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COMPARATIVE NOTES ON MICROPYLE STRUCTURE IN "CORDULEGASTROID"[1] AND "LIBELLULOID"[1] ANISOPTERA

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The morphology of the micropyle and other chorionic features of eggs of *Neopetalia* is similar to that of Cordulegastridae, although with 8 rather than 6 or 7 atrial (micropylar) openings. Libelluloids have a different micropylar structure, but the present results show that this is more diverse than hitherto suspected. The previously reported morphology of Synthemistinae (J.W.H. TRUEMAN, 1991, *Odonatologica* 20: 441-452) and of several corduliids and Libellulidae (J.J. BECNEL & S.W. DUNKLE, 1990, *Odonatologica* 19: 235-241; – TRUEMAN, 1991, *ibid.*) is here confirmed, but it is shown that *Gomphomacromia* has a unique micropyle with up to 4 openings. This finding casts doubt on the current understanding of the Gomphomacromiinae and supports the placement of *Gomphomacromia* at or near the base of the libelluloids.

INTRODUCTION

Several recent comparative studies (MILLER, 1987; IVEY, et al. 1988; BECNEL & DUNKLE, 1990; TRUEMAN, 1991) using scanning electron microscopy (SEM) have begun to reveal patterns in the evolution of micropyle morphology of the eggs of Anisoptera. The most pervasive is the apparent progressive reduction in a number of atrial openings (I use the descriptive nomenclature of TRUEMAN,

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[1] The anglecized terms "cordulegastroid" and "libelluloid" are intended only as informal designations for phenetically cordulegastrid-like and libellulid-like taxa. CARLE & LOUTON (1994) presented evidence implying that Cordulegastroidea (sensu FRASER, 1957), can be monophyletic only if confined to the Cordulegastridae (s.s.) alone; if accepted, this in turn implies possible changes in the definition of Libelluloidea (sensu FRASER, 1957). In addition, the same authors suggest the paraphyly of the Corduliidae, a conclusion for which I have substantial independent evidence. Thus I also use the term "corduliid" only informally.

1991, throughout), culminating in the libelluloids, which heretofore have been thought to have only 2 openings (BECNEL & DUNKLE, 1990; TRUEMAN, 1991). In addition, the Cordulegastridae and, most clearly, the libelluloids, have a distinctive conical micropylar projection (Dr. J.W.H. Trueman, pers. comm., 1993; cf. also BECNEL & DUNKLE, 1990, figs 2, 6) that is lacking or indistinct in other taxa. Both of these patterns have been associated with increasingly rapid egg deposition, especially in exophytic species, which presumably would require precise orientation of the atrial openings relative to the female fertilization pore (BECNEL & DUNKLE, 1990).

I had the opportunity to examine eggs of 2 genera whose phylogenetic affinities have been uncertain or controversial, along with those of several other little known taxa. The first, *Neopetalia*, has recently (CARLE & LOUTON, 1994) been shown to be related more closely to Cordulegastridae than to the Aeshnidae as previously supposed (e.g., by FRASER, 1957). As seen below, the structure of their eggs is consistent with this relationship.

Gomphomacromia is a problematic genus in the loosely defined corduliid complex. FRASER (1957) placed it along with a diverse and rather arbitrary assemblage of genera, ranging structurally and geographically from *Pseudocordulia* to *Oxygastra*, in his Gomphomacromiinae. More recently, THEISCHINGER & WATSON (1984) recognized a possible relationship with the Synthemistinae, based on larval characteristics. Its micropyle structure, however, has proven to be unique among known libelluloids and is possibly plesiomorphic within that group of taxa. Finally, I report on several other species that represent genera and some higher taxa not previously described.

This paper is dedicated to the memory of Dr J.A.L. Watson, in particular recognition of his contributions to our knowledge of the Australian corduliids.

