ONTGENY OF THE PROTOID TRILOBITE STENOBLEPHARUM, AND RELATIONSHIPS OF A NEW SPECIES FROM THE UPPER ORDOVICIAN OF ARGENTINA

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ABSTRACT—Silicified material from the Early Caradoc part of the Las Aguaditas Formation in San Juan Province, Argentina, includes a nearly complete growth series for a new species of the tropidocoryphid Stenoblepharum Owens, 1973. Cladistic analysis of Stenoblepharum indicates that S. astini new species is most closely allied to the Early Caradoc S. strasburgense (Cooper, 1953) from Virginia. Chinese species of Stenoblepharum are sister group to a Baltico/Laurentian clade. A single adult-like protaspis stage occurs in the life cycle of S. astini, closely resembling the protasps of Decorooprotus. It is preceded by a non-adult-like first protaspis instar that appears to be characteristic of Proetoidea in general but contrasts markedly with the early larval stages of other taxa in Proetoidea.

INTRODUCTION

Middle to Late Ordovician (Llanvirn to Caradoc) silicified faunas from the Precordiller a of Argentina contain a range of superbly preserved trilobites. This work is one of a series documenting the ontogeny, taxonomy, and phylogenetic relationships of trilobites from the Las Aguaditas Formation southwest of Jáchal, San Juan Province (Chatterton et al., 1997).

Only a single species of the Proetoidea, Stenoblepharum astini new species, is known from the Las Aguaditas Formation at its type locality, Quebrada de Las Aguaditas. The section crops out on the eastern flank of the Cordón de Los Blanquitos in the northern part of the San Juan Precordillera (see Chatterton et al., 1997, fig. 1, for locality map). Numerous horizons from the Early Caradoc Nemagrapthus gracilis Zone (Brassa, 1994, in press) have yielded silicified specimens of S. astini (Figure 1). The Las Aguaditas Formation is composed of a rhythmic succession of calcareous and marly beds with intercalated breccias deposited on a carbonate margin to foresets facing (Astini, 1995).

In this work we describe the ontogeny of Stenoblepharum astini new species from protaspids through holaspis periods, the best known proetoid ontogeny to date, and consider relationships within Stenoblepharum Owens, 1973a.

SYSTEMATIC PALEONTOLOGY

Figured specimens are housed in collections of the Cátedra de Estratigrafía y Geología Histórica, Universidad Nacional de Córdoba (prefix CEGH-UNC), and the Division of Invertebrate Paleontology, Peabody Museum of Natural History, Yale University, New Haven (prefix YPM).

Proetoidea Salter, 1864
Tropidocoryphidae Pribyl, 1946
Stenoblepharum Owens, 1973a

Type species.—Paraproetus warburgae Pribyl, 1964, from the Boda Limestone (Ashgill), Dalarna, Sweden (revised Owens, 1973a); also known from the Chair of Kildare Limestone (Ashgill), Ireland (Dean, 1974).

Diagnosis.—Dorsal exoskeleton relatively strongly arched (tr.); preglabellar field of equal length to or shorter than anterior cranial border (longer only in plesiomorphic species); glabellar furrows lightly incised; L0 moderately to strongly shortened distally; interocular fixigenae narrow; rostral plate trapezoidal to subtriangular, strongly narrowing backwards, connective sutures adaxially convex, three to five pygidial axial rings; three or four pleural furrows; anterior band of pygidial pleurae elevated as crest; pygidial border absent; dorsal sculpture of fine striations and granulation.

Phylogenetic analysis.—A new species from the Las Aguaditas Formation shows obvious affinities to certain taxa classified as Stenoblepharum Owens, 1973a. To resolve phylogenetic structure within this genus, we outline a cladistic analysis for adequately known species of Stenoblepharum. This provides a basis for the emended generic diagnosis above. Character codings were made for S. warburgae (Pribyl, 1964); S. dactylum (Xia, 1978; revised Zhou and Xiang, 1993); S. kullbergense (Warburg, 1925; revised Owens, 1973a); S. norwegicum Owens, 1973a; S. planum Zhou and Xiang, 1993; S. strasburgense (Cooper, 1953) and, S. zalesskyi (Opik, 1937). These were coded from published sources except for S. strasburgense, for which new collections were examined, and S. zalesskyi, for which the types were studied at the Institute of Geology, Estonian Academy of Sciences, Tallinn. Dean's (1974) Irish material of S. warburgae was examined in the Natural History Museum, London, but the species' coding was based solely on specimens from the type stratum, the Boda Limestone, in Sweden (Owens, 1973a). Coding for S. dactylum includes conspecific material figured by Ji (1986), accepting the synonymy of Zhou and Xiang (1993).

Owens' (1973b) hypothesis that Stenoblepharum was derived from Decorooprotus, accepted by Lütke (1980), provides an appropriate outgroup to root the tree, but the monophyly of Decorooprotus (sensu Owens, 1970, 1973b, b) is doubtful. Several of the better known Llandeilo and Caradoc species of Decorooprotus were thus considered to determine possible basal states for Stenoblepharum. These are: D. fennisi (Bancroft) pristinus Owens, 1973b; D. furuvgerensis Owens, 1970; and D. solenotus Owens, 1970. Owens (1973b, text-fig. 11) and Lütke (1980, fig. 419
Table 1—Character matrix for species of *Stenoblepharum* and allied taxa. Characters 1–18 are as described in the text. State 0 is plesiomorphic, states 1 and 2 are apomorphic. "?" indicates missing data.

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26) interpreted a few other lineages as Upper Ordovician branchings from *Decropoetopus*, with one (Eremiproetinae) possibly derived from *Stenoblepharum*. To evaluate this idea we have considered the earliest species referred to *Eremiproetus* (the Ashgill *E. agellus* Owens, 1973a; but see Holloway, 1980, for a critique of the generic assignment of "E." *agellus*).

