

The Prospect of Compact Estuarine Lagerstätten

Charles E. Savrda, Patrick S. Bingham, Terrell K. Knight, and Ronald D. Lewis

Department of Geology and Geography

Auburn University

Auburn, AL 36849-5305

ABSTRACT

A thin, laterally restricted but exceptionally fossiliferous clay lens—informally dubbed the Ingersoll shale—within the Upper Cretaceous Eutaw Formation, eastern U.S. Gulf coastal plain, provides insights regarding the origins of a class of fossil conservation lagerstätten we call compact estuarine lagerstätten (CELs). The Ingersoll shale accumulated in a restricted channel wherein preservation of a diverse paleoflora, amber with fossil inclusions, and feathers was favored by rapid tidal deposition of clay-rich carbonaceous sediments, anoxic pore waters, early diagenetic pyrite mineralization, and perhaps microbial sealing and/or replacement. Although potentially easily overlooked, similar compact lagerstätten formed by comparable taphonomic factors may be common in other estuarine successions.

Exploration for additional CELs, guided by sequence stratigraphic principles, may yield other small but spectacular glimpses of life in the past.

COMPACT LAGERSTÄTTEN

Fossil conservation lagerstätten are sedimentary deposits that contain unusually well-preserved fossil biotas, commonly including soft parts (Seilacher et al., 1985; Allison, 1988). Given their importance to paleontology and sedimentary geology, it is critical to understand the processes by which they form and to develop criteria that can be used to prospect for additional exceptionally preserved fossil biotas (Bottjer et al., 2002; Allison et al., 2008).

Many conservation lagerstätten accumulated over extended time periods in sizeable depocenters—meromictic lakes (e.g., Allison et al., 2008), stratified marine basins (e.g., Seilacher, 1982), anoxic or hypersaline lagoons (e.g., Papazzoni and Trevisani, 2006), or large estuaries (e.g., Baird et al., 1986)—and, hence, are relatively thick and/or laterally extensive. However, conditions conducive to exceptional fossil preservation may develop in small and transient depocenters as well, forming relatively compact lagerstätten that, due to limited breadth and thickness, may go unnoticed. We posit that transgressive estuarine sequences hold particularly high potential for discovery of new compact lagerstätten, and we term these deposits compact estuarine lagerstätten (CELs). As demonstrated by the recently discovered Ingersoll shale, a small yet extraordinarily fossiliferous deposit in the Cretaceous (Santonian) Eutaw Formation of eastern Alabama (Bingham et al., 2008), the various processes that lead to exceptional preservation may act synergistically in certain restricted estuarine environments. Because associated facies typically occur as components of incised valley fills,

the distribution of CELs formed in these settings can be predicted in the context of sequence stratigraphy.

INGERSOLL SHALE

Fossil Biota

The Ingersoll shale is characterized by a mainly terrestrial fossil biota, the most important elements of which are fossil plants, amber, and feathers. Plant remains are abundant and diverse (Fig. 1). Angiosperms are represented by forty-one leaf morphotypes as well as by rare flowers, seeds, and purported fruits, whereas gymnosperms and ferns are represented by leaves (seven morphotypes each), cones, and megaspores. Commonly, leaves are preserved intact and attached to stems, and cones and megaspores are preserved in three dimensions. Amber occurs as *in situ* rods within plant parts and as isolated detrital clasts. Amber clasts entomb plant debris, fecal pellets, fungal hyphae, and terrestrial arthropods, including mites, scale insects, and spiders (e.g., Fig. 2). The deposit has yielded the largest collection of feathers (cover photo and Fig. 3) derived thus far from North American Mesozoic strata; all are contour feathers, some with detailed anatomical features such as barbules and barbicels. The wealth of paleontologic information contained in this fossil assemblage is quite remarkable, especially when the limited volume of the host sediment is considered.