MATERIAL AND METHODS

Eggs of several species were taken from the ovipositors or vulvar laminae of dried museum specimens, sometimes after softening with a wetting agent and air drying; they were not treated further except for coating. Mature, chorionated oocytes were dissected from females *Oxygastra curtisii* (alcohol preserved specimen), *Heteronaias heterodoxa, Idionyx yolanda, Neocordulia batesi,* and *Zoraena bilineata* (dried specimens). Oocytes were dissected fresh from mature *Gynacantha tibiata* and *Uracis imbuta*, but these were extracted in chloroform (as a part of a study unrelated to this one) for 2 weeks prior to examination. Eggs of *Neopetalia* were supplied by F. Carle from a dry specimen. After collection and drying, eggs were mounted on stubs, sputter coated with gold-palladium, and examined using a Hitachi S-510 scanning electron microscope at 10kV accelerating voltage and original magnifications ranging from 60X to 1000X.

RESULTS AND DISCUSSION

Table I

Egg dimensions and micropyle characteristics of selected cordulegastroids and libelluloids. – [Measurements are taken from electron micrographs and thus may be affected by distortion during drying. Usually a single egg was measured; a range of sizes is given for multiple eggs]

Species	Length (mm)	Width (mm)	Projection length (μm)[a]	Projection type[b]	Number of openings[c]
Cordulegastroids					
Neopetalia punctata	1.03	0.55	55	convex cone	8
Zoraena bilineata	0.66	0.45	36	convex cone	6
Libelluloids					
Choristhemis flavoterminata	0.49	0.31	41	hyperboloid, recessed tip	2
Cordulia aenea	0.73	0.32	47	concave cone	2
Gomphomacromia paradoxa	0.62	0.39	40-46	hyperboloid, projecting tip	4[d]
Heteronaias heterodoxa	0.53	0.42	28	concave cone	2
Idionyx yolanda	0.48	0.28	50	concave cone	2
Idomacromia proavita	0.62	0.32	44	concave cone	2
Neocordulia batesi	0.35	0.25	32	concave cone	2
Oxygastra curtisii	0.61-0.64	0.28-0.30	47-55	concave cone	2
Uracis imbuta	0.68	0.36	26	concave cone	2

[a] Length of micropyle projection.

[b] Shape of micropyle projection. A "convex cone" is generally conical but with convex sides (e.g., Figs 2, 3), "concave cone" conical with concave sides (e.g. Figs 5-11), "hyperboloid" columnar with strongly concave sides below the atrial openings (Figs 4, 12; TRUEMAN, 1991).

[c] Number of atrial openings.

[d] Possibly 2 or 3 in some specimens (see text).

Dimensions and micropyle characteristics of the eggs examined are summarized in Table I. These data, along with a comparison of Figures 1-3, clearly indicate the affinities of *Neopetalia* with the Cordulegastridae, rather than Aeshnidae, in the much less elongate overall shape and the well-differentiated, conical micropylar projection. On the other hand, neopetaliids and cordulegastrids are distinct from the libelluloids in having the atrial openings much more numerous and differently shaped, the micropylar projection not concave-sided, and the exochorion apparently thicker. Although *Neopetalia* has more atrial openings than any known cordulegastrid (BECNEL & DUNKLE, 1990; Dr J.W.H. Trueman, pers. comm., 1993; present study), I do not attach much phylogenetic importance to this fact at present, in view of the apparent variability in number even within species that have many atrial openings (BECNEL & DUNKLE, 1990).