An alternative to Owens' (1973a, b) and Lütke's (1980) derivation of *Stenoblepharum* from *Decropoetopus* (Tropidocoryphidae) is the view of Přibyl and Vaněk (1987) that *Stenoblepharum* "shows a clear-cut proetid character". This obviously impacts upon the selection of an appropriate outgroup. Přibyl and Vaněk's evidence was "a broad glabella without marked preglabellar field and tropidium, the shape of the pygidium with a small number of rings and ribs, i.e., characters that are usually absent in the representatives of the subfamily Tropidocoryphinae" (Přibyl and Vaněk, 1987, p. 68). Přibyl and Vaněk's arguments are weakened by several facts: most species of *Stenoblepharum* have a glabellar shape very similar to that of many *Decropoetopus*; the preglabellar field is usually well marked in *Stenoblepharum*; they do not account for the typically tropidocoryphid imbricate (Owens, 1973b) pygidial rib structure in *Stenoblepharum*; and, the striated sculpture of *Stenoblepharum* (Štěpánek, 1937, pl. 3, fig. 3) resembles *Decropoetopus* but not Proetidae. Characteristic (possibly synapomorphic) proetid characters such as occipital lobes, a panderian opening at the base of the genal spine, and thoracic preamnuli are absent in *Stenoblepharum*. Accordingly, we have maintained Owens' and Lütke's hypothesis.

Characters.—Eighteen characters as described below were coded for eight species of *Stenoblepharum*, "Eremiproetus" *agellus*, and an outgroup, *Decropoetopus* (Table 1). States in *Decropoetopus solenotus* and *D. furubergerense* coded identically for the characters considered here that varied within *Stenoblepharum*, so only a single outgroup coding is shown. Ten characters are binary (0/1), and eight are multistate (0/1/2).

1. Length of preglabellar field: 0) distinctly longer than anterior border; 1) about equal in length to anterior border; 2) much shorter than anterior border.

This character is polarized the same by ontogeny and outgroup comparison. The ontogeny of *S. astini* displays a shortening of the preglabellar field, transforming from states 1 to 2.

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Figure 1—Stratigraphic column for the Las Aguaditas Formation at Quebrada de Las Aguaditas, after Astini (1995). Sampled occurrences of *Stenoblepharum astini* new species are indicated by dots, and vertical line represents known range of species. Letters and numbers to right of column indicate collections at fossiliferous horizons ('a' through 'n' correspond to horizons LA-A through LA-N in text).
Stenoblepharum planum possesses state 0 in the smallest figured cranidia (Zhou and Xiang, 1993, pl. 2, fig. 5), transforming to state 1 in some larger holaspides, confirming a general trend towards ontogenetic shortening of the preglabellar field. Stenoblepharum dactylum and S. planum are polymorphic for this character, with larger specimens of each coding as either of states 0 or 1.

2. Course of anterior section of facial suture, between $\gamma$ and $\beta$: 0) divergent (more than 10 degrees); 1) subparallel (less than 10 degrees).

3. Medial lengthening of anterior cranidial border: 0) border of even length (sagittally/exsagittally); 1) border longer medially than abaxially.

Ontogeny polarizes this character identically to outgroup rooting with Decoroprotus. The medial lengthening of the anterior border that distinguishes S. dactylum and S. planum is derived from a condition in juvenile stages in which the border is of even length across its width (S. planum; Zhou and Xiang, 1993, pl. 2, fig. 5).

4. Glabellar shape: 0) weakly bell-shaped, expanded against L1; 1) thimble-shaped, without significant widening against L1.

5. Strong ridges along outer edge of cephalic border: 0) absent (border bearing several weak lineations); 1) absent on cranidium, one strong ridge on librigenal border; 2) two strong ridges on cranidium and librigena.

Juvenile cranidia and librigenae of S. astinii reveal a pair of fairly strong lineations along the outer edge of the border. These are presumably homologous with the prominent pair of lineations maintained in large holaspides of S. kullsbergense, S. norvegicum, and S. warburgae but considerably suppressed in holaspid ontogeny in S. astinii. This character can be coded decisively for all species except S. zalesskii, for which the librigena is unknown. Either of states 0 or 1 may be applicable for S. zalesskii, whereas state 2 is not (based on the cranidium).

6. Depth of occipital furrow abaxially: 0) not significantly shallowing, continuous with axial furrow; 1) effaced distally, not continuous with axial furrow.

7. Length of L0 abaxially: 0) with minor shortening (exsagittal length of L0 near axial furrow more than 60 percent of sagittal length); 1) moderately shortened (exsagittal length 40–60 percent of sagittal length); 2) strongly shortened (exsagittal length less than 40 percent of sagittal length).

8. Position of occipital node: 0) at midlength of L0; 1) anterior to midlength of L0; 2) posterior to midlength of L0.

This character exhibits variation within particular species, but in cases where the node ranged from midlength to either anterior or posterior, the more common condition was coded (e.g., posterior in astinii and planum, anterior in strasburgerae). Because of this variability, experiments with additive coding were not attempted.

9. Width of interocular fixigeniae: 0) wide (more than 25 percent width of cranidium across gamma); 1) narrow (less than 25 percent width of cranidium across gamma).

The definitions of wide and narrow interocular fixigenae distinguish Stenoblepharum (narrow) from Decoroprotus (wide). However, within Stenoblepharum it may prove possible to identify a subgroup of taxa at the narrow end of the range (e.g., S. norvegicum and S. warburgae), but the continuous range of variation between species has not led us to identify additional states.

Ontogeny of S. astinii provides the same polarization as outgroup comparison, with relatively wide fixigenae (state 0) in earlier growth stages transforming to narrower (state 1).

