Graptolite synrhabdosomes: biological or taphonomic entities?

Juan Carlos Gutiérrez-Marco and Alfred C. Lenz

Abstract.—Synrhabdosomes, structures made of mostly radially arrayed graptolite rhabdosomes attached by distal regions of their virgulae, have been considered as biological entities by some in the past, but as taphonomic structures by others more recently. Our survey of at least 200 synrhabdosomes, more than 90 of which derive from one locality in northwestern Spain, shows that all synrhabdosomes are most probably entirely monospecific assemblages composed of a more or less finite number of rhabdosomes, all of which are consistently straight or only weakly curved, and all of which bear simple, or relatively simple, thecae. We conclude, therefore, that synrhabdosomes are biological entities, and we suggest that they formed infrequently as, perhaps, temporary structures to increase food-gathering efficiency during times of lower plankton supply in local, relatively restricted water masses.

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Introduction

Synrhabdosomes have been recognized since at least the time of Hall (1865) but were best made known by Ruedemann (1895, 1904, 1908, 1947) through his many illustrations and reconstructions of them as float-associated structures, and it was Ruedemann (1904: p. 483) who first coined the name “synrhabdosome” and recognized the structures as third-order “supercolonies” (i.e., the joining together of second-order rhabdosomal colonies). Until recently, the vast majority of synrhabdosomes were known mainly among diplograptid graptolites, so much so that Bulman (1970: p. V11) in his definition parenthetically remarks that they are “usually biserial.” Over the last twenty years, a number of new recoveries, particularly among the monograptids, have been made. These include Silurian monograptids (Hundt 1965; Rickards 1975), Early Devonian monograptid (Jackson et al. 1976), Silurian biserial (Bjerreskov 1976), Early Silurian biserial (Chen 1984), Early Ordo- vician dichograptids (Zalasiewicz 1984), Late Silurian monograptid (Lenz and Melchin 1986), Ordovician biserial (Rigby 1993), and Silurian biserial (Ge and Chen 1995).

Synrhabdosomes characteristically are structures in which a number of individual rhabdosomes are more or less radially arrayed around a central point of attachment/entanglement by their virgulae, the only known exception being the biserial Rhaphidograptus torenquisti attached by the virgellae (Bjerreskov 1976). The relative rarity of synrhabdosomes raises a number of questions in regard to their biological nature; that is, are they biological entities (for reproductive purposes?) as suggested by Bulman (1970), Rickards (1975, 1996), Zalasiewicz (1984), Underwood (1993), and Ge and Chen (1995), merely a passive entanglement or “sticking together” of a number of rhabdosomes as suggested by Rigby (1993), or facultative biological entities as suggested by Melchin and DeMont (1995)? Furthermore, if the former, what was their purpose or function, and if entanglements, why are all synrhabdosomes (almost) always monospecific assemblages; and, in any of the three options, why are they normally so rare?

The present study is prompted by the recent recovery of 15 synrhabdosomes of several monograptid species from upper Wenlock and middle Ludlow strata in the Canadian Arctic and, particularly, by a large population of synrhabdosomes of a single upper Wenlock species from northwestern Spain.

The Arctic Islands material consists of 15
synrhabdosomes collected from among the many dozens seen on bedding plane surfaces at several stratigraphic levels and three sections. All synrhabdosomes are monospecific assemblages; all are associated with far more numerous isolated rhabdosomes, including many of the same species, on the same bedding plane; all are attached by their virgulae; and all appear to be made of mature rhabdosomes. Species making up the synrhabdosomes are all common in the Arctic and comprise the upper Homerian species Pristigraptus dubius, Colonograptus ludensis, C. praedeubeli, and C. scheididoneus, and the mid-Ludlow species Monograptus ceratus (Lenz 1990, 1994, 1995). In addition, the mid-Ludlow species Saetograptus fritschi linearis is also recorded from the Arctic (Lenz and Melchin 1986). The rhabdosomes of all the above species are essentially straight.

The synrhabdosome-bearing surfaces of upper Homerian strata bear numerous specimens of plectograptine retiolitids, many with long spines, whereas the middle Ludlow synrhabdosome is associated with numerous curved monograptid species such as Bohemograptus bohemicus (s.l.). None of the curved monograptids forms synrhabdosomes while, on the other hand, clumps of plectograptines are often randomly oriented and clearly physically entangled.