Eggs of *Choristhemis* (Fig. 4) have not previously been described, but their

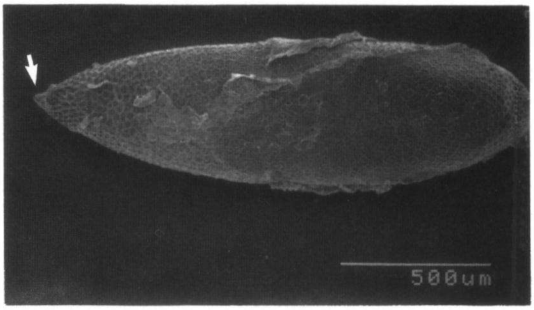


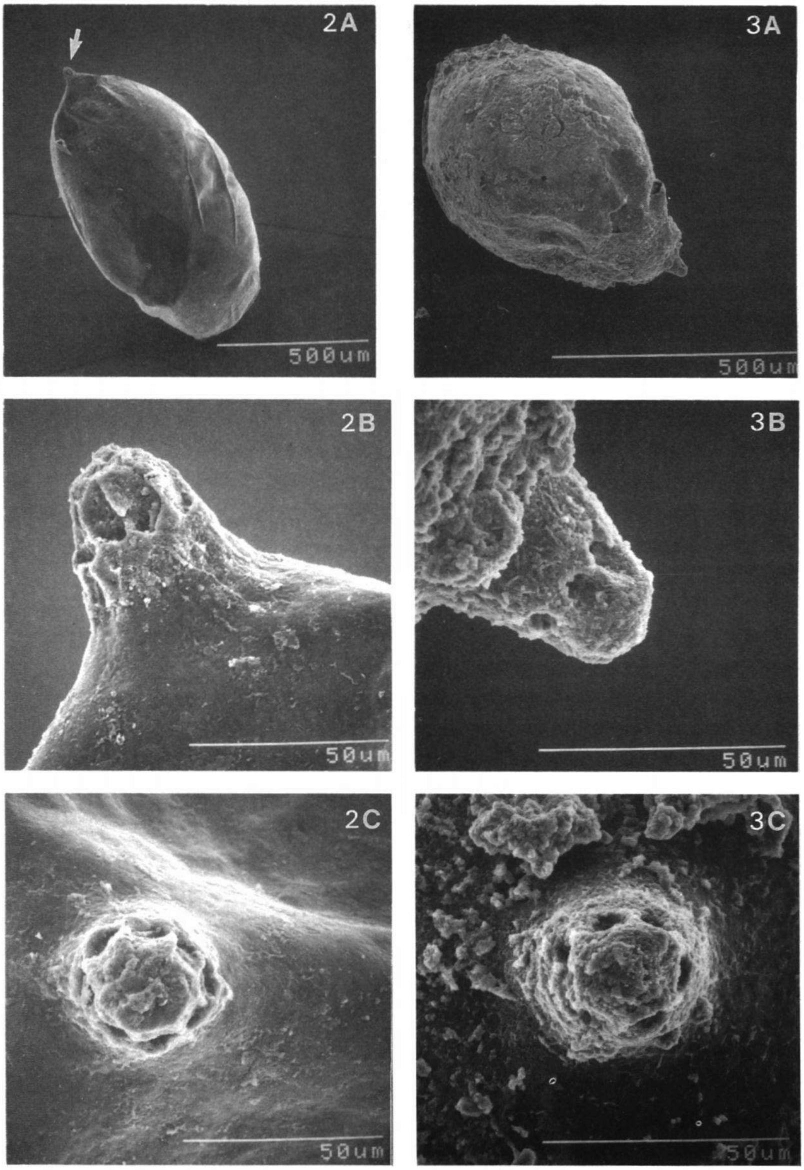
Fig. 1. *Gynacantha tibiata* Karsch, egg, lateral view. Arrow indicates micropylar projection. – [Dimensions are 1.66 x 0.51 mm]

micro-pyle is like that of other syn-themistines (TRUEMAN, 1991), with a slender "hyperbolic" projection and 2 recessed, terminal atrial openings.