Stratigraphic and Paleoenvironmental Context

The Ingersoll shale, comprising dark gray, carbonaceous, pyritiferous clay with subordinate sand and silt laminae towards the base, forms a lenticular body with maximum thickness and width of 80 cm and 30 m, respectively. This small lens occurs in the lower part of the Eutaw Formation, which in eastern Alabama and western Georgia accumulated in a mixed-energy estuarine system (Frazier, 1997; Savrda and Nanson, 2003), approximately 1 m above the disconformable contact with the underlying fluvial Tuscaloosa Formation (Fig. 4). Both the base and top of the Ingersoll shale are erosional. The base truncates *Ophiomorpha*-bearing, cross-stratified, coarse-grained sands and planar-bedded sands and clays deposited in tidal-channel and tidal-flat settings. The lens is overlain by highly bioturbated, carbonaceous sandy muds and muddy sands that accumulated in a proximal estuarine central bay. A firmground ichnofossil assemblage developed in the upper 5 cm of the lens reflects truncation at the top of the Ingersoll shale in response to bay-shoreline ravinement during transgression. Based on geometry, facies associations, and sedimentologic characteristics, we interpret the Ingersoll shale to have accumulated in a restricted tidal channel in the lower reaches of a bayhead delta.

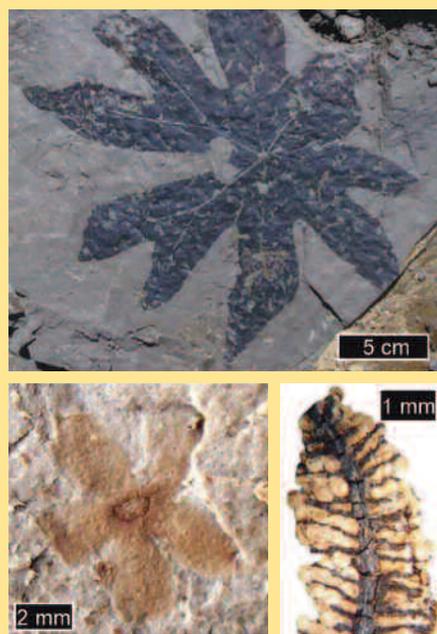


Figure 1. Examples of well-preserved fossil plants in the Ingersoll shale, including a large intact angiosperm leaf (top), small flower (bottom left), and a water-fern sporocarp containing mega- and microsporangia (bottom right).

Environmental and early diagenetic conditions and fossil preservation in the Ingersoll shale are addressed further in the following discussion of taphonomic factors. We refer the reader to Bingham et al. (2008) for details.

PRESERVATION MECHANISMS AND THEIR ROLE IN ESTUARIES

Factors that may contribute to exceptional preservation in conservation lagerstätten include (1) rapid burial, particularly by muds; (2) oxygen deficiency; (3) early diagenetic mineralization; (4) microbial processes, including replacement or sealing of organic remains; and (5) entombment in relatively sterile media (Seilacher et al., 1985; Allison, 1988; Bottjer et al., 2002; Briggs, 2003). These factors are not mutually exclusive, and their importance varies among lagerstätten. In the Ingersoll shale, all of five factors played a role in fossil preservation. Predictably, multiple preservation processes have similarly interacted to form as-yet unrecognized compact lagerstätten in estuarine settings comparable to that of the Ingersoll shale.

Rapid Burial

Rapid burial insulates organic remains from the destructive effects of bottom

currents, scavenging, and bioturbation. For many lagerstätten, burial was caused by episodic deposition of tempestites, turbidites, other gravity flows, or volcanic ash (Brett et al., 1997). However, in some settings, including certain estuarine environments, steady background accumulation rates may be sufficiently high to bury and conserve organic remains.

Estuaries form by transgressive inundation of fluviably incised coastal plains (Dalrymple et al., 1992). Drowning of incised valleys creates accommodation space, which is then rapidly filled mainly by river-derived sediments. Although sediment-accumulation rates in estuaries are not everywhere adequate to enhance preservation, prerequisites may be met in environments characterized by both unusually high sedimentation rates and little or no reworking. Such environments include intertidal and shallow subtidal settings prone to accumulation of tidal rhythmites, which reflect continuous deposition of mm-scale graded packages in response to diurnal or semidiurnal tidal cycles (Kvale et al., 1999).