The northwestern Spain synrhabdosomes are, unlike any other known occurrences, astonishingly numerous (more than 90 specimens: Fig. 1), so much so that it is often difficult to recognize the components of any one synrhabdosome. All synrhabdosomes are made up of the late Wenlock species Colonograptus deubeli, and all appear to be made of mature rhabdosomes attached by their virgulae. In addition, a single synrhabdosome composed of mature specimens of Colonograptus? cf. gerardi was found in early Ludlow strata in the same area.

In Table 1, we have summarized all known species of synrhabdosomes. Omitted from the list are questionable forms; for example, aggregations of rhabdosomes of Orthograptus socialis in the lower Ashgill of Scotland (Williams 1987: Fig. 8H) and Newfoundland (Williams 1991: Pl. 2, Fig. 17), Paraclimacograptus? flamandi from the Telychian of central Spain, and immature colonies of Saetograptus ex gr. chimaera from upper Ludlow strata of southwestern Portugal (the latter two examined in this study), that may represent poorly preserved or collapsed synrhabdosomes, or may be only random congregations of individual rhabdosomes.

### Rhabdosomal Characteristics

**Taxonomic Composition.**—Synrhabdosomes are exclusively monospecific assemblages, generally of adult rhabdosomes, but include some showing different growth stages (see especially Bulman 1931; Ruedemann 1947). Of the approximately 200 synrhabdosomes analyzed in this study, either directly or by examination of photographs, only a very few have been considered by others to be composed of more than one species (e.g., Hernández Sampelayo 1950; Riva in Clark 1972; Goldman and Mitchell 1994), and all of these are made up of diplograptids or monograptids. Our reexamination of most of these supposedly mixed taxa suggests either some doubt as to whether all components are part of the actual synrhabdosome or, more importantly, that the mode of preservation of individual rhabdosomes has obscured crucial parts of the morphology (e.g., hidden spines or other such diagnostic features), leading to incorrect identifications. For example, in the case of Ruedemann’s (1947) types NYSM 3914 and 3920,
purportedly a mixture of Orthograptus rude-
manni and O. ruisai and/or Lasiograptus sp. (see Goldman and Mitchell 1994), a careful ex-
amination suggests that all rhabdosomes, while
not ideally preserved, are equally spine
and, therefore, assignable to a single species.
In contrast, the multigeneric synrhabdosome
reported from the Upper Ordovician of south-
western Spain by Hernández Sampelayo
(1950) appears, upon reexamination, to be lit-
tle more than a pseudoradiate aggregation of
poorly preserved rhabdosomes probably de-
"rived from Silurian strata. Furthermore, even
in those rare cases where there is an apparent
mixture of species, the morphology of one
species is suspiciously close to that of the oth-
er species. This factor was alluded to by Gold-
man and Mitchell (1994). In sum then, we sug-
gest that there is very strong reason to doubt
the existence of "hybrid" synrhabdosomes; in-
stead we suggest that all are monospecific.

Morphology of the Taxa Comprising Synrh-
habdosomes.—With the exception of synrhab-
dosomes formed of various species of the cone-
shaped Rhabdinopora, individual rhabdosomes
of diplagnostids and monagnostids, the
groups comprising the vast majority of syn-
rhabdosomes, are all essentially straight or, at
most, gently curved, and the vast majority are
single-aligned stipes that are either uniseri-
or biserial pleural. The only apparent excep-
tions are the monopleural Cryptograptus schae-
feri (see Bulman 1931) and the dichagnostid
Expansograptus cf. simulans (see Zalasiewicz
1984), the latter possessing two separated stipes
that are, however, only gently curved and di-
 verge at approximately 180° and thus behave
as if they were more or less straight. Furth-
more, the thecae of all synrhabdosomes are
relatively simple; i.e., they are exclusively
tubes or slightly elaborated tubes with few or
no spines in the monagnostids, and simple
cuplike or tubelike with no, or short, simple
spines in the diplagnostids. Synrhabdosomes
have not been recognized in the following
groups: diplagnostid taxa bearing long thecal
or basal spines (e.g., Climacograptus spiniferus,
C. bicornis); monagnostids with complex the-
cae (e.g., almost all true Monograptus, and all
streptagnostids, globosagnostids, cucullo-
graptids, and neocuculagnostids); strongly
curved or spiraled rhabdosomes (e.g., Spiro-
graptus, Oktaviites, Torquigraaptus, Rastrites,
Demirastrites); multi-stiped taxa such as Cyro-
graptus, Linograptus, Nemagraptus); dichogra-
toids with more than two stipes; or any retiol-
itetid.