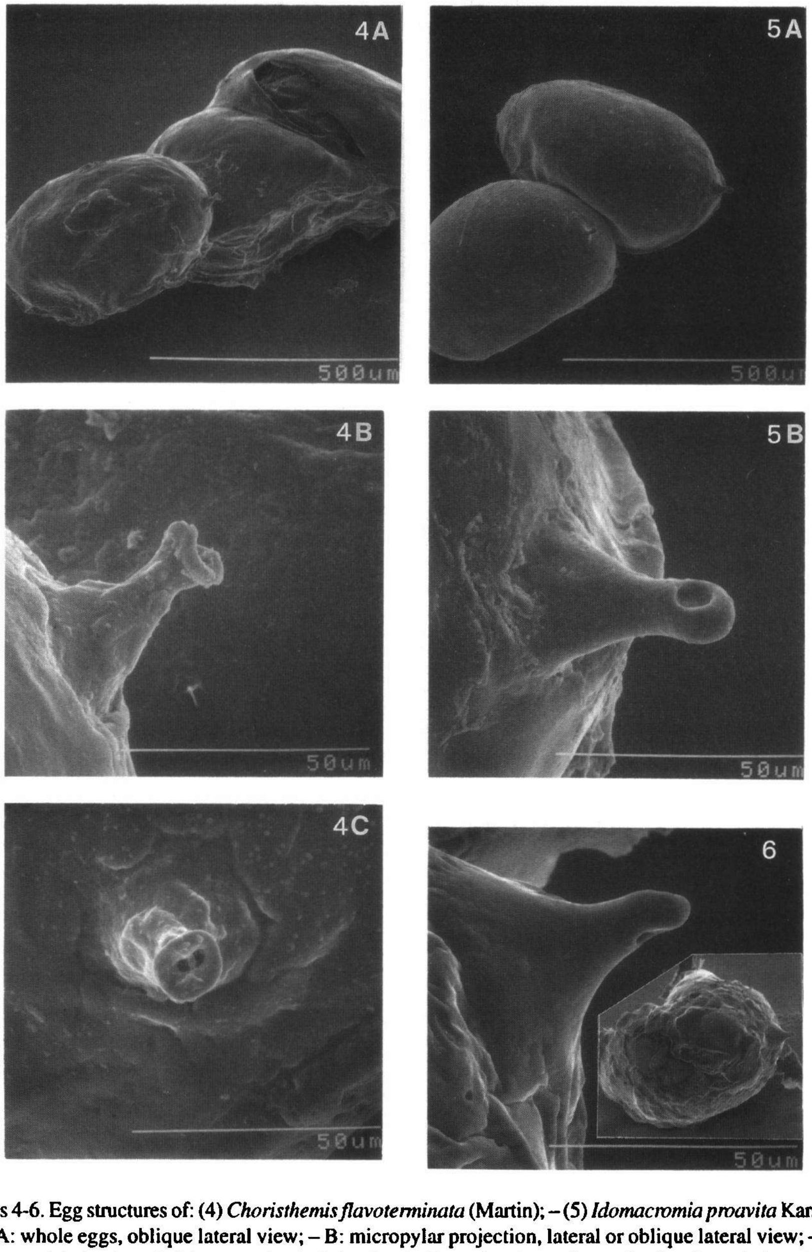
The eggs of most other libelluloids share a very similar and constant micropyle structure, with 2 subterminal atrial openings directly opposite each other on a conical, concave-sided micropylar projection. Except for *Gomphomacromia*, described below, all of the other corduliids studied here conform to this pattern. This includes *Idomacromia* and *Idionyx* (Figs 5, 6), which are each in distinctive subfamilies (in FRASER's 1957 taxonomy) that have not been previously examined. Other supposed "gomphomacromiines", i.e., *Oxygastra curtisii* and *Neocordulia batesi* (Figs 7, 8) also have the typical libelluloid structure. Other chorionic features, as well as overall shape, also are rather uniform, with a thin, unadorned exochorion, except in *Cordulia* (Fig. 9), which is covered with low, rounded bumps, and *Heteronaias* (Fig. 10), which has a reticulated pattern on its nearly spherical eggs. *Idionyx, Neocordulia* and *Heteronaias* show evidence of a gelatinous layer although, since none of these eggs were deposited in water, that layer is not expanded and thus might be hard to detect in other species if it were very thin.