10. Width of eye socle: 0) narrowest at midlength, widening anteriorly and posteriorly; 1) of even width; 2) widening anteriorly.

States 1 and 2 are autapomorphies for single species (S. kullsbergense and S. astinii, respectively). This character is coded as non-additive to allow its cladogram character to be determined by best fit to other characters.

11. Depth of border furrow at base of genal spine: 0) deep; 1) shallow.

This character identifies a distinction between the shallow continuation of the border furrows onto the genal spine in S. astinii and S. strasburgerae versus other species. Even where the furrow is shortened to a small notch (Zhou and Xiang, 1993, pl. 2, fig. 2) it is deeper than in astinii and strasburgerae.

12. Height of pygidium: 0) low (height less than 30 percent of pygidial width); 1) high (height more than 30 percent width of pygidium).

This character is used as a measure of the high degree of exoskeletal vaulting that characterizes Stenoblepharum. Other features that could be used to express the same apomorphy would be the height of the thoracic segments or a measure of convexity of the cranidium. There is considerable variation within Stenoblepharum, ranging from a height of about 45 percent of pygidial width in S. astinii to 31 percent in S. norvegicum.

13. Number of pygidial axial rings: 0) six; 1) four or five; 2) three.

14. Number of pygidial pleural furrows: 0) five; 1) four; 2) three.

15. Curvature of pygidial pleural furrows: 0) curved distally; 1) approximately straight.

16. Impression of pygidial interpleural furrows: 0) shallower than pleural furrows; 1) subequally deep to pleural furrows.

17. Height of anterior band of pygidial pleural: 0) gently raised above posterior band (imbricate cross-section); 1) crest-like elevation above posterior band.

18. Pygidial marginal denticles: 0) absent; 1) two pairs; 2) three pairs.

Several other characters were surveyed but found to be affected by preservation and photography. These included the tendency towards obsolescence of the lateral glabellar furrows and the degree of expression of striate sculpture on the exoskeletal surface. Stenoblepharum norvegicum demonstrates the variability in definition of the glabellar furrows shown by other species as well, ranging from indistinct (Owens, 1973a, fig. 10) to clearly marked (Owens, 1973a, fig. 10L). Expression of striate sculpture ranges from prominent and similar to Decoroprotus (S. zalesskii) to subdued (S. warburgae), but is variable within species (S. astinii).

Two analyses were undertaken, running the data with and without “Eremiprotus” agellus. Cladograms were computed with PAUP Version 3.1.1 (Swofford, 1993) on a Macintosh LC 475. The small number of characters (18) and taxa (nine or ten) permits rapid, exact solutions using the branch-and-bound option. Separate runs were undertaken with all multistate characters non-additive (unordered) and then with two different combinations of ordered multistate characters. Four multistate characters (1, 7, 13, and 14) could plausibly be regarded as ordered transformation series (one state is morphologically intermediate between two others, e.g., L0 with weak, moderate, or strong distal shortening), and the trees generated with these assumptions about character relationships were examined. A fifth multistate character (18), if left unordered as coded, does not necessarily group derived states 1 and 2 as homologous, although both pertain to the presence of marginal spines on the pygidium. A third run was done with characters 1, 7, 13, 14, and 18 ordered. All PAUP trials employed ACCTRAN optimization (Swofford and Maddison, 1987). Polyomorphism in character 1 for S. dactylum and S. planum has been optimized by PAUP with both states coded for those species.
Analysis without "E." _agellus, all characters unordered, yields two shortest cladograms of 32 steps (consistency index 0.812), the strict consensus of which is shown in Figure 2.1. The only taxon whose placement differs between the two cladograms is _S. zaleskii_, which is resolved either as sister to _astinii + strasburgense_ or further down-tree, as sister to _astinii + strasburgense_ (kullsbergense (norvegicum + warburgiae)).

With characters 1, 7, 13, and 14 ordered, three shortest cladograms of 33 steps (c.i. 0.788) are found. These include the two trees produced by unordered analysis, and yield a strict consensus with one less resolved node (Figure 2.2) as the position of _S. kullsbergense_ became ambiguous. Ordering character 18 to recognize the homology of marginal spines in _Stenoblepharum_ (despite a different number, two or three) produces two shortest cladograms (Figure 2.3), of 33 steps, in which _S. zaleskii_ is sister to _astinii + strasburgense_. The position of _S. kullsbergense_ is the only source of ambiguity between the two cladograms. It should be noted that all three trials resolve the Chinese clade (dactylum + planum) as sister to all other species of _Stenoblepharum_, a Baltic/Laurentian clade.

Including "Eremiproetus" _agellus_ in the analysis produced the same results for ingroup relationships. The run with all characters non-additive yielded three shortest cladograms of 34 steps and 0.765 consistency. These include the two trees generated in the prior unordered analysis (with the addition of having "E." _agellus_ resolved outside of _Stenoblepharum_). The third topology, however, resolves "E." _agellus_ as part of the ingroup for _Stenoblepharum_, one node up-tree of _dactylum + planum_. The strict consensus is thus identical to Figure 2.1 except for adding "E." _agellus_ to a basal ingroup trichotomy. To show character distributions, one of these minimal length cladograms (Figure 3) was selected using the successive approximations weighting option of PAUP. Character weights were set by their rescaled consistency indices, a measure of the "cladistic reliability" (Farris, 1969) of the characters. This favours one of the two topologies that places "E." _agellus_ outside _Stenoblepharum_.

Ordering characters 1, 7, 13, and 14 also yields three shortest cladograms (35 steps; c.i. 0.743), of which the strict consensus is identical to that shown in Figure 2.2 except for the addition of "E." _agellus_ basally, as sister to a monophyletic _Stenoblepharum_. Finally, analysis with character 18 ordered in addition to 1, 7, 13, and 14 yielded two 35-step trees identical to those producing Figure 2.3 (except for the basal position of _agellus_).