Tidal rhythmite deposition, previously implicated as a key control on fossil preservation in other conservation lagerstätten (e.g., see Feldman et al., 1993), played an important role in the small Ingersoll tidal channel. Well-developed tidal rhythmites in the lower, sandier parts of the Ingersoll shale (Fig. 5) indicate virtually uninterrupted sedimentation space with diurnal tidal cycles at rates as high as 1 m/yr (Bingham et al., 2008). Deposition at these rates likely was the most important factor contributing to the preservation of delicate feathers and intact plant remains in the Ingersoll shale lagerstätte.

Preservation potential of fossil remains is greatest when the burial medium is mud, particularly clay. Clayey sediments more readily cast structural details of buried remains and may produce soupy substrate barriers that inhibit burrowing and scavenging by benthic organisms. Muds and mudrocks are also less permeable, limiting the extent of leaching and fossil degradation in deeper burial diagenetic and post-uplift weathering regimes.

Central zones of estuarine systems (e.g., central bays in wave-dominated or mixed energy estuaries) are characterized by energy minima (Dalrymple et al., 1992) and, hence, are most prone to the accumulation of muds. In the case of the Ingersoll shale, rapid filling of the tidal channel by clay-

dominated sediment occurred in seaward parts of a bayhead delta when transgressive expansion of the central bay resulted in decreased hydraulic gradients and lower flow regimes in the channel. Not surprisingly, feathers and intact plant parts are most common in clay-dominated middle and upper parts of the Ingersoll shale.

Oxygen Deficiency

Low dissolved oxygen concentrations favor fossil preservation in aquatic settings by limiting or precluding destructive activities of benthic organisms (scavenging, bioturbation, substrate irrigation), and by mediating early diagenetic mineralization. For many lacustrine and marine lagerstätten, deposition occurred beneath anoxic *bottom waters* formed by long-term thermohaline basin stratification. Although some estuarine systems may experience periodic stratification and hypoxia (e.g., Officer et al., 1984), they normally are not prone to development of stable anoxic bottom-water masses. Nonetheless, estuarine subenvironments may be characterized by anoxic *pore waters*, which can enhance preservation.

Development of reducing substrate pore waters beneath a shallow, oxygenated water column requires high organic influx. Organic production in estuaries is typically high, particularly in climatic regimes that support coastal marsh and swamp



Figure 2. Amber clasts (top) and a scale insect entombed in amber (bottom) from the basal part of the Ingersoll shale.



Figure 3. Composite image of the largest feather recovered from the Ingersoll shale. Inset (SEM of feather) shows minute, carbonized rod-shaped bodies. Do these reflect sealing/replacement by bacteria? Or, are they preserved feather pigment bodies?

vegetation, and organic accumulation rates can be considerable in relatively low-energy, mud-dominated subaqueous settings. Consequently, microbial degradation of sedimentary organic matter may result in anoxic pore waters that inhibit infauna and limit bioturbation (Feldman et al., 1993).

The impact of high organic supply on substrate redox conditions in estuarine subenvironments is manifest in the Ingersoll shale. Organic contents are high (1.16 to 3.62%), reflecting input of mostly terrestrial plant detritus from adjacent swamps but

also a contribution from marine plankton (e.g., dinoflagellates). Consequent development of anoxic conditions at or just below the sediment-water interface is indicated by abundant early-formed pyrite and general lack of bioturbation. The bulk of the Ingersoll shale contains only narrow (1–2 mm), shallowly emplaced (<1 cm), flattened burrows produced by sediment-swimming worms. These ill-defined ichnofossils locally penetrate and disrupt leaf fossils. However, sulfidic pore waters in concert with highly fluid clay substrates precluded colonization of the channel bottom by a deeply burrowing and destructive infauna.

Diagenetic Mineralization

Exquisite preservation in conservation lagerstätten is commonly tied to precipitation of early diagenetic minerals—e.g., phosphate, silica, carbonates, or pyrite—that entomb, replace, or permineralize organic remains (Briggs, 2003). The nature of early diagenetic mineralization depends on water chemistry (e.g., salinity, redox conditions) and availability of reactive organic matter. Mineralization of fossils in estuarine lagerstätten commonly entails sideritization or pyritization, the relative importance of which is controlled by salinity. Preservation of soft parts within siderite nodules, such as those in Mazon Creek-type deposits, is commonly attributed to the influence of relatively fresh, Fe-rich waters and limited sulfate supply (e.g., Baird et al., 1986). In contrast, pyritization is more prevalent in substrates overlain by marine waters and characterized by open diagenetic systems that provide an unlimited supply of sulfate for microbial sulfate reducers (Brett and Allison, 1998).

