HWML), Division of Parasitology, University of Nebraska State Museum, Lincoln, Nebraska. The holotype is a trophozoite on slide HWML 39724 (author’s slide REC9700221A) and is marked by an etched circle. The remaining trophozoites, gamonts, and associations in HWML 39725 (28 slides, author’s slides REC9700204; REC9700205; REC9700206; REC9700209A, B, C; REC9700210A, B; REC9700215A, B, C; REC9700216A, B, C; REC9700218A, B; REC9700219B; REC9700220A, B; REC9700221B; REC9700222A, B, C; REC9700225A, B, C; REC9700229A, B) are paratypes.

**Etymology:** I broke off my field work on this species to return for the birth of my first child and completed the work during the first weeks of his life. The specific epithet is given in honor of my son, Ellis Teague Clpton, who followed me to Cedar Point Biological Station to collect beetles when he was 1 wk old.

**Remarks**

*Xiphopcephalus ellisi* is the first species of *Xiphopcephalus* described from the New World. Gamonts of *X. ellisi* possess an ovoid to elongate ovoid deuteromere that is distinct from the serpentine deuteromeres of *Xiphopcephalus serpentina* Devdhav and Amoji, 1977, and *Xiphopcephalus gonocephali* Patil and Amoji, 1985. The eimerite proper distinguishes *X. ellisi* from species with cordate (*Xiphopcephalus latipes* Patil and Amoji, 1985; *Xiphopcephalus karnatakaensis* Devdhav and Amoji, 1977) or gladiate (*Xiphopcephalus gladiator* [Blanchard, 1905]; *Xiphopcephalus africanus* Théodoridès, Desportes, and Jolivet, 1965) epimerites. *Xiphopcephalus africanaus* is independently distinguished by a diamere with distinct marginal paraglycogen deposits bordering an agranular central channel. This structural combination is not observed among *X. ellisi*. The epimerite structure of *X. ellisi* is most similar to that of *Xiphopcephalus reitteri* Patil and Amoji, 1985, but these taxa are morphometrically disparate. Gamonts of *X. ellisi* range 737.4–1,756.8, their average length being readily twice that of the largest reported gamont of *X. reitteri* (TL 545.0–650.0; Patil and Amoji, 1985).

*Xiphopcephalus reitteri* also possesses a distinctive, terminal “ectoplasmic tail” that is retained into syzygy (Patil and Amoji, 1985). The ectoplasmic tail does not occur among *X. ellisi* but remains autapomorphic for *X. reitteri*.

**ACKNOWLEDGMENTS**

I appreciate the use of facilities at the University of Nebraska’s Cedar Point Biological Station (CPBS), Keith County, Nebraska. Special thanks to the CPBS Director and Assistant Director, John Janovy, Jr., and Mary Batterson, for accommodating my wife and new son at the station. This material is based upon work supported by the National Science Foundation under grant DEB-97-05179.

**LITERATURE CITED**