Morphology of the Synrhabdosome.—Typically,
synrhabdosomes are composed of radially ar-
ranged rhabdosomes at the same stage of de-
velopment and appear to be attached by their
virgulae or nemata (see Rickards 1996, for the
distinction) to a more or less central point. The
only exception to this is Rhapdidograptus toern-
quisti, which is attached by the virgella. Less
commonly and clearly for taphonomic rea-
sons, synrhabdosomes are preserved in a sem-
istellate or pie-shaped pattern, in which all
virgulae converge toward a common center.
These observations are suggestive of a life
configuration as a broad, cone-shaped struc-
ture.

Generally speaking, the length of the vir-
gulae between the distal ends of the rhabdo-
somes and the central point of attachment of
the virgulae is more or less uniform in any one
synrhabdosome, regardless of whether the
rhabdosomes are mature, immature, or, as in
the rare cases, where there is a mixture of ma-
ture and immature rhabdosomes. Further-
more, although the lengths of the free virgulae
range considerably depending on the species
involved, there seems to be no correlation be-
tween the maturity of the rhabdosomes and
the lengths of the free virgulae; that is, syn-
rhabdosomes made up of immature rhabdo-
somes appear not to have virgulae noticeably
longer than those made up of mature rab-
dosomes. Rather, the lengths of the free vir-
gulae seem to be related only to the species
makeup of the synrhabdosome.

Close examination of the virgulae of the
central area of some well-preserved synrhab-
dosomes shows large numbers of "virgular
threads," greater than the number of rab-
dosomes, suggesting distal multiple bifur-
cations and intertwining of virgular threads
(e.g., Saetograptus varians in Palmer and Rick-
ards 1991: Fig. 110). This construction is prob-
ably homologous to the nemal tufts illustrated
in some planktic "dictyonemids" (Rhabdino-
pora spp., of the R. parabola and "meta-
ne' groups [Bulman 1964: Fig. 7; Lin 1988, with earlier references)] that were also able to form synrhabdosomes (Bulman 1950; Erdtmann 1982) and, possibly, to the fine nemata in some "petalograptids" (see Schauer 1971; Palmer and Rickards 1995: Fig. 106).

In the center of better-preserved material examined in this study, individual virgulae are often observed to lead directly into a small central knot or cluster of threads, less than 1 mm in diameter. This has also been noted by other authors (Ekström 1937; Jackson et al. 1976) and was even described by Bulman (1948, 1950), who noted accessory processes or a branching tangle at the virgular ends in synrhabdosomes. Ordovician dichograptoids show a different central development, in which the nemata in synrhabdosomes may be short, twisted, and locally thickened, in contrast to the single nema in individual colonies of the same species (Zalasiewicz 1984).

Possibly related to this, some early Llandovery taxa develop diverse and complex virgellar structures (e.g., some species of Akidograptus, Dimorphograptus, Rhaphidograptus, Glyptograptus, Normalograptus [see Schauer 1971]), one of them leading to a virgellar type of synrhabdosome (R. toernquisti [Bjerreskov 1976]).

The number of rhabdosomes making up a synrhabdosome is very variable, ranging from 3 or 4 to more than 30; however, when considering only diplograptids and monograptids, the minimum numbers are much higher (Table 1). Silurian examples, including the large population of Spanish synrhabdosomes, range from 15 to 34, and the many diplograptid synrhabdosomes illustrated by Ruedemann (1947) contain 18–38. Overall, the average number of rhabdosomes constituting diplograptacean and monograptacean synrhabdosomes is about 20, this number obviously representing a minimum, since it is very likely that some individual rhabdosomes may have been lost in splitting of the rock or are covered by sediment or other rhabdosomes.

The diameter of complete synrhabdosomes, lying flat on bedding planes and fully radially arrayed, varies through more than an order of magnitude. For example, small samples of synrhabdosomes of Orthograptus ruedemannii and Colonograptus deubeli may be no more than 7–12 mm, whereas those of the largest O. calcatus incisus or O. quadrimeronatus may be as much as 150 mm.