Ingersoll shale substrates clearly were most influenced by sulfate-rich marine waters. Siderite has not been detected, but pyrite occurs throughout the Ingersoll shale as nodules and disseminated framboids. Compaction of clay around pyrite nodules, along with pyrite sulfur isotopic evidence (see Bingham et al., 2008), indicates that sulfide precipitation occurred very rapidly at shallow substrate depths in open connection with normal marine channel waters. Although pyritization of fossils in the Ingersoll shale is not pervasive, early mineralization was important locally in conserving three-dimensional aspects of plant reproductive bodies (cones and megaspores) and parts of some feathers.

Microbial Processes

Microbial processes are generally required to induce anoxia in bottom and pore waters, and they govern precipitation of early diagenetic minerals. Moreover, microbes may play more direct roles in fossilization. Bacterial or algal mats, formed atop substrates or in the water column before descending to the bottom, may coat organic remains and thus form protective barriers or seals against physical and chemical degradation (e.g., Seilacher et al., 1985; Harding and Chant, 2000).

The extent to which bacterial sealing or replacement contributed to preservation of Ingersoll shale fossils is still under investigation. Previously, we reported evidence indicating that bacteria played a role in preservation of Ingersoll feathers (Bingham et al., 2008). SEM studies show that feather barbules and barbicels are now composed of small (~1 μ long), carbonized, elongate ovate structures (Fig. 3 inset). Following interpretations made for similar structures observed in feathers from the Eocene Messel Shale (Davis and Briggs, 1995), we inferred that Ingersoll feathers were coated or replaced by bacterial mats. The affinity of these structures, however, requires further consideration in light of the recently demonstrated resemblance between bacteria and melanosomes (pigment-bearing organelles) in modern and fossil feathers (Vinther et al., 2008).

Amber Accumulation

Amber serves as an excellent medium for preservation of any small organic feature that happens to be trapped in viscous and sticky plant exudates. Resins exuded in subaerial environments may preserve the remains of plants, microbes, insects, and other arthropods, terrestrial or aerial vertebrates, and traces of organism activity, such as fecal pellets, spider webs, and nests (e.g., see Poinar, 1993, 1998; Grimaldi et al., 2000). Fossils mummified in amber are typically rendered in three dimensions, and their microscopic anatomical detail, including labile tissues (e.g., Henwood, 1992), is commonly retained.

Formation of amber-rich deposits requires (1) a terrestrial plant community that includes common resin-producers and (2) a mechanism for transport and hydraulic concentration of resin clasts or resin-bearing plant parts in depositional settings that are conducive to amber preservation (see Martínez-Delclòs et al., 2004). Both of these requirements likely were met with