Uracis imbuta, the only libellulid (s.s.) examined, is of some interest because the form of the ovipositor in convergently similar to that of cordulegastrids, although the posterodorsal "valves" are secondary extensions of the 9th sternite rather than homologs of the second gonapophyses. Oviposition behavior of *Uracis* was reported to be reminiscent of *Cordulegaster* by DE MARMELS (1990), raising the possibility that, if micropyle morphology is indeed adapted to facilitate oviposition, eggs of *Uracis* might show some *Cordulegaster*-like characteristics. The evidence (Fig. 11), however, gives but little support to this hypothesis. The micropylar projection is slightly less prominent and less concave than other known libelluloids, although it may be somewhat obscured by the apparent remnants of a gelatinous layer. The standard libelluloid complement of 2 atrial openings is retained.

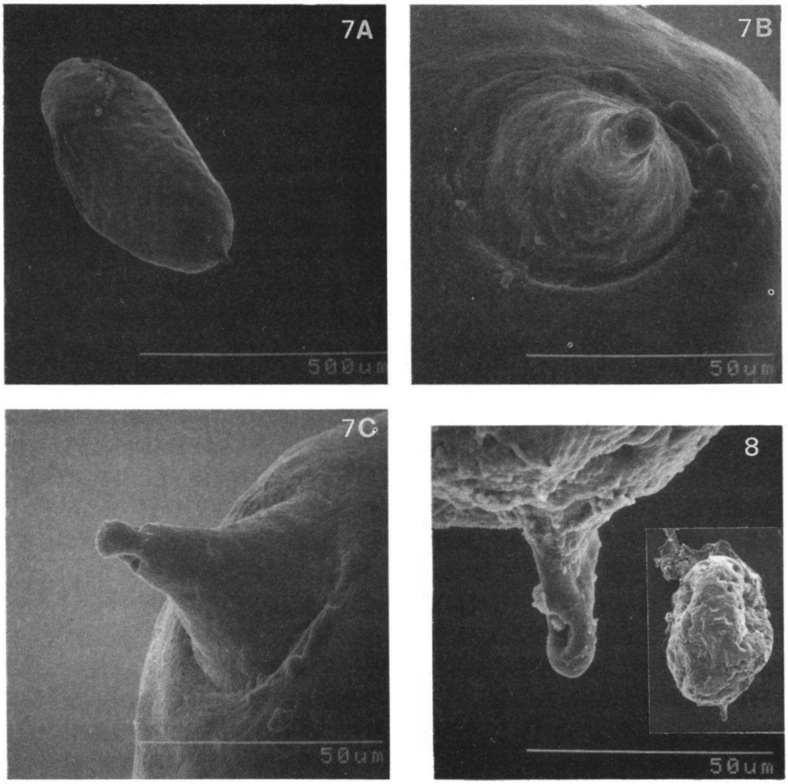
The micropyle of *Gomphomacromia paradoxa* is strikingly different from all others in typically having 4 atrial openings (Fig. 12). This was observed in several eggs from 2 different females; some other eggs may have had 2 or 3 asymmetrically positioned openings, although in each of these cases distortion of the



Figs 2-3. Egg structures of: (2) *Neopetalia punctata* (Hag.); – (3) *Zoraena bilineata* Carle. – [A: whole egg, lateral view, arrow indicates micropylar projection; – B: micropylar projection, lateral view; – C: same, axial view]



Figs 4-6. Egg structures of: (4) *Choristhemis flavoterminata* (Martin); – (5) *Idomacromia proavita* Karsch. – [A: whole eggs, oblique lateral view; – B: micropylar projection, lateral or oblique lateral view; – C: same, axial view]; – (6) *Idionyx yolanda* Sel. – [Main figure is micropylar projection, lateral view; inset is whole egg, partly crushed, at 0.1 x scale of micropyle]