Associated Species.—In many cases, synrhabdosomes constituting one species are associated with other species on the same bedding plane. In the Canadian Arctic, for example, synrhabdosomes, as well as many single specimens, of the late Wenlock Colonograptus? schedidoneus are associated with C. praeudeubeli and Pristograptus dubius, neither of which is represented by synrhabdosomes, and with retiolitids, which often form tangled masses but not synrhabdosomes. In like manner, a single synrhabdosome of the mid-Ludlow species Monograptus ceratus is associated with numerous, single specimens of Bohemograptus bohemicus tenuis and Saetograptus fritschi linearis.

Biostratigraphic Distribution.—The biostratigraphic distribution and numbers of species forming synrhabdosomes is shown in Figure 2. Although it is difficult to read too much into such a small sampling, there appear to be peaks in the lower Caradoc and upper Wenlock. There also appears to be a peak in the Tremadoc, although this may be somewhat artificial because, with one exception, all components are species/subspecies of a single genus, Rhadinopora. The apparent rarity, or absence, of synrhabdosomes in upper Arenig, Ashgill, lower Llandovery, and upper Llandovery is striking, since all are times of high, or relatively high, global species diversity.

An examination of a specific period, the late Wenlock, may be instructive. The interval appears to show the highest diversity of synrhabdosome-forming species, whereas the species diversity of monograptids was relatively low, although they were undergoing rapid evolution following the "lundgreni extinction event" (Koren' 1991), and their thecal and rhabdosomal morphology was uniformly fairly simple (Lenz 1995). At the same time period, however, diversity of retiolitids was moderate (Lenz 1993), but none shows any evidence of synrhabdosome formation.

Taphonomy and Paleoenvironmental Aspects.—Synrhabdosomes everywhere seem to be most probably associated with black or dark gray silts or shales deposited in anoxic and, probably, relatively deep environments. They are
Table 1. Tabulation of the known occurrences of synrhabdosomes, numbers of specimens (in parentheses), and number of rhabdosomes in each synrhabdosome.