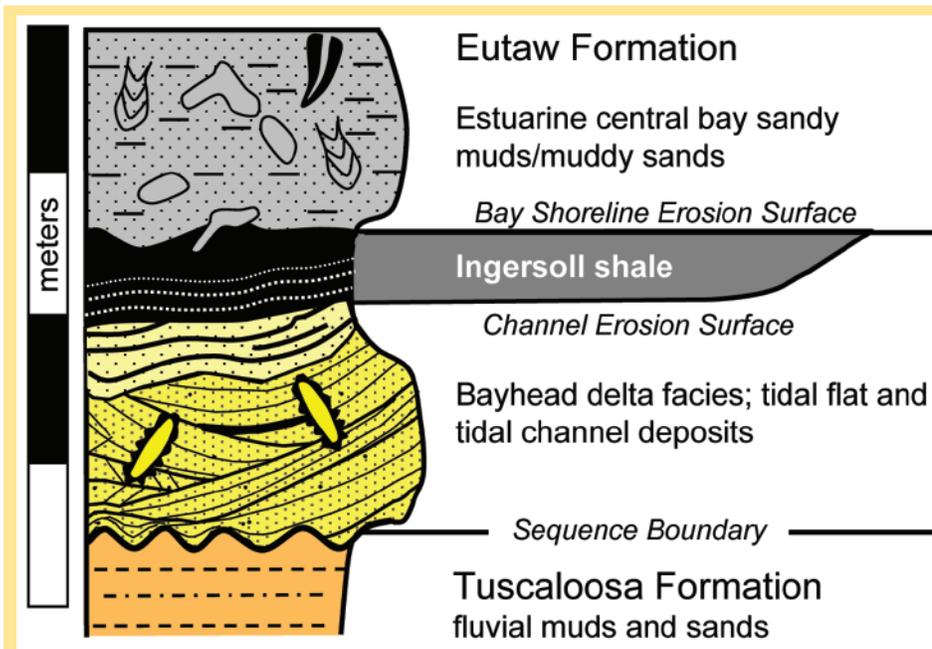


Figure 4. Schematic representation of the Ingersoll shale lens and bounding facies in the lower part of an incised valley fill, Eutaw Formation. The Ingersoll shale accumulated in a restricted tidal channel in a lower bayhead-delta setting during transgressive expansion of an estuarine central bay. Amber clasts are most abundant in the basal, sandier part of the lens, whereas intact plant parts and feathers are prevalent in overlying clays.

some frequency in Cretaceous and younger estuarine environments, particularly in bayhead-delta settings. Depending on age, climate, and vegetation type, coastal swamp vegetation could have produced copious amounts of resin, and resin masses could have been concentrated as bed load in the fluvial and/or tidal channels. Preservation of accumulated resin masses would be enhanced by rapid burial beneath organic-rich sediments.

Requirements for amber accumulation and preservation were satisfied in the Ingersoll estuarine system. Resin-producing trees, most likely conifers in the family Cupressaceae, in coastal swamps supplied amber clasts and amber-bearing plant parts that subsequently were transported to the tidal channel. Amber clasts, typically in the size range of 1 to 15 mm (Fig. 2), are most abundant on or within sand laminae in the lower parts of the lens, reflecting transport and concentration on the channel bed during relatively high-energy phases of tidal cycles. Most Ingersoll amber clasts are transparent and lack chalky crusts that form by weathering and oxidation. This reflects rapid burial by clay-rich laminae and the development of reducing conditions in pore waters during later phases of channel filling.

Amber clasts in some deposits have experienced a complex history of transport

and may be age and facies incongruent (Martínez-Delclòs et al., 2004). In contrast, amber clasts that accumulated in small estuarine channels such as that filled by the Ingersoll shale likely had relatively simple and short transport histories. Consequently, amber and fossil inclusions more reliably reflect the plants and terrestrial organisms that occupied contemporaneous neighborhoods in the estuarine system.

The Five Processes Combined

As shown above, estuarine systems provide mechanisms for rapid deposition of fine-grained, organic-rich sediment. Resulting oxygen deficiency limits biological disruption and promotes microbial growth and early diagenetic mineralization. These coastal settings also may add preservation traps in the form of land-plant generated amber, also preserved by rapid burial and reducing conditions. The fortuitous cooperation of these processes in small ephemeral depocenters results in CELs.

PROSPECTING FOR COMPACT ESTUARINE LAGERSTÄTTEN

The Ingersoll shale exemplifies how conservation lagerstätten of limited areal extent and thickness can be formed in relatively isolated, transient estuarine

depocenters. Another example of a compact lagerstätte formed in comparable settings is provided by the Triassic Grès à Voltzia (NE France). Therein, fossils are well preserved in small carbonaceous and pyritiferous clay lenses that record rapid deposition in stagnant temporary tidal pools formed during a fluvial-to-marine transition (Briggs and Gall, 1990). Unlike the Ingersoll shale, the latter clay bodies, which may qualify as CELs, contain arthropods, fish, and wholly soft-bodied organisms, reflecting the potential variability of biotas preserved in estuarine deposits.

Isolated environments predisposed to rapid accumulation of organic-rich, reducing clayey sediments undoubtedly have recurred in many ancient estuarine systems. Hence, we contend that CELs may be common in estuarine successions but, due to their small volume and superficially unremarkable field expression, they easily escape detection. Notably, the Ingersoll shale lagerstätte may have gone unrecognized were it not for the few curious hammer blows by one of us (PSB) that serendipitously yielded the first Ingersoll feather.