In summary, all experiments with taxon addition and ordering of multistate characters supported four clades within _Stenoblepharum_ (astinii + strasburgense; norvegicum + warburgiae; dactylum + planum; all other species as sister to dactylum + planum). The position of _S. kullsbergense_ and _S. zaleskii_ is more ambiguous, being resolved differently depending on assumptions about character transformations. Either may be sister species to all other Baltic and Laurentian _Stenoblepharum_. Present evidence does not provide strong support for "Eremiproetus" _agellus_ being derived from within _Stenoblepharum_. As observed by Zhou and Xiang (1993), inclusion of the Chinese species requires a broadening of the diagnosis of _Stenoblepharum_ from that originally proposed by Owens (1973a), as the dactylum/planum clade lacks certain derived features of the Baltic/Laurentian group.

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1. characters unordered; 2. strict consensus of three shortest cladograms (33 steps; c.i. 0.788) with characters 1, 7, 13, and 14 ordered; 3. strict consensus of two shortest cladograms (33 steps; c.i. 0.788) with characters 1, 7, 13, 14, and 18 ordered.
The discovery of an Early Caradoc clade occurring in eastern Laurentia (Virginia) and the Precordillera permits an ecological observation in addition to the biogeographic component. Owens (1973a) noted that Stenoblepharum was largely restricted to algal reef environments, as association that appears to be limited to Ashgill species from Scandinavia. The Early Caradoc clade from eastern Laurentia and the Precordillera (strusburgense + astinii), however, inhabited a different ecological setting, as these species occur in outer shelf micrites. The same biogeographic component, Eastern Laurentia + Precordillera, was determined for contemporary species of the odontopleurid Ceratocara (Chatterton et al., 1997).

**Stenoblepharum astinii** new species

**Figures 4–8**

*Diagnosis.*—Stenoblepharum lacking preglabellar field in large holaspides; glabella subquadrate, gently bulged outward against L1, weakly narrowing anteriorly, with anteromedian margin gently convex forward; glabellar furrows shallow but distinctly impressed; posterior margin of L0 not strongly convex backwards; median occipital tubercle usually behind midlength (sag.) of L0; anterior sections of facial suture gently divergent; eye socle widening anteriorly, with shallow furrow at base; rostral plate subtriangular; pygidial axis very wide, 50–55 percent width of pygidium; articulating furrow of similar depth to first pygidial ring furrow; three pygidial pleurae terminate as small denticles; pygidial doublure moderately wide.

*Description.*—Cranidial length (sag.) slightly greater than width across palpebral lobes; axial furrow narrow, shallow against L0, moderately deep against glabella; glabellar length (sag.) about equal to maximum width across L1; glabella moderately convex (sag.), especially strongly curved down anteriorly; glabellar furrows lightly impressed; S1 gently curved, running posteroomedially from axial furrow at about 45 degrees, effacing at less than half distance to S0, S2 usually shallower than S1, gently convex forward, much less posteroomedially directed than S1; distal edge of S2 opposite γ; S3 often undefined, gently directed anteroomedially; S0 short, moderately deep; length (sag.) of L0 30 percent its width (tr.), about 20 percent length of cranidium; L0 very gently convex forward medially, shortened abaxially to 60–75 percent of sagittal length, with posterior margin weakly arched backwards medially in large specimens; small, subdued median node usually well behind midlength of L0; striate sculpture on L0 arranged as concentric, anteriorly convex arcs; glabellar striations less anteriorly arched than those on L0; striations subdued but continuous across glabellar furrows; anterior cranial margin gently convex forward; anterior border of even length (sag., exsag.), gently upturned, bearing a few weak terrace ridges; anterior border furrow narrow, only moderately deep; palpebral lobe slightly more than 50 percent length of glabella; interocular fixigena moderately sloping down to axial furrow.
FIGURE 4—1–19, *Stenoblephas* a*stinii* new species. Las Aguditas Formation (Early Caradoc), Quebrada de Las Aguditas, San Juan Province, Argentina. Stratigraphic horizons are indicated by letters following section prefix LA. All secondary electron micrographs except 5, 17, 19, backscattered electron micrographs. 1, dorsal view of metaprospsis, CEGH-UNC 14544, ×88, LA-K; 2, dorsal view of metaprospsis, CEGH-
Libigneca lacking tropidium; eye socket moderately wide, gently widening anteriorly such that its height exceeds width (tr.) of librigenal field, with base defined by break in slope and weakly impressed furrow; field covered with dense granules; lateral and posterior border furrows narrow, moderately deep; low, closely spaced terrace ridges weakly defined on outer edge of lateral border and genal spine in dorsal view, prominent in lateral and internal views; genal spine moderately long, with very shallow extension of border furrow along anterior half, no panderonder opening at base of genal spine.

Rostral plate broadly triangular, length (sag.) about 33 percent maximum width across rostral suture; connective sutures strongly convergent backwards, gently convex forwards; rostral plate bearing about seven terrace ridges.

Hypostome with maximum width across anterior wing about 90 percent maximum length; anterior margin of hypostome gently to moderately convex forwards; rear edge of short (sag., exsag.) anterior border developed as a low, transverse or anteriorly convex ridge; anterior lobe of middle body bearing strong sinuous, sublongitudinal lineations that abruptly efface at juncture with posterior lobe; lineations also strong between anterior wing and lateral shoulder; middle furrow shallow, directed inwards at about 45 degrees, effaced medially; posterolateral margin with three pairs of denticles; posteromedian angulation varying from weak to prominent, sometimes extending back equal to or farther than last pair of posterolateral marginal denticles; doubleure narrow.