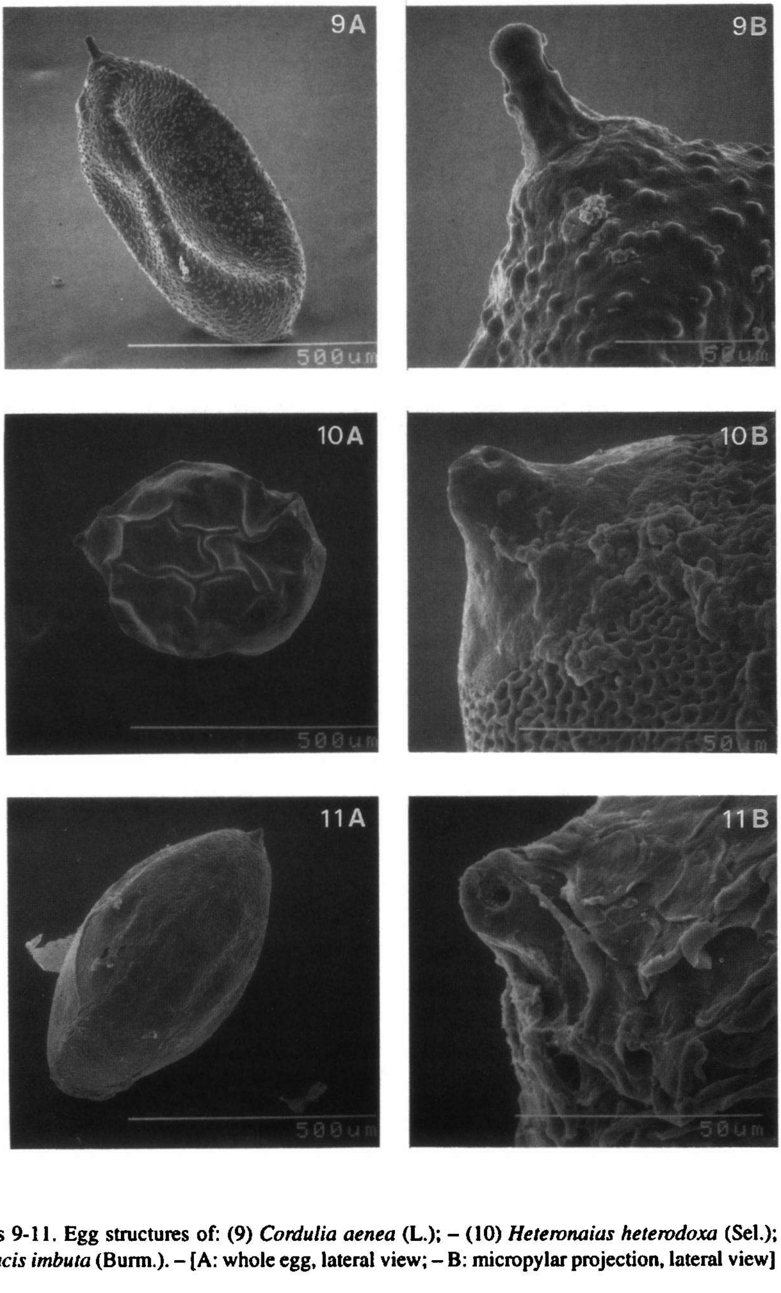


Figs 7-8. Egg structures of: (7) *Oxygastra curtisii* (Dale). – [A: whole egg, oblique lateral view; – B: micropylar projection, oblique axial view; – C: same, oblique lateral view]; – (8) *Neocordulia batesi* (Sel.). – [Main figure is micropylar projection, lateral view; inset is whole egg at 0.1 x scale of micropyle].

micropylar projection may have caused the apparent variability. Variation certainly occurs among species in the genus. Two *G. etcheverryi* eggs had 3 openings arranged in radial symmetry while a single *G. fallax* egg had 2 nearly contiguous openings (May, unpublished).

The sides of the micropylar projection of *G. paradoxa* and *G. etcheverryi* are concave and flare outward distally as in the synthemistines; however, the atrial openings are not recessed and are slightly subterminal. The small central projection between the openings is similar to the tapering tip of other corduliids, especially *Oxygastra*, perhaps suggesting a similar mechanism for positioning the oocyte for fertilization (Dr. F. Carle, pers. comm., 1994).