How can we prospect for as-yet undiscovered CELs? A regional sequence stratigraphic framework should provide a starting point for exploration. Efforts should be directed at lowstand incised valley fills (IVF), wherein transgressive estuarine facies are most commonly represented. Within IVF, the search likely will be most fruitful if focused on bayhead facies associations, which predictably would be

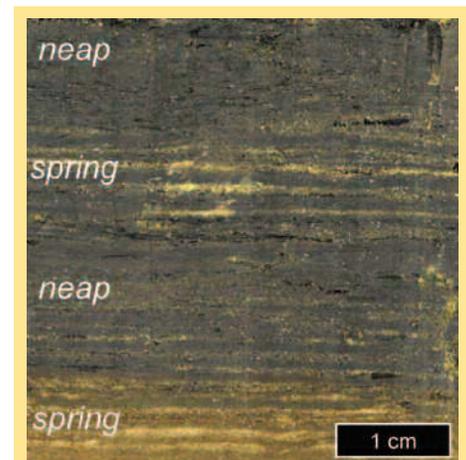


Figure 5. Tidal rhythmites in the lower part of the Ingersoll shale. Systematic variations in sand-clay couplet thickness reflect neap-spring tidal cyclicity in a diurnal tidal system.

more common and better preserved in lower and landward parts of estuarine packages. Carbonaceous muds and mudrocks within these associations obviously represent the most interesting targets. Our own search for hidden CELs in other Gulf coastal plain Cretaceous successions has already begun. Find those estuarine carbonaceous clay bodies, draw your hammers, and dig in.....carefully!

ACKNOWLEDGEMENTS

Mr. Michael Ingersoll graciously provided access to the Ingersoll shale exposure. David Grimaldi (American Museum of Natural History) assisted in analysis of amber and inclusions. Studies of the Ingersoll shale were supported by NSF grant EAR-0633839 (to CES and RDL) and grants-in-aid from the GCAGS and GSA (to PSB and TKK).