Pygidial length (sag.) 50 percent of width (tr.); axial furrow narrow, shallow; axis about 50–55 percent of pygidial width; first axial ring strongly convex (tr.), sloping upwards posteriorly, with crest distinctly raised above slope of axis (sag.); third ring only moderately convex (tr.); first ring furrow narrow, moderately deep; second and third ring furrows shallow, usually gently convex backwards; unsegmented terminal piece about 35 percent length of axis in large specimens; axial terminus bluntly rounded; post-axial sector 22–29 percent length (sag.) of pygidium, steeply declined; posteromedian margin gently convex backwards between third pair of marginal spines; anterior and posterior pleural bands subequal in length (exsag.) across rib; pleural furrows at least moderately deep, flexed backwards distally, terminating just above ventrolateral margin of pygidium; interpleural furrows impressed equally to pleural furrows; doubleure moderately wide, narrowing slightly medially, with about three strong terrace ridges; sculpture of lineations strongest on first axial ring but sometimes discernable on inner part of pleurae; entire dorsal surface of pygidium (except furrows) densely covered with coarse granules.

Discussion. — Closest comparisons can be made with Stenoblepharum strasburgense (Cooper, 1953), from the Edisbury Formation (Early Caradoc) of Virginia. Proetoid holaspis pygidia figured by Hu (1971) as Phasoleops conus (Hu, 1971, pl. 23, figs. 28–31) are regarded here as belonging to S. strasburgense (see also Adrain and Chatterton, 1995a, p. 310), whereas the assigned crania (including the holotype) are those of an aulacopleurid. Additional material was referred to S. strasburgense by Hu (1975), although the assigned pygidium (Hu, 1975, pl. 2, figs. 21–24) is much less similar to that of S. astini than is that figured as P. conus by Hu (1971). The supposed conus pygidium (here regarded as that of S. strasburgense) bears three marginal denticles and has relatively deep interpleural furrows, thus being very similar to that of S. astini, whereas the alleged strasburgense pygidium of Hu (1975) has an entire margin and faint interpleural furrows. There is no question of misassociation of sclerites for S. astini, as it is the only species of Proetidae or Tropidophyridae at all levels from which it is known. The association of a denticulate pygidium in S. zaleskyi (Opik, 1937), a species for which Owens (1973a, p. 155) noted the cranium to be “remarkably similar to that of Stenoblepharum strasburgense” provides additional evidence that the pygidium of S. strasburgense should be denticulate. Also, we have processed and picked samples from the Edisbury Formation that include S. strasburgense, and have identified crania and libignecae of a co-occurring Decoropectus-like proetoid to which we refer the Decoropectus-like pygidium assigned to Stenoblepharum by Hu (1975).

Stenoblepharum astini and S. strasburgense share at least four compelling derived characters that suggest a sister species relationship. These are the shallow extent of the border furrow onto the librigenal spine (versus a short but sharply impressed furrow in S. warburgiae and S. norwegicum), a very short preglabellar field, pygidial interpleural furrows that are deepened equal to the pleural furrows, and the development of denticulate terminiae on the three pairs of pygidal pleurae. Stenoblepharum astini is distinguished from S. strasburgense by its more quadrate (versus subparabolic) glabellar outline; the complete loss of the preglabellar field medially; more distinct glabellar furrows; a less posteriorly convex margin of LO with less marked shortening of L0 distally; an occipital tubercle that is usually posterior to the midlength of L0, rather than anterior; shallow furrow defining the base of the eye socle; the eye socle widening anteriory, rather than anteriorly and posteriorly; longer, more slender genal spine; a wider pygidial axis (50–55 percent width of the pygidium versus 40–45 percent); a less marked difference in depth between the first pygidial ring furrow and the articulating furrow (the latter being much deeper in S. strasburgense); and, a narrower pygidial doubleure that lacks the weak posteromedian embayment of S. strasburgensen (Hu, 1971, pl. 23, fig. 30).

The other Early Caradoc species, the Estonian S. zaleskyi (Opik, 1937), is known solely from two crania and a pygidium from the Kukruse Stage. All of the cranial differences between S. astini and S. strasburgense noted above pertain also to the former and S. zaleskyi. S. astini further differs from S. zaleskyi in the following: more subdubed sculpture of lineations on the cranium; 33 directed anteromedially, rather than posteromedially (best shown on the holotype cranium of S. zaleskyi,
Figure 5—1–21, *Stenoblepharum astinii* new species. Las Aguaditas Formation (Early Caradoc), Quebrada de Las Aguaditas, San Juan Province, Argentina. Stratigraphic horizons are indicated by letters following section prefix LA. All secondary electron micrographs except 1, 11, 14, 22, backscattered electron micrographs. 1, dorsal view of left librigena, CEGH-UNC 14563, ×80, LA-H; 2, dorsal view of left librigena, CEGH-UNC 14564, ×80, LA-H; 3, dorsal view of left librigena, CEGH-UNC 14565, ×60, LA-K; 4, dorsal view of left librigena, CEGH-UNC 14566,
Tr 2208); anterior section of the facial suture that is gently divergent between \( \gamma \) and \( \beta \), rather than markedly divergent; three, rather than two, pairs of pygidial denticles; and, stronger impression of the interpleural furrows proximally.

The other Caradoc species from Baltica, Stenoblepharum kullsbergenense, bears closer comparison to \( S. \) asinii than does the Ashgill clade of \( S. \) warburgae and \( S. \) norwegicum, although these similarities are pleisomorphies shared with Decoroeproetus and Chinese Stenoblepharum. Conspicuous shared primitive characters of \( S. \) asinii and \( S. \) kullsbergenense include the posterior bulge in the glabellar outline, distinctly impressed glabellar furrows, and \( L0 \) not being strongly shortened distally.