The micropyle structure of *G. paradoxa* may well be plesiomorphic for the Libelluloidea (sensu FRASER, 1957). This hypothesis is supported especially by the high number of atrial openings and also by the combination of hyperboloid shape with a projecting tip and subapical atrial openings, thus incorporating char-



Figs 9-11. Egg structures of: (9) *Cordulia aenea* (L.); – (10) *Heteronaias heterodoxa* (Sel.); – (11) *Uracis imbuta* (Burm.). – [A: whole egg, lateral view; – B: micropylar projection, lateral view]

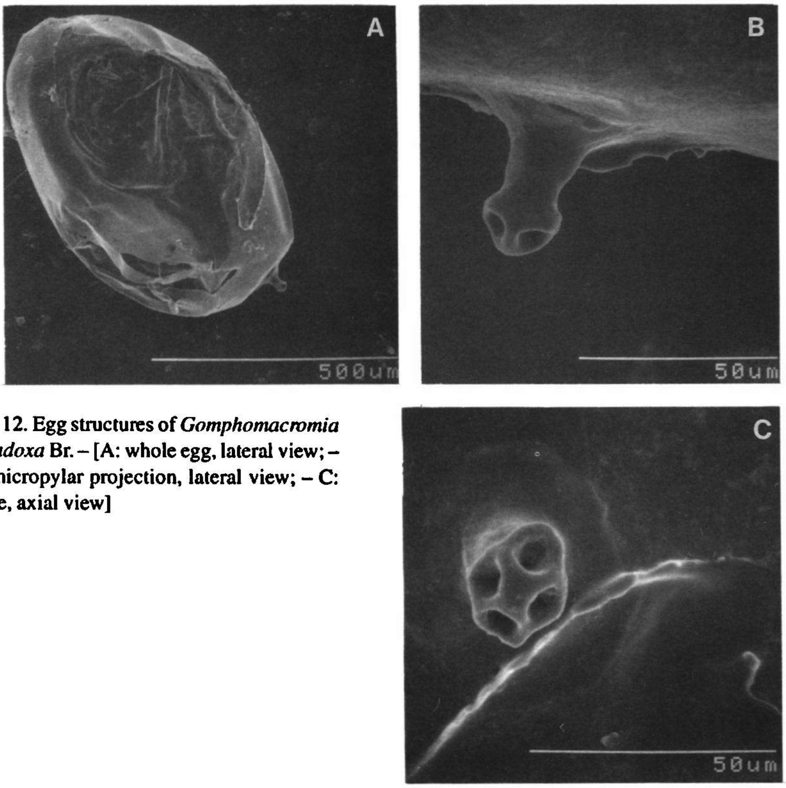


Fig. 12. Egg structures of *Gomphomacromia paradoxa* Br. – [A: whole egg, lateral view; – B: micropylar projection, lateral view; – C: same, axial view]

acteristics of both the Synthemistinae and the higher libelluloids. The latter characters are neither very complex nor very distinctly developed in *Gompomacromia*, however, so I regard these suggested homologies as tentative, although the interpretation is in accord with the observations of THEISCHINGER & WATSON (1984) on adults and larvae of these taxa. Micropyle structure certainly suggests, however, that the Gomphomacromiinae of FRASER (1957) and others is a paraphyletic group, because its supposed members, *Neocordulia, Oxygastra* and *Hesperocordulia* (TRUEMAN, 1991) share the apomorphic atrial opening number with other libelluloids (at least Cordulephyinae [TRUEMAN, 1991], Corduliinae, Idionychinae, Idomacromiinae, Libellulidae, and Macromiinae [BECNEL & DUNKLE, 1990]) but not with *Gomphomacromia*. Abundant independent evidence supports separation of *Gomphomacromia* from most other "gomphomacromiines" (THEISCHINGER & WATSON, 1984; May, unpublished), although the true relationships among the various taxa are not yet clear.

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