<table>
<thead>
<tr>
<th>Family</th>
<th>Genus/species</th>
<th>References (in parentheses are numbers of synrhabdosomes illustrated in literature or in possession)</th>
<th>Number of rhabdosomes in each synrhabdosome</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anisogaptidae</td>
<td>Rhabdinopora spp.</td>
<td>Hahn 1912 (?); Bulman 1927 (1); 1950 (37); Ruedemann 1947 (1); Tomczyk 1962 (17); Erdtmann 1982 (1)</td>
<td>2–5</td>
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<td></td>
<td>Anisograptus monseni</td>
<td>Bulman 1941 (1)</td>
<td>&gt;2</td>
</tr>
<tr>
<td>Dichograptacea</td>
<td>Expansograptus cf. simulans</td>
<td>Zalasiewicz 1984 (5)</td>
<td>4–8</td>
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<td></td>
<td>Azgyograptus lapworthi</td>
<td>Zalasiewicz 1984 (1); Beckly and Maletz 1981 (2?)</td>
<td>15</td>
</tr>
<tr>
<td>Glossograptacea</td>
<td>Corynoides americanus</td>
<td>Ruedemann 1908, 1947 (1); Riva 1974 (1); Finney 1986 (1) (all same specimen)</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td>Cryptograptus schaferi</td>
<td>Bulman 1931 (1)</td>
<td>±16</td>
</tr>
<tr>
<td>Diplogaptacea</td>
<td>Orthograptus spinigerus</td>
<td>Ruedemann 1925, 1947 (17)</td>
<td>20?</td>
</tr>
<tr>
<td></td>
<td>O. quadriramuncranatus</td>
<td>Ruedemann 1895, 1908, 1947 (12); Riva in Clark 1972 (1 or 2?); Rigby 1993 (&gt;1)</td>
<td>10–26</td>
</tr>
<tr>
<td></td>
<td>O. ruedemanni and O. rivai</td>
<td>Ruedemann 1895, 1947 (&gt;70); Walters 1977; Goldman and Mitchell 1994; Goldman 1995 (all from Ruedemann’s material)</td>
<td>10–15</td>
</tr>
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<td></td>
<td>O. eucharis</td>
<td>Hall 1865 (1); Ruedemann 1947 (same specimen)</td>
<td>18</td>
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<td>O. calcaratus incisus</td>
<td>Ruedemann 1947 (1)</td>
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<td></td>
<td>“O.” cf. attenuatus</td>
<td>Ge and Chen 1995 (1)</td>
<td>13</td>
</tr>
<tr>
<td></td>
<td>Climacograptus? putillus</td>
<td>Ruedemann 1947 (&gt;1)</td>
<td>8?</td>
</tr>
<tr>
<td></td>
<td>Pseudoclimacogr. modestus</td>
<td>Ruedemann 1947 (2); Decker 1952 (1); Bulman 1948 (1)</td>
<td>16–36</td>
</tr>
<tr>
<td></td>
<td>Eoglyptograptus dentatus</td>
<td>Bulman 1931 (1); Ruedemann 1947 (1)</td>
<td>28–29?</td>
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<tr>
<td></td>
<td>Pseudoplexograpthus sp.</td>
<td>Ekström 1937 (2)</td>
<td>17?, 20?</td>
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<td>“Glyptograptus euglypha pygmaeus”</td>
<td>Ruedemann 1908, 1947 (1)</td>
<td>9?</td>
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<td>Monograptacea</td>
<td>Hallograptus mucranatus</td>
<td>Ruedemann 1908, 1947 (3)</td>
<td>8?</td>
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<td>Lasigograptus pusillus</td>
<td>Ruedemann 1947 (&gt;1)</td>
<td>?</td>
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<td></td>
<td>Normalogr. mohawkensis</td>
<td>Riva in Clark 1972 (1)</td>
<td>26?</td>
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<td></td>
<td>Normalogr. normalis</td>
<td>Chen 1984 (2)</td>
<td>20?</td>
</tr>
<tr>
<td></td>
<td>Rhaphidogr. toernquisti</td>
<td>Bjerreskov 1976 (4)</td>
<td>17–25</td>
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<td>Petalograptus fusiformis</td>
<td>Palmer and Richards 1991 (1)</td>
<td>12</td>
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<td>Pristigraptus dubius</td>
<td>Arctic Canada, this study (1)</td>
<td>11?</td>
</tr>
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<td></td>
<td>Colonomgraptus ludensis</td>
<td>Czech Republic, pers. comm., Storch 1996 (1)</td>
<td>11</td>
</tr>
<tr>
<td></td>
<td>Colonomgraptus dubeli</td>
<td>Northwestern Spain, this study (&gt;90)</td>
<td>20–26</td>
</tr>
<tr>
<td></td>
<td>C. schididonensis</td>
<td>Arctic Canada, this study (5)</td>
<td>17–28</td>
</tr>
<tr>
<td></td>
<td>C. praedebeli</td>
<td>Arctic Canada, this study (1)</td>
<td>17</td>
</tr>
<tr>
<td></td>
<td>C. ludensis</td>
<td>Arctic Canada, this study (8)</td>
<td>16–34</td>
</tr>
<tr>
<td></td>
<td>C. aff. colonus</td>
<td>Rickards 1975 (17)</td>
<td>2?</td>
</tr>
<tr>
<td></td>
<td>C. cf. gerardi</td>
<td>Northwestern Spain, this study (1)</td>
<td>&gt;11</td>
</tr>
<tr>
<td></td>
<td>C.? tubufelixis</td>
<td>Hundt 1965 (1)</td>
<td>?</td>
</tr>
<tr>
<td></td>
<td>Sactograptus varians</td>
<td>Rickards 1975 (1); Siveter et al. 1989 (&gt;1); Palmer and Rickards 1991 (1)</td>
<td>4,12</td>
</tr>
<tr>
<td></td>
<td>S. fritschi linearis</td>
<td>Lenz and Melchin 1986 (1)</td>
<td>15</td>
</tr>
<tr>
<td></td>
<td>Monograptus ceratus</td>
<td>Arctic Canada, this study (1)</td>
<td>15</td>
</tr>
<tr>
<td></td>
<td>M. fanicus</td>
<td>Jackson, Kerr, and Morrow 1976 (1)</td>
<td>9</td>
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<tr>
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<td>M. weigelti</td>
<td>Hundt 1965 (1)</td>
<td>?</td>
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<tr>
<td></td>
<td>M. spp. (2 species?)</td>
<td>Hundt 1965 (2)</td>
<td>?</td>
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</tbody>
</table>

Rarely known from light-colored and/or shallow-water deposits, one such exception being an apparently transgressive shallow marine subtidal sequence in the upper Arenig of north Wales (Beckly and Maletz 1991). Characteristically, in situ benthic faunas are absent, but vagrant nektan such as nautiloids, phyllocarids, or eurypterids may be present. Referring specifically to northwestern Spain, many of the numerous synrhabdosomes are tightly overlapping and form more or less linear "superclusters" (Fig. 1), parallel to what appear to be low-amplitude ripples, and sometimes lie on top of eurypterid fragments, suggesting a degree of being "snagged" by topographic irregularities. Weak bottom currents were clearly present in some sites, suggesting selective distributions of synrhabdo-
somes on certain bedding planes and, thus, a degree of strength or coherence to synrhabdosomal structures, greater than previously assumed.