It is not currently possible to make a meaningful comparison with the Ordovician proetoid from Mendoza described by Rusconi (1955) as Proetus pichuywelchensis. The subquadrate glabellar outline, lack of a preglabellar field, obscure glabellar furrows, and the three pairs of pygidial pleurae figured by Rusconi (1955, pl. 5, fig. 7) are suggestive of \( S. \) asinii. The taxa are at least specifically distinct, as indicated by Rusconi’s description of seven pygal axial rings and the extent of the axis near to the pygal terminus in pichuywelchensis. The figured specimen was not located in the collections of the Museo de Historia Natural de Mendoza during a visit by the authors in 1994. New collections from the same unit, the Empeza Formation, show a species of Decoroeproetus to be the typical proetoid.

The hypostome has not previously been known for any Stenoblepharum species, so that of \( S. \) asinii provides new data for considering relationships of the genus. The middle body is much less inflated (sag., tr.) than in early cornuproetoids (Interproetus; Thomas, 1978, pl. 11, fig. 11b) or in Decoroeproetus (Owens, 1973b, pl. 10, figs. 3b,c). The three pairs of marginal spines of Stenoblepharum asinii are, however, known from some species of Decoroeproetus (Holloway, 1980, pl. 5, fig. 1).

The rostral plate of Stenoblepharum asinii (Figure 5.11) resembles that of \( S. \) warburgae (Owens, 1973b, text-fig. 1B.5) in the strong posterior convergence of the connective sutures, although the overall outline of the plate differs substantially. The connective sutures are much straighter than in \( S. \) warburgae, maintaining an even convergence backwards such that the rostral plate is more nearly triangular in outline.

**Protaspis period.**—One non-adult-like and one adult-like (sensu Speyer and Chatterton, 1989) protaspis stage are known for \( S. \) asinii. They are hereafter cited as anaprotaspis and metaprotaspis stages, respectively. The assignment of the typically proetoid metaprotaspis (Figure 4.1–4.4) is straightforward, but the association of the anaprotaspis (Figure 8.1–8.13) requires discussion.

Positive evidence for the association of the anaprotaspis with Stenoblepharum asinii is based on the following: 1) this instar fits the growth trajectory for that species (Figure 9), not violating Dyar’s or Przibram’s laws (Chatterton et al., 1990, p. 260); 2) anaprotaspides similar in form have been found by one of us (B.D.E.C.) in other proetoid-bearing samples (see below). Chatterton (1971, pl. 21, fig. 8–11) assigned an Australian Lower Devonian protaspis of the type that we associate here with Stenoblepharum to a species of Phacops. No Phacopina such as pterygotomorphs co-occur with \( S. \) asinii in the Las Aguaditas Formation. However, a proetid, Devonoproetus talenti (Chatterton, 1971), occurs in the same samples as the Stenoblepharum-like Lower Devonian anaprotaspis. An unpublished sample discovered by B.D.E.C. in the Middle Devonian of the Mackenzie Mountains, Canada, also contains protaspides of this type, associated with only two species of trilobites, one a species of the proetid Diuchenella, and the other the stygiid Ancyropsy. Stygiid early protaspides are known (see Failliana in Chatterton, 1980), and are quite distinct from the protaspides described here.

Negative evidence in support of the hypothesis that this type of larva is proetid involves the absence of anaprotaspides of the type described here from numerous appropriately-aged samples that lack proetids or tropidocoryphids, but with well preserved trilobite growth stages (e.g., other levels in the Las Aguaditas Formation; in Chatterton, 1980; Shaw, 1968; and in numerous unpublished samples of Ordovician to Devonian age in collections of B.D.E.C.).

The discovery that proetoids possess a distinctive, non-adult-like first larva may have implications for the debate over the monophyly (Fortey and Owens, 1979; Fortey, 1990) or polyphyly (Bergström, 1977) of the order Proetida Fortey and Owens, 1975. These new data demonstrate that Proetida contains taxa with at least two different early life history strategies. Within this order, aulacopleurids, scharyids, hystricurids, dimeropygids, and some telephinds have been described with smallest larval stages that are more generally adult-like (Chatterton, 1980; 1994; Adrain and Chatterton, 1995a, 1995b; Chatterton and Speyer, in press). These protaspides are as small as, but morphologically very distinct from, the anaprotaspides assigned to Stenoblepharum and Devonoproetus. They have a much less bulbous form, a reentrant posterior margin, and only one pair of marginal spines. All of the groups within Proetida that have the more adult-like first protaspis usually have a distinct pattern of raised tubercles on the cephalon and protopygidium in later protaspis stages, as well as in early meraspis degrees. Proetids and tropidocoryphids, with a bulbous anaprotaspid, are usually smooth and lack a pattern of raised tubercles. While the proetoid anaprotaspis retains clear evidence for its librissome/pytophorid affinities, its novel characters are its inflation, degree of effacement, and very long hypostome. It is not presently clear whether the two early life history strategies (Proetoidea versus hystricurids-dimeropygids-aulacopleurids-schariyids) imply that Proetida may have more than one origin within Libristoma. An alternative would be to maintain that their similar metaprotaspides (the proetide protaspis sensu Fortey, 1990) are a synapomorphy uniting all these taxa, and the disparity in earlier larval ontogeny results from apomorphies in different groups.

