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The Status of the Sauropterygian Reptile Genera *Ceresiosaurus*, *Lariosaurus*, and *Silvestrosaurus* from the Middle Triassic of Europe

Olivier Rieppel

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The Status of the Sauropterygian Reptile Genera *Ceresiosaurus, Lariosaurus,* and *Silvestrosaurus* from the Middle Triassic of Europe

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The Status of the Sauropterygian Reptile Genera *Ceresiosaurus, Lariosaurus,* and *Silvestrosaurus* from the Middle Triassic of Europe

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Abstract

The geographic and stratigraphic occurrence of the Middle Triassic sauropterygian genera *Ceresiosaurus, Lariosaurus,* and *Silvestrosaurus* is summarized, and their skeletal morphology is critically reviewed. A cladistic analysis using parsimony supports the synonymy of all three genera, among which *Lariosaurus* takes priority. The genus *Lariosaurus* includes five species, *balsami, buzzii, calcagnii, curionii* n. sp., and *valceresii,* with only partially resolved interrelationships. The sister group of *Lariosaurus* is the genus *Nothosaurus.* Lariosaurs diversified during Ladinian times in the northwestern Tethyan coastal area, after the genus *Nothosaurus* had invaded the Alpine intraplatform basin facies.

Zusammenfassung

Die geographische und stratigraphische Verbreitung der Gattungen *Ceresiosaurus, Lariosaurus,* und *Silvestrosaurus* wird zusammengefasst, und die Morphologie ihrer Vertreter kritisch diskutiert. Eine kladistische Analyse stützt die Synonymie aller drei Gattungen, von welchen *Lariosaurus* Priorität hat. Innerhalb der Gattung *Lariosaurus* werden fünf Arten unterschieden: *balsami, buzzii, calcagnii, curionii* n. sp., und *valceresii.* Schwestergruppe der Gattung *Lariosaurus* ist die Gattung *Nothosaurus.* Die Lariosaurier diversifizierten während des Ladins im nordwestlichen Küstenbereich der Tethys, nachdem die Gattung *Nothosaurus* in die Alpine Fazies vorgedrungen war.

Introduction

Lariosaurus balsami Curioni, 1847, ranks among the earliest fossil reptiles described from the Middle Triassic of the southern Alps. The holotype from the black shales of Perledo in northern Italy was originally described and figured by Balsamo-Crivelli (1839) as a representative of the "famiglia dei Paleosauri." Curioni (1847) described a second, distinctly smaller specimen from the same deposits as "*Macromirosaurus Plinj*" (etymologically correctly spelled as *Macromerosaurus* by Cornalia [1854] and most later authors, including Curioni [1863]), and formally named Balsamo-Crivelli's specimen *Lariosaurus balsami.* Although the name *Macromirosaurus* (*Mac-*

romerosaurus) suggests a relatively large humerus, Curioni (1847, p. 161) noted that femur length exceeded humerus length by almost 30% ("maggiore di quasi una terza parte"; actual measurements on the holotype of *Macromirosaurus plinii* indicate that humerus length is 86.8% of the femur length). This feature was believed to distinguish *Macromirosaurus* from similar specimens, one from Perledo, with a humerus longer than the femur, the other from Viggiù (Varese, northern Italy), with humerus and femur of approximately equal length. The controversy (see Rieppel, 1987, for a detailed account and further references), which unfolded with the description by Cornalia (1854) and Curioni (1863) of additional specimens from Middle Triassic black shales of north-

ern Italy (Viggiù and Besano), highlighted the problem faced by these earlier authors in distinguishing *Lariosaurus* and *Macromirosaurus* from pachypleurosaurs (*Neusticosaurus* [*Pachypleurosaurus*] *edwardsii*; Sander, 1989), and culminated in Curioni's (1863, p. 266) claim that all fossil saurians from Perledo had to be referred to a single taxon, *Lariosaurus balsami*. By implication, Curioni (1863) accepted *Macromirosaurus plinii* as a junior synonym and a juvenile representative of the latter species. With his review of the fossil reptiles from Perledo, Peyer (1933–1934) proved Curioni's (1863) claim was wrong by demonstrating that pachypleurosaurs do occur in the black shales of Perledo (*Neusticosaurus pusillus,* redescribed by Rieppel, 1995a), and he brought the debate over the validity of *Macromirosaurus* to an end by recognizing the specimen as *Lariosaurus balsami* var. *plinii.* Peyer's (1933–1934) monograph also included an amended diagnosis for the genus *Lariosaurus* and its only known species, *L. balsami,* and therewith provided the basis for all future work on *Lariosaurus.*

Following Peyer's monographic revision, several additional lariosaur specimens were described, all of which were referred to *Lariosaurus balsami* Curioni (Zapfe & König, 1980; Sanz, 1983b; Ticli, 1984; Mazin, 1985) and which collectively document the abundance and the wide geographic distribution of this species. Among these specimens, however, the original of Mazin (1985) is noteworthy for a number of unique characters (discussed below), and it will here be designated the holotype of a new species to be diagnosed below (*Lariosaurus curionii* n. sp.).

It was not until 1987 that a second species of *Lariosaurus* was described from the upper Ladinian Kalkschieferzone of Monte San Giorgio, southern Switzerland, *Lariosaurus lavizzarii* Kuhn-Schnyder, 1987. Based on a nondiagnostic juvenile specimen, the latter species was synonymized with *Lariosaurus balsami* by Tschanz (1989), who in turn described *Lariosaurus buzzii* from the Grenzbitumenzone (Anisian–Ladinian boundary) of Monte San Giorgio, Switzerland. If indeed a *Lariosaurus,* this specimen would be the earliest representative of its genus, and it would occur only slightly earlier and in the same geographic setting as the purported sister group of *Lariosaurus,* the genus *Ceresiosaurus* (Peyer, 1931; see Sues, 1987, and Storrs, 1991, 1993, for a phylogenetic analysis including these two genera). The genus *Ceresiosaurus* was erected by Peyer (1931) on the basis of three articulated

specimens and some isolated postcranial elements collected from the lower Meridekalke (lower Ladinian) of Monte San Giorgio.

Dissatisfied with the character analysis presented by Tschanz (1989), Kuhn-Schnyder (1990) erected a separate genus, *Silvestrosaurus,* to include *buzzii.* In the same year, the description of yet another species of *Lariosaurus* was published, *Lariosaurus valceresii* Tintori and Renesto, 1990, from the Kalkschieferzone of Valceresio, northern Italy. The discovery of a juvenile specimen from the same locality (Renesto, 1993) once again activated the discussion surrounding the validity of *Lariosaurus lavizzarii* Kuhn-Schnyder and the status of *Silvestrosaurus buzzii* (Tschanz, 1989). Indeed, the question as to how many species of *Lariosaurus* and related genera should be recognized has remained unanswered.

It is the purpose of this paper to review the status of the genera *Ceresiosaurus, Lariosaurus, Silvestrosaurus,* and their constituent species on the basis of a comprehensive review of all material available in public repositories (see Appendix II). For the purpose of the ensuing discussion, the three genera *Ceresiosaurus, Lariosaurus,* and *Silvestrosaurus* are considered members of a monophyletic clade, collectively referred to as "lariosaurs."

INSTITUTIONAL ABBREVIATIONS—BSP, Bayerische Staatssammlung für Paläontologie, München; MCL, Museo Civico, Lecco; MCSNM, Museo Civico di Storia Naturale, Milano; MNHL, Muséum d'Histoire Naturelle, Lausanne; PMZ, Paläontologisches Institut und Museum der Universität, Zürich; PVHR, Université Paris VI, Laboratoire de Paléontologie et de Paléoanthropologie, Paris; SB, Museo y Laboratorio de Geologia, Seminario de Barcelona; SMF, Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt a.M.; UGR, Ufficio Geologico di Roma.

Materials and Methods

The personal inspection of all of the material of *Lariosaurus* deposited in public repositories forms the basis for this review. However, all of the material discussed in this paper (except the small specimen of *Lariosaurus* from the Natural History Museum in Lausanne; see Appendix II) has previously been described and figured in detail (see particularly Ticli, 1884; Boulenger, 1898; Mariani, 1923; Peyer, 1931, 1933–1934; Sanz,
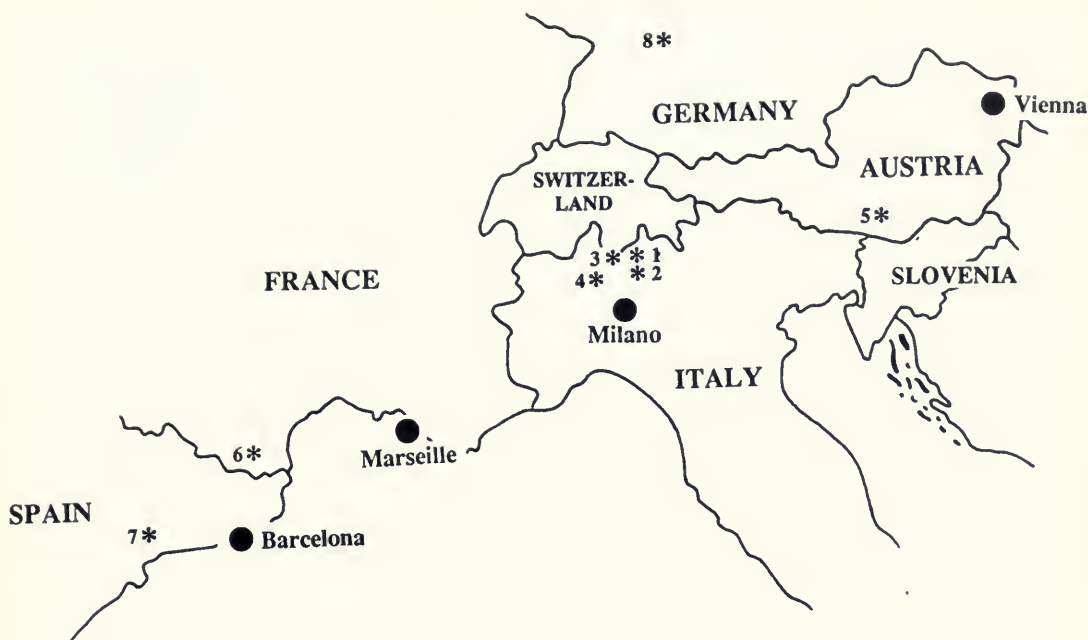
FIG. 1. Locality map for the sites that have yielded *Lariosaurus*. **1,** Calcare di Perledo, Perledo and Esino; **2,** Calcare di Perledo, Lecco; **3,** Grenzbitumenzone and lower Meridekalke and Kalkschieferzone, Monte San Giorgio; **4,** Kalkschieferzone, Cà del Frate; **5,** Partnach-Plattenkalk, Gailtaler Alps (Kellerberg Quarry near Villach); **6,** Black shales, Amélie-les-Bains; **7,** Muschelkalk, Montral and Alcover; **8,** Keuper, Sulzheim (near Würzburg).

1976, 1983b; Mazin, 1985; Kuhn-Schhnyder, 1987; Tschanz, 1989; Renesto, 1993; Rieppel, 1994a). Unfortunately, all specimens of *Ceresiosaurus* but the one kept at the Natural History Museum in Basel are currently unavailable for investigation, which limits character analysis for this taxon to one adult specimen and the original description by Peyer (1931). It is for these reasons that the anatomy of lariosaurs is here described in terms of character definitions only. Illustration of lariosaur anatomy is by photographic plates based on specimens available for photography and is designed to complement plates and figures already existing in the literature. Illustrations in this paper cannot replace the excellent plates published by Peyer (1933–1934). Peyer's monograph has been reprinted by the Servicio Geologico d'Italia, which is why Curioni's material kept at the Ufficio Geologico di Roma was not available for photography.

The Stratigraphic and Geographic Distribution of *Lariosaurus*

A variety of localities have yielded *Lariosaurus* specimens, as enumerated below (see Fig. 1 for

geographic locations and Fig. 2 for stratigraphic relations):

Calcare di Perledo

The holotype of *Lariosaurus balsami* (lost in World War II; Fig. 3) and all the specimens referred to that taxon by Curioni (1847, 1863) came from the black shales of Perledo above Varenna at Lake Como, northern Italy (southern Alps). Additional specimens from the same deposits were described by Boulenger (1898; Fig. 4) and Mariani (1923; Fig. 5). Among these specimens, the original holotype (a cast of which is kept at the Museo Civico di Storia Naturale in Milano, uncatalogued) was the largest; the next largest specimen (kept at the Bayerische Staatssammlung für Paläontologie und Historische Geologie, Munich, BSP AS I 802) was selected as the neotype for *Lariosaurus balsami* by Kuhn-Schnyder (1987; Peyer, 1933–1934, Pl. 32).

The precise age of these historical fossil collections from Perledo cannot be determined unequivocally today because precise stratigraphic and locality data are lacking. Tintori et al. (1985) noted that most of the historical fossil material
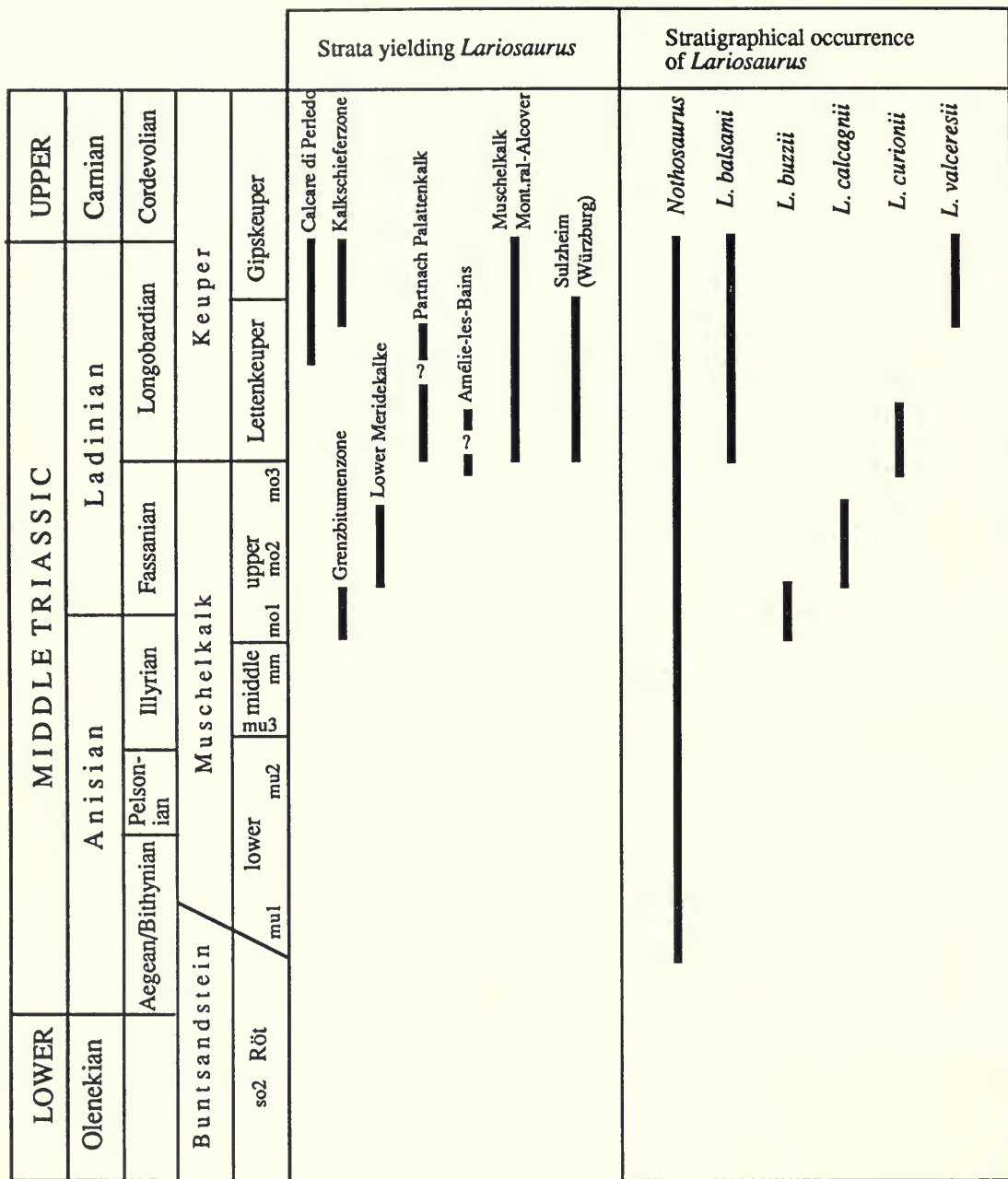
FIG. 2. The stratigraphic distribution of *Lariosaurus* species.

appears to have been collected in the surroundings of the village of Perledo, i.e., in the upper part of the Calcare di Perledo, recognized as the Perledo Member of the Perledo-Varenna Formation, of upper Ladinian age (Gaetani et al., 1992). At this locality and time, *Lariosaurus balsami* occurs to-gether with the pachypleurosaur *Neusticosaurus pusillus* Seeley (Rieppel, 1995a).

An isolated left foot from Esino, close to Perledo, was described by Boulenger (1891, p. 292) under the name *Eupodosaurus longobardicus* before he realized that the specimen is, in fact, *La-*

Fig. 3. Holotype of *Lariosaurus balsami* (cast, uncatalogued, kept at the Museo Civico di Storia Naturale, Milano).

Fig. 4. *Lariosaurus balsami* (SMF R-13, original of Boulenger, 1898).

FIG. 5. *Lariosaurus balsami* (MCSNM uncatalogued, original of Mariani, 1923).

riosaurus balsami (Boulenger, 1898) and had previously been described by Curioni (Curioni, 1863, Pl. 7, Fig. 1). Two further specimens of *Lariosaurus balsami* were collected in equivalent deposits in the surroundings of Lecco, south of the type locality of the Calcare di Perledo, and described by Ticli (1984; Figs. 6, 7).

Kalkschieferzone

The Kalkschieferzone (Senn, 1924; Furrer, 1995) is the upper member of the Meridekalke (Wirz, 1945), of uppermost Ladinian age. Outcrops in Val Mare, Monte San Giorgio, the southern Alps (Switzerland) have yielded the juvenile specimen described by Kuhn-Schnyder (1987) as *Lariosaurus lavizzarii*. No pachypleurosaurs or other fossil reptiles have yet been collected in Swiss outcrops of the Kalkschieferzone (Furrer, 1995).

Equivalent outcrops in Valceresio (at Cà del Frate near Viggiù, Varese, northern Italy) have yielded the holotype of *Lariosaurus valceresii* Tintori and Renesto, 1990, as well as a juvenile specimen of *Lariosaurus* (Renesto, 1993; Fig. 8). The Cà del Frate locality has also yielded the holotype of the pachypleurosaur *Neusticosaurus* (*Pachypleurosaurus*) *edwardsii* (Cornalia, 1854), but from an older quarry located in earlier strata of late lower Ladinian age; the taxon otherwise occurs in lower to middle Ladinian deposits of Monte San Giorgio (Sander, 1989).

Grenzbitumenzone

The Grenzbitumenzone of Monte San Giorgio (Anisian–Ladinian boundary, southern Switzerland) has yielded the holotype of *Silvestrosaurus buzzii* Tschanz, 1989, along with abundant material of other sauropterygians (the pachypleurosaur *Serpianosaurus* Rieppel, 1989a, and the nothosaur *"Paranothosaurus"* [a junior synonym of *Nothosaurus:* Rieppel & Wild, 1996]).

Lower Meridekalke

The Meridekalke lie on top of the Grenzbitumenzone at Monte San Giorgio. Lower Meridekalke outcrops (Cava inferiore beds, Cava superiore beds, and Cassina beds; Furrer, 1995) of lower Ladinian age have yielded *Ceresiosaurus calcagnii* (Peyer, 1931), along with abundant pachypleurosaur material (*Neusticosaurus*; Sander, 1989).

Partnach-Plattenkalk

The Partnach-Plattenkalk (Warch, 1979; also known as Partnachschichten or "Plattenkalk" [Zapfe & König, 1980]), spans the entire Ladinian. Outcrops in the Gailtaler Alps (northern Alps, Kärnten, Austria) have yielded *Lariosaurus* cf. *L. balsami* (Zapfe & König, 1980; Warch, 1984; Rieppel, 1994a) along with *Neusticosaurus* (*Psi-*

FIG. 6. *Lariosaurus balsami* (MCL 202, original of Ticli, 1984).

lotrachelosaurus) *toeplitschi* Nopcsa, 1928a (see also Rieppel, 1993b) and other indeterminate pachypleurosaur remains. According to Zapfe and König (1980), the greater part of the quarry that yielded *Lariosaurus* specimens is located in the upper unit of the Partnach-Plattenkalk, of late Ladinian age. Warch (1984) emphasized that *Lariosaurus* was found immediately above an intercalated bed of marly shales at the middle of the lithological column of the Partnach-Plattenkalk, which indicates a middle Ladinian age.

A very incomplete skeleton from the Gailtaler Alps was described as *Proneusticosaurus carinthiacus* by Arthaber (1924). The exact locality for this fossil remains doubtful, as it was labeled "Bleiberg?" only. Bleiberg is an important mining area with exposures of the Wetterstein-Kalk of late Ladinian and early Carnian age (Zeeh,

FIG. 7. *Lariosaurus balsami* (MCL 663, original of Ticli, 1984).

FIG. 8. *Lariosaurus balsami* (Museo Civico di Szienze Naturali di Induno Olona P 550, original of Renesto, 1993).

1994), which yielded an ichthyosaur (*Shastasaurus carinthiacus* Huene, 1925; see also McGowan, 1994). Lithological clues seem to indicate, however, that the specimen is not from the Wetterstein-Kalk but rather from the Partnach-Plattenkalk, as are the other *Lariosaurus* specimens from the Gailtaler Alps (Warch, 1984). Indeed, the specimen in question has nothing in common with *Proneusticosaurus* Volz, 1902, redescribed by Rieppel and Hagdorn (1997). Instead, it represents the badly eroded pelvic region of a *Lariosaurus* (Zapfe & König, 1980), of a size comparable to the neotype of *Lariosaurus balsami,* and hence distinctly larger than the other *Lariosaurus* from the same deposits (Fig. 9).

Black Shales of Amélie-les-Bains

An incomplete specimen of *Lariosaurus* was collected along with microvertebrate remains in the black shales of Amélie-les-Bains, eastern Pyrenees. The microvertebrate (fish) fauna (Mazin & Martin, 1983), as well as the occurrence of *Lariosaurus,* may suggest a Middle Triassic (Ladinian) age (Mazin, 1985), but no detailed stratigraphic studies have addressed the age of these fossiliferous outcrops as yet. The specimen of *Lariosaurus* from this locality was referred to *L. balsami* by Mazin (1985), but is here designated as the holotype of a new species.
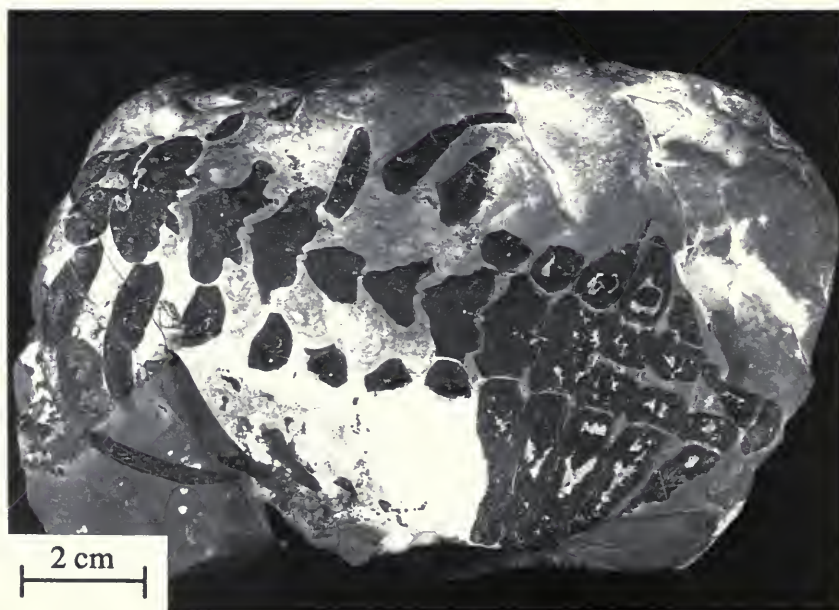

FIG. 9. Holotype of *Proneusticosaurus carinthacus* Arthaber, 1924.

Spanish Muschelkalk

The "Muschelkalk superior" of northeastern Spain (outcrops located between Mont-ral and Alcover, Province Tarragona) has yielded a rich vertebrate fauna, including marine reptiles reviewed by Sanz et al. (1993). The age of these deposits has been determined as middle to upper Ladinian (Esteban Cerda et al., 1977; Hemleben & Freels, 1977; Via Boada et al., 1977). Preservation in these calcareous shales is unique in that dolomitization destroyed all original skeletal material, rendering morphological analysis of the material rather difficult. Sauropterygians from that locality have been identified as *Lariosaurus balsami, Nothosaurus cymatosauroides,* and a problematic pistosaur (Sanz, 1976, 1983a,b; Sanz et al., 1993; Alafont & Sanz, 1996). A recent survey of the fauna indicated the presence of *Ceresiosaurus* (an incomplete specimen held at the Centre d'Historia Natural de la Conca de Barbera, Montblanc), while some of the specimens referred to *Lariosaurus balsami* by Sanz (1976, 1983b) may in fact represent an as yet undescribed pachypleurosaur taxon. *Lariosaurus* generally has an elongated skull with an elongated and constricted rostrum and an upper temporal fossa between one and two times as long as the longitudinal diameter of the orbit. Some small sauropterygians from the Montral–Alcover area show a relatively short preorbital skull without constriction, large orbits, and a postorbital skull that, as a whole, measures approximately 70% of the longitudinal diameter of the orbit (for example, the specimen DeLucas I, figured by Sanz, 1983b, Pl. 3, Fig. B). That these skull proportions should be a juvenile character of *Lariosaurus* is unlikely in view of the juvenile specimens described by Kuhn-Schnyder (1987) and Renesto (1993). On the other hand, the specimens share with *Lariosaurus* and the Chinese pachypleurosaur *Keichousaurus* a distinctive humerus morphology (discussed below), as well as the broadened ulna.

Germanic Keuper

The lower Keuper (Lettenkeuper) of the Germanic Triassic (upper Ladinian) has yielded a distinctly broadened ulna (Rieppel, 1994b, Fig. 61A), which on the basis of its morphology can be referred to *Ceresiosaurus.* The upper Keuper (Gipskeuper, uppermost Ladinian) of Sulzheim near Würzburg (southern Germany) has yielded

the poorly preserved skeleton of a sauropterygian described by Schultze and Wilczewski (1970), who compared the specimen either to *Ceresiosaurus* or to *Lariosaurus.* The Lettenkeuper has also yielded the type material of *Neusticosaurus pusillus* Seeley, 1882.

Previous Cladistic Analyses of Lariosaur Interrelationships

Sues (1987) first recognized the sister-group relationship of *Lariosaurus* and *"Ceresiosaurus,"* and considered those two clades to represent the sister group of *Nothosaurus.* These results were corroborated by subsequent studies of Storrs (1991) and Rieppel (1994b). In an analysis presented by Sanz et al. (1993), eusauropterygian (*sensu* Tschanz, 1989) relationships are shown to be fully unresolved in a strict consensus tree, but in their preferred cladogram (Sanz et al., 1993, Fig. 14), these authors again support a sister-group relationship for *Lariosaurus* and *"Ceresiosaurus,"* which together form the sister-group of *Nothosaurus* (and *"Paranothosaurus"*).

I reanalyzed the data matrix published by Sanz et al. (1993, Table I) using the software package PAUP (version 3.1.1) developed by David L. Swofford (Swofford, 1990; Swofford & Begle, 1993). With the branch-and-bound search option implemented, and rooting the ingroup on their outgroup (which represents an all-0-ancestor), I obtained six most parsimonious trees (MPTs) with a tree length (TL) of 46, a consistency index (CI) of 0.826, and a rescaled consistency index (RC) of 0.723. The sister-group relationship of *Lariosaurus* and *"Ceresiosaurus"* is supported in all six trees, and in all six trees this clade falls into an unresolved polytomy with *Nothosaurus, "Paranothosaurus,"* and all other Eusauropterygia (which in turn form a monophyletic clade *sensu* Tschanz, 1989). *Nothosaurus* and *"Paranothosaurus"* fail to come out as sister groups because of the unknown character states for characters 17 and 25.

Whereas Rieppel (1993a) considered *"Silvestrosaurus"* as a subjective junior synonym of *Lariosaurus* because its diagnosis is based on plesiomorphy, Storrs (1993) added *"Silvestrosaurus"* to his analysis of sauropterygian interrelationships and found it to be the sister group of a clade comprising *Lariosaurus* and *"Ceresiosaurus."* To test the validity of *"Silvestrosaurus"* as

a separate taxon, I reanalyzed the data matrix published by Storrs (1993) with all 88 characters included (of which characters 10, 40, 50, 54, 55, and 72 are uninformative and hence were ignored). Heuristic search settings employed random stepwise addition (10 replications), and branch swapping (on minimal trees only) was effected by tree bisection and reconnection. Rooting the monophyletic ingroup on a paraphyletic outgroup including Captorhinomorpha, *Petrolacosaurus*, Younginiformes, and *Claudiosaurus* yielded four equally parsimonious trees (TL = 187, IC = 0.688, RC = 0.527). The strict consensus tree shows "*Silvestrosaurus*" in an unresolved trichotomy with the "*Ceresiosaurus*"–*Lariosaurus* clade, on the one hand, and the *Nothosaurus*–"*Paranothosaurus*" clade on the other. Three out of the four MPTs (75%) show "*Silvestrosaurus*" to pair with the *