In like manner, the large numbers of synrhabdosomes on a single bedding plane figured by Ruedemann (1895, 1947) (Fig. 3 herein) have been interpreted differently by Ruedemann (1895), Rickards (1975), and Kirk (1978). Significantly, the last two authors centered their attention only on a minor part of the rock surface; that shown in Ruedemann (1947: Pl. 81, Fig. 33). A reexamination of the entire rock surface, however, reveals a concentration of synrhabdosomes aligned on a minor part of the slab, whereas the remainder of the surface is free of fossils or shows only a band of siculae and graptolite fragments lying in a different orientation (Fig. 3). A differential current sorting of the different size and density components is suggested, again pointing to the considerable "cohesion" of the synrhabdosomes.

Finally, the biostratinomic congregations of synrhabdosomes by weak bottom currents observed in the Spanish Silurian, as well as in some Appalachian Ordovician material, also argue in favor of the relative durability of rhabdosomal attachment in each synrhabdosome, reinforcing the suggestion of a true biological association for such structures. Accordingly, synrhabdosomes appear capable of resisting moderate displacement in low-energy conditions for some period of time, only gradually undergoing progressive detachment of their constituent rhabdosomes, as shown by the presence in many aggregations of larger numbers of detached but radially arrayed nemata, relative to the remaining number of rhabdosomes in any one structure (e.g., Ruedemann 1895, 1947; Bulman 1941).

**Biological Entity or Physical Entanglement?**

Triggered, in part, by the life-reconstructions of synrhabdosomes by Ruedemann (1895, 1908, 1947), and reinforced by the comments of Kozlowski (1949), the interpretation accepted by most earlier workers was that synrhabdosomes are biologically generated structures (Bulman 1970), possibly related to sexual or asexual reproduction. More recently, however, their rarity and seeming randomness of their occurrences, and the presence of supposed mixed-taxon synrhabdosomes, has led to the suggestion that some, at least, may merely be aggregations or spurious assem-

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**Figure 2.** Biostratigraphic distribution of species forming synrhabdosomes from the Tremadoc to Pragian (Lower Devonian). Abbreviations are as follows: Tr = Tremadoc; LA = lower Arenig; UA = upper Arenig; Ln = Llanvirn; LC = lower Caradoc; UC = upper Caradoc; As = Ashgill; LV = lower Llandovery; MV = middle Llandovery; UV = upper Llandovery; LW = lower Wenlock; UW = upper Wenlock; LL = lower Ludlow; ML = middle Ludlow; UL = upper Ludlow; Pr = Priodoli; Lk = Lochkovian; Pg = Pragian.
Synrhabdosomal grouping of *Orthograptus ruedemanni* (Gurley) from the Utica Shale, Dolgeville, New York. Free-hand drawing of part of sample NYSM 4922, reproduced from Ruedemann (1895: Pl. 5). Note that current orientation of synrhabdosomal groupings are distinctly different from those of a band of numerous siculae and small fragment of graptolites. The “central structures” shown by Ruedemann in some of the synrhadosomes are not recognizable on the original slab.

blages “stuck together.” This latter interpretation has been promoted by Rigby (1993) and Goldman and Mitchell (1994).