**Anaprotaspis.**—First protaspis instar (Figure 8.1–8.13) approximately equidimensional to very slightly longer than wide, length (sag.) 0.38–0.46 mm, width (tr.) 0.36–0.42 mm; axial
Figure 6—1–16. Stenoblepharum astinii new species. Las Aguaditas Formation (Early Carboniferous), Quebrada de Las Aguaditas, San Juan Province, Argentina. Stratigraphic horizons are indicated by letters following section prefix LA. All secondary electron micrographs except 5, 6, 12, 13, backscattered electron micrographs. 1, ventral view of transitory pygidium, presumed degree 1, CEGH-UNC 14584, ×53, LA-K; 2, ventral view of transitory pygidium, CEGH-UNC 14585, ×53, LA-K; 3, dorsal view of transitory pygidium, CEGH-UNC 14586, ×61.3, LA-K; 4, dorsal view of transitory pygidium, CEGH-UNC 14587, ×53, LA-K; 5, dorsal view of transitory pygidium, CEGH-UNC 14588, ×53, LA-K; 6, dorsal view of transitory pygidium, CEGH-UNC 14589, ×62, LA-E; 7, dorsal view of transitory pygidium, CEGH-UNC 14590, ×50.5, LA-K; 8, dorsal view of transitory pygidium, CEGH-UNC 14591, ×52.3, LA-K; 9, dorsal view of ultimate transitory pygidium, CEGH-UNC 14592, ×53, LA-K; 10, dorsal view of transitory pygidium, CEGH-UNC 14593, ×51.4, LA-K; 11, posterodorsal view of ultimate transitory
furrow shallow to inconspicuous, running backward from pair of distinct pits close to anterior margin, and disappearing backward; glabella barrel-shaped; sculpture difficult to discern on dorsal surface, consisting of fine ridges and grooves parallel to margin on narrow incurved doublure; three pairs of short, sharp, conical spines project from margins, anterior pair projects sublaterally from about 35 percent length of protaspid, where facial suture crosses doublure; middle pair of spines projects posterolaterally and slightly dorsally from about 65 percent length of protaspid; posterior pair of spines projects backward and downward from near posterior margin, with spines separated by almost 25 percent width of protaspid. Librigena small, curved, submarginal, lacking genal spine and eye, restricted to anterior 35–50 percent of protaspid. Rostral plate wide, more than 50 percent width of protaspid, short, with fine transverse sculpture of ridges and grooves; connective sutures strongly convergent backward. Hypostome elongate ovoid in outline, with three very short lateral marginal spines and extended, pointed postero-
suture converging forward and weakly convex outward between γ and anterior border furrow, then continuing to converge inward across anterior border; eye ridge weakly raised, running anteromedially across genal field; posterior protocranial border furrow absent; juncture between protocranium and protopygidium marked by very shallow furrow on pleurae. Protopygidium subsemicircular, margins entire, with shallow posteromedian embayment; axis short, terminating well in advance of border; one well-defined axial ring; pleurae unfurrowed; border narrow anterolaterally, evenly lengthening posteromedially; doublure flattened, narrow (sag., exsag.), gently lengthening medially, lacking terrace ridges but with raised rim along inner margin. Polygonal sculpture well-developed on anterior protocranial border and protopygidial border and surrounding (outer) parts of protaspis, subdued on axis, network of polygons with concentric pattern.

Meraspis and holaspid periods.—Some meraspid cranidia and transitory pygidia can be identified as degree 0. The craniidium (Figure 4.5) differs from that of the metaprotaspis in the generally stronger incision of the axial furrow, the well-impressed posterior border furrow, and the absence of a transverse glabellar furrow (S3). The degree 0 transitory pygidium (Figure 4.6) retains the shallow posteromedian embayment of the metaprotaspis and likewise lacks marginal spines. A second axial ring is defined, but is not strongly set off from the terminal piece, and the pleurae remain unfurrowed. The presumed degree 1 craniidium (Figure 4.8) has a more adult-like course of the facial suture, with the anterior section running subparallel from γ (rather than converging as in M0 and the protaspis), and is markedly bulged outward against the palpebral lobe. The presumed degree 1 transitory pygidium (Figure 4.10, 4.11) is the first to have a denticulate margin, two pleural tips terminating
with small denticles. Polygonal sculpture remains well-defined (Figure 6.17), in contrast to the granulate, and then striate and granulate, sculpture developed later in ontogeny. The transformation from polygonal to granulate sculpture has occurred by degree 3, for which an articulated axial shield is known (Figure 5.12).

Changes occurring through the meraspid and holaspid periods include: the preglabellar field gradually shortens until its complete closure, with the median depression in the field (Figure 4.12–4.14) eliminated; the glabella progressively broadens, changing from a narrow, conical shape (Figure 4.13, 4.15) to a more quadrate shape (Figure 4.17, 4.18); S1 is most pronounced in meraspsids (Figures 4.13, 5.12), setting off triangular lateral lobes; the occipital node becomes progressively smaller; and, the interocular fixigenae narrow. The genal spine becomes relatively longer and more slender; the posterior border and border furrow become more marked on the librigena; one (Figure 5.4) then two (Figure 5.7) lineations develop along the outer edge of the border to extend onto the genal spine, but are suppressed in large holaspids; and, the eye socle, poorly defined on small librigenae (Figure 5.8), becomes enhanced by deepening of the furrows both at the base of the visual surface and beneath the socle. A sculpture of more or less longitudinal lineations on the anterior lobe of the middle body is lacking in the smallest known hypostomes (Figure 5.10, 5.15), with lineations becoming progressively more abundant; in small hypostomes (Figure 5.15) width across the anterior wings is less than across the lateral shoulder, whereas large specimens (Figure 5.20) are considerably broadened across the wings, and the shoulder is less laterally inflected. The number of segments in the transitory pygidium that terminate with marginal spines increases from three (Figure 6.1) to four (Figure 6.2, 6.3), to five (Figure 6.5), to a maximum of six (Figure 6.4, 6.6–6.8), a number that is apparently retained through a few meraspid degrees, and then decreases again to five (Figure 6.10), four (Figure 6.3, 6.11, 6.14), and the holaspis number of three (Figure 6.13, 6.15, 6.16, 6.18), as segments are shed into the thorax. Assuming that the holaspis possessed ten thoracic segments as in S. warburgae, the five and four-segmented stages may be identified as degrees 8 and 9, respectively. The articulated degree 3 meraspid (Figure 5.12) possesses five stronger marginal spines in the transitory pygidium and a small sixth pair, the transitory pygidium being the same length as other six-spined specimens (Figure 6.6, 6.7). Within the holaspis period, the impression of the second and third ring furrows decreases considerably (Figure 7.19 versus 7.17), and the relative length of the axial terminal piece is much greater in large holaspides than in late meraspsids.

Discussion of ontogeny.—Growth series are known for a few proetoids that bear comparison to Stenoblepharum astinii. The most closely related taxon for which ontogeny is known is S. strasburgense (Cooper, 1953), described by Hu (1975). Hu described two “forms” of protaspides for S. strasburgense, one larger than the other. His illustrations (Hu, 1975, fig. 3A, B) suggest that the larger form has a less tapering anterior part of the glabella, more obvious eye ridges, and a clearly defined pygidial border furrow. The fragmentary nature of Hu’s protaspides makes his identification of two possible instars in the protaspid period of S. strasburgense very uncertain. Two of Hu’s protaspides (his pl. 2, figs. 1, 3) are illustrated upside-down. There is little compelling evidence that more than a single instar is represented, and the poor preservation does not allow morphological differences from the metaprotaspid stage of S. astinii to be detected. The transitory pygidia assigned to S. strasburgense by Hu (1975, pl. 2, figs. 12, 17, 19) are here considered misassigned, and likely belong to the other co-occurring tropichordophy (Hu, 1975, pl. 2, figs. 21–24). Comparable meraspid stages in S. astinii have well-defined marginal denticles that are lacking in the transitory pygidia figured by Hu. It is very unlikely that the marginal denticles of holaspides of S. strasburgense (Hu, 1971, pl. 23, figs. 28–31; see discussion above) would have such a different meraspid origin from that known for S. astinii.

Early growth stages of Stenoblepharum astinii are also very similar to those of the proetoid in Beechers Trilobite Bed (Caradoc), New York. This ontogenetic series includes a protaspis originally described by Beecher (1893, 1895) as Triarthrus becki, but recognized by Whittington (1957, “Protaspis A”) as that of a proetoid. Subsequently Cise (1973) treated the juvenile stages as those of Triarthrus eatoni, but Whittington’s proetoid assignment is strongly supported. Briggs and Edgecombe (1993) indicated that the proetoid early growth stages are very likely those of “Protoetus” beecheri Ruedemann, 1926. The largest available specimens of the Beecher Bed proetoid are juveniles and not well preserved (Figure 10), but are consistent with an assignment to Decoroprotod. Accordingly we assign the proetoid early growth stages to Decoroprotodon beecheri (Ruedemann, 1926). Conspicuous similarities between the metaprotaspid of S. astinii and that of D. beecheri include the short preglabellar field, the subparallel glabella, the relative size of the protopygidium and proportions of its border, and its single axial ring. They differ in the following states for the S. astinii protaspis:
rites, the type material includes: numerous holaspis crania, librigenae, hypostomes, and pygidia; one rostral plate; meraspis crania, librigenae, hypostomes, and transitory pygidia; and, metaprotaspides.

**Stenoblepharum strasburgense** (Cooper, 1953)

*Proetus* (s.l.) *strasburgensis* Cooper, 1953, p. 19, pl. 1, figs. 15–18, not 19 = "Decoroproetus" n. sp.

Phaseolops conus Hu, 1971, pl. 23, figs. 28–31 only.


Discussion.—Because of the confusion over sclerite assignments to this species in previous works (see discussions above), a new synonymy is provided.

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**REFERENCES**


**FIGURE 10—1–4. Decoroproetus beecheri** (Ruedemann, 1926), Beecher’s Trilobite Bed, Frankfort Shale (Caradoc), Rome, New York. All magnifications x 10. 1, dorsal view of axial shield of late meraspis (degree 8 or 9), YPM 27810; 2, molt assemblage of librigenae and hypostome associated with Figure 10.1, presumed to belong to same individual, YPM 27810; 3, dorsal view of cranium with articulated right librigena, late meraspis, YPM 32986; 4, external mould of transitory pygidium, YPM 32988.

Glabella narrows very slightly forward; preglabellar field slightly longer; less marked transverse furrow at S3; slenderer S1; and, juncture between protocranidium and protopygidium marked by a shallower furrow on the pleurae.

The best known proetid ontogeny in previous works is that of *Devonoproetus talenti* (Chatterton, 1971). Chatterton documented two protaspis stages for *D. talenti*, with the larger of these bearing greater similarity to the metaprotaspis stage of *S. astini* (note and the original assignment of an anaprotaspis to *D. talenti* above). In general, however, the second metaprotaspis of *Devonoproetus* is less similar to that of *Stenoblepharum* than is the metaprotaspis of *Decoroproetus beecheri*, most obviously differing in its significant anterior narrowing of the glabella. It may well prove that this greater similarity between *Decoroproetus* and *Stenoblepharum* protaspides can be used as additional evidence for their close affinities (or possibly to distinguish tropidocoryphids from proetids). The test will be early ontogeny from appropriate non-proetid outgroups in order to determine whether the “tropidocoryphid” similarities are shared derived states.

Etymology.—In honor of Dr. Ricardo Astini, who ably guided us through the stratigraphy at Quebrada de Las Aguaditas.

Types.—Holotype, cranium CGH-UNC 14562 (Figure 4.19), from horizon LA-J, Las Aguaditas Formation, Quebrada de Las Aguaditas. Paratypes CGH-UNC 14544–14561, 14563–14610, 14624, from type locality, horizons LA-D, E, F, H, J, and LA-S-B. Selected from several hundred available slabs.