REFERENCES

- ALLISON, P.A., 1988, Konservat-Lagerstätten: Cause and classification: *Paleobiology*, v. 14, p. 331-334.
- ALLISON, P.A., MAEDA, H., TUZINO, T., and MAEDA, Y., 2008, Exceptional preservation within Pleistocene lacustrine sediments of Shiobara, Japan: *Palaaios*, v. 23, p. 260-266.
- BAIRD, G.C., SROKA, S.D., SHABICA, C.W., and KUECHER, G.J., 1986, Taphonomy of Middle Pennsylvanian Mazon Creek area fossil localities, northeast Illinois: Significance of exceptional fossil preservation in syngenetic concretions: *Palaaios*, v. 1, p. 271-285.
- BINGHAM, P.S., SAVRDA, C.E., KNIGHT, T.K., and LEWIS, R.D., 2008, Character and genesis of the Ingersoll shale, a compact continental fossil-lagerstätte, Upper Cretaceous Eutaw Formation, eastern Alabama: *Palaaios*, v. 23, p. 391-401.
- BOTTJER, D.J., ETTER, W., HAGADORN, J.W., and TANG, C.M., eds., 2002, *Exceptional Fossil Preservation: A Unique View on the Evolution of Marine Life*, Columbia University Press, New York, 403 p.
- BRETT, C.E., and ALLISON, P.A., 1998, Paleontological approaches to the environmental interpretation of marine mudrocks, in Schieber, J., Zimmerle, W., and Sethi, P., eds., *Shales and Mudstones I*, E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart, p. 301-349.
- BRETT, C.E., BAIRD, G.C., and SPEYER, S.E., 1997, Fossil Lagerstätten: Stratigraphic record of paleontologic and taphonomic events, in Brett, C.E., and Baird, G.C., eds., *Paleontological Events: Stratigraphic, Ecological, and Evolutionary Implications*, Columbia University Press, New York, p. 3-40.
- BRIGGS, D.E.G., 2003, The role of decay and mineralization in the preservation of soft-bodied fossils: *Annual Review of Earth and Planetary Sciences*, v. 31, p. 275-301.
- BRIGGS, D.E.G., and GALL, J.-C., 1990, The continuum in soft-bodied biotas from transitional environments: a quantitative comparison of Triassic and Carboniferous Konservat-Lagerstätten: *Paleobiology*, v. 16, p. 204-218.
- DALRYMPLE, R.W., ZAITLIN, B.A., and BOYD, R., 1992, Estuarine facies models: Conceptual basis and stratigraphic implications: *Journal of Sedimentary Petrology*, v. 62, p. 1130-1146.
- DAVIS, P., and BRIGGS, D.E.G., 1995, Fossilization of feathers: *Geology*, v. 23, p. 783-786.
- FELDMAN, H.R., ARCHER, A.W., KVALE, E.P., CUNNINGHAM, C.R., MAPLES, C.G., and WEST, R.R., 1993, A tidal model of Carboniferous Konservat-Lagerstätten formation: *Palaaios*, v. 8, p. 485-498.
- FRAZIER, W.J., 1997, Upper Cretaceous strata in southwestern Georgia and adjacent Alabama: *Atlanta Geological Society Field Trip Guidebook*, p. 1-22.
- GRIMALDI, D., SHEDRINSKY, A., and WAMPLER, T.P., 2000, A remarkable deposit of fossiliferous amber from the Upper Cretaceous (Turonian) of New Jersey, in Grimaldi, D., ed., *Studies on Fossils in Amber, with Particular Reference to the Cretaceous of New Jersey: Paleontology of New Jersey Amber Part VII*, p. 1-76.
- HARDING, I.C., and CHANT, L.C., 2000, Self-sedimented diatom mats as agents of exceptional preservation in the Oligocene Florissant lake beds, Colorado, United States: *Geology*, v. 28, p. 195-198.
- HENWOOD, A., 1992, Exceptional preservation of dipteran flight muscle and the taphonomy of insects in amber: *Palaaios*, v. 7, p. 203-212.
- KVALE, E.P., JOHNSON, H.W., SONETT, C.P., ARCHER, A.W., and ZAWISTOSKI, A., 1999, Calculating lunar retreat rates using tidal rhythmites: *Journal of Sedimentary Research*, v. 69, p. 1154-1168.
- MARTÍNEZ-DELCLÒS, X., BRIGGS, D.E.G., and PEÑALVER, E., 2004, Taphonomy of insects in carbonates and amber: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 203, p. 19-64.
- OFFICER, C.B., BIGGS, R.B., TAFT, J.L., CRONIN, L.E., TYLER, M., and BOYNTON, W.R., 1984, Chesapeake Bay anoxia: Origin, development, and significance: *Science*, v. 223, p. 22-27.
- PAPAZZONI, C.A., and TREVISANI, E., 2006, Facies analysis, palaeoenvironmental reconstruction, and biostratigraphy of the "Pesciari di Bolca" (Verona, northern Italy): An early Eocene fossil-lagerstätte: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 242, p. 21-35.
- POINAR, G.O., Jr., 1993, Insects in amber: *Annual Reviews of Entomology*, v. 46, p. 145-159.
- POINAR, G.O., Jr., 1998, Trace fossils in amber: a new dimension for the ichnologist: *Ichnos*, v. 6, p. 47-52.
- SAVRDA, C.E., and NANSON, L.L., 2003, Ichnology of fair-weather and storm deposits in an Upper Cretaceous estuary (Eutaw Formation, western Georgia, USA): *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 202, p. 67-83.
- SEILACHER, A., 1982, Posidonia Shales (Toarcian, S. Germany)-Stagnant basin model revalidated, in Gallitelli, E.M., ed., *Paleontology, Essential of Historical Geology: Proceedings of the First International Meeting on "Paleontology, Essential of Historical Geology," STEM Mucchi, Modena*, p. 279-298.
- SEILACHER, A., REIF, W.-E., and WESTPHAL, F., 1985, Sedimentological, ecological and temporal patterns of *Fossil-Lagerstätten*: *Philosophical Transactions of the Royal Society of London*, v. B 311, p. 5-23.
- VINTHER, J., BRIGGS, D.E.G., PRUM, R.O., and SARANATHAN, V., 2008, The colour of fossil feathers: *Biology Letters*, p. 1-4 (published online: doi:10.1098/rsbl.2008.0302).

Accepted February 2009