First, and most importantly, we consider it likely that all known synrhadosomes are monospecific assemblages and all, with the exception of *Rhaphidograptus toernquisti*, illustrated by Bjerreskov (1976), are anchored by their virgulae; second, as noted above, the number of rhabdosomes in a synrhadosome appears to be finite, something not to be expected in random aggregations; and third, all mid-Ordovician and younger synrhadosomes are composed of essentially straight biserials or monograptids with relatively simple thecae. It seems particularly striking that there are apparently no known synrhadosomes constructed of strongly curved and/or spiraled species (e.g., species such as *Oktawites spiralis*, *Spirograptus turriculatus*, *Bohemograpthus bohemicus*, *Cyrtograptus* spp.), or of any kind of Silurian retiolitid. On the other hand, numerous, clearly entangled aggregations of retiolitids have been observed in Silurian rocks in the Arctic. Finally, the sheer number of discrete, monospecific synrhadosomes from northern Spain, as well as those of *Orthograptus ruedemanni* originally illustrated by Ruedemann (1895) and reillustrated herein (Fig. 3), adds further strong evidence of a natural assemblage. We feel, therefore, that the evidence for synrhadosomes being biologically generated structures, although probably facultative, rather than obligate, associations (cf. Melchin and DeMont 1995), is overwhelming, a suggestion apparently supported by Underwood (1993). We further conclude that the suggestion of Rigby (1993) that “marine snow” might bind rhabdosomes together is inadequate to explain the consistent monospecific makeup of all the studied synrhadosomes, or the apparent relative strength of synrhadosomal structures. Furthermore, we fail to see how “marine snow” could be so “selective” as to bind rhabdosomes only at distal parts of the virgulae, to bind only species with straight rhabdosomes and with relatively simple thecae, or to account for distal virgular modifications seen in many synrhadosomal specimens.

Whether the distal ends of virgulae in synrhadosomes continued to lengthen in conjunction with the distal growth of rhabdosomes is difficult the ascertain. However, the observation (discussed above), that virgular lengths appear to be species-related, rather than astogenetically related, suggests that continued growth was possible. The mechanism, however, is not understood.

**Function of the Synrhadosome**

Synrhadosomes have been attributed to float mechanisms (Ruedemann 1895, 1908, 1947; see also Hundt 1965), to some aspect of sexual or even asexual reproduction (Ruedemann 1895; Kozlowski 1949, 1971; Bjerreskov 1976; Zalasiewicz 1984; Underwood 1993; Ge and Chen 1995; Rickards 1996), or interpreted
as evidence of benthic assemblages preserved in situ (Kirk 1978). The first suggestion is dis-
counted since, as pointed out by Bulman (1970) and Kozlowski (1971), each rhabdosome
already has its own buoyancy mecha-
nism, and the so-called float devices illus-
trated by Ruedemann (1895) are, in fact, not rec-
ognizable (Rickards 1975; Walters 1977; Gold-
man and Mitchell 1994; personal examination
of the Ruedemann material by J. C. G.-M.) and
therefore are probably nonexistent; certainly
none of the many specimens viewed by us
shows any sign of an extra-rhabdosomal
structure, whereas they may show an inextric-
table central entanglement of virgular
“threads,” and/or a central knot-like struc-
ture. Furthermore, if synrhabdosomes were
float-related structures, it is difficult to under-
stand why all post-Lower Ordovician syn-
rhabdosomes known to us are made up exclu-
sively of straight, or only weakly curved,
rhabdosomes bearing relatively simple thecae.

The suggestion that synrhabdosomes are in
situ benthic assemblages (Kirk 1978) is consid-
ered untenable in view of clear evidence of
current control on synrhabdosomal distribu-
tions, and because the vast majority of all syn-
rhabdosomes are found in black shales indic-
tive of anoxic environments.

The reproductive aspect is obviously im-
possible to test and, except by analogy with
the living Cephalodiscus (Kozlowski 1949), we
feel the suggestion has little support. The facts
that synrhabdosomes are relatively rare struc-
tures and that post-Lower Ordovician syn-
rhabdosomes are made up of a more or less
finite number of essentially straight, mono-
specific rhabdosomes with relatively simple
theca prompt an alternative interpretation.

Computer modeling studies of Fortey and
Bell (1987) have shown that in multibranched
graptolites, stipe number, branch position,
and branching pattern in any rhabdosome is
constrained by factors improving the feeding
strategy through a maximum water sampling.
Experimental studies of Rigby and Rickards
(1989) further suggest that most, if not all,
graptolites, whether multibranched or unise-
rial, probably spiraled to varying degrees
through the water column as a strategy for in-
creasing feeding efficiency. Extrapolating
from these two studies, we therefore suggest
that synrhabdosomes are best interpreted as
feeding structures, a suggestion somewhat
obliquely made by Underwood (1993). Assum-
ning that rhabdosomes were attached to
some central point, most probably by virgular
“threads” branching into a central point or
knot, that the rhabdosomes were radially ar-
rayed in a cone-shaped structure, and finally
that such structures spiraled through the wa-
ter column, then feeding efficiency would be
substantially increased when compared with
that of the single, straight rhabdosome. Pre-
sumably the increased frictional drag on the
whole synrhabdosome also would optimize
its passive buoyancy in deeper environments
where such large structures could effectively
exploit the cool, dense water masses. This, in
conjunction with local, oxygen-depleted en-
vironments acting as marginal nutrient res-
ervoirs, would promote the formation of syn-
rhabdosomes in those few species living in or
near, and able to exploit, such abnormal local
environments.

In essence, therefore, the synrhabdosome
would in many ways mimic the straight- and
multi-stiped Early Ordovician dichograptoids
or even, to some extent, Silurian cyrtograptids
and linograptids. A feeding strategy interpre-
tation would, we feel, explain the finite num-
ber of rhabdosomes as well as the fact that
they are all straight. The interpretation further
explains that strongly curved or spiraled
monograptids or cyrtograptids, as well as
those with complex and ornate thecal struc-
tures, are unlikely to have formed synrhab-
dosomes simply because of the physical im-
possibility of preventing thecal/stipe interfer-
ence; further, because of their design, they are
naturally spiraling structures often with elab-
orate thecal structures and thus are already
optimally efficient feeding structures. We feel
this would apply even if locomotion was by
means of winglike extensions of the cephalic
shield of the zooids as proposed by Melchin
and DeMont (1995), the only requirement be-
ing that the rowing movement of the muscular
appendages of all the zooids be coordinated
throughout the synrhabdosome “super colo-
ny.”
Rarity or Patchiness of Synrhabdosomes

If, as suggested, synrhabdosomes are primarily feeding structures, the question of their rarity arises (although the same question arises when considering them to be related to sexual reproduction). In either interpretation, their relative rarity must be accounted for. To put it in the form of a question, if the synrhabdosomal structure is good/efficient for a few taxa with straight rhabdosomes, why don’t many more, even all, species of straight biserials and monograptids form synrhabdosomes? Furthermore, why then are synrhabdosomes not the rule rather than the exception?

The suggestion by Rickards (1975) that synrhabdosomes were held together by a small mass of soft axial extrathecal tissue helps, in part, to explain their ephemeral nature, although, as suggested above, they were more likely welded together, relatively firmly, by means of a small central cluster of post-virgular “threads.” This suggestion is supported by the seeming resiliency and not-easily-entangled nature of the rodlike virgulae of most graptoloids (see Kirk 1978). Furthermore, as already noted, virgulae of synrhabdosomes are often complexly bifurcated, whereas those of the vast majority of single rhabdosomes are simple rods, providing strong evidence that the latter are not remnants of disaggregated synrhabdosomes. It appears significant to us that when synrhabdosomes are found, they are often relatively common and are most often found in only specific parts of the stratigraphic column. This is certainly true of the Canadian Arctic and Spanish occurrences, and it has been claimed for the Upper Ordovician of the Appalachians (Ruedemann 1895; Rigby 1993) and the Silurian of south-central Wales (Siveter et al. 1989). If as suggested, above, synrhabdosomes were feeding structures, then it is possible they might have served only as temporary “emergency feeding devices,” forming only at times of local, lowered food (plankton) supply in marginal environments. Their preservation could then be looked upon as a series of rare but coincidental events, i.e., infrequent formation of synrhabdosomal structures during times of local, lowered food supply; periodic overturning and/or rise of anoxic waters in relatively local cell-like areas (see Berry et al. 1987), causing mass killing of synrhabdosomal colonies and single rhabdosomes; and rapid burial and/or encapsulation in totally anoxic waters prior to burial. This is in contrast to Underwood (1993), who suggests that synrhabdosomes form only in high-nutrient waters, although we find totally untenable his suggestion that synrhabdosomal movement would be severely restricted in these waters and that they are, by implication, inefficient feeders.

A further explanation of the patchiness of synrhabdosome distribution might lie in the presence of relatively small, persistent eddies as seen in the present-day oceanic waters. Haury et al. (1978) noted considerable patchiness in the distribution of plankton communities in the Sargasso Sea, due to the short-duration (years to tens of years) existence of “cold core rings” that may be up to 100–200 km in diameter and hundreds of meters in depth. By analogy, a particular graptolite community could have been confined to one “ring” with nutrient levels relatively much lower than adjacent regions outside the ring, and it would be only in those rings with lower nutrient supply that synrhabdosome formation would be triggered in one or a few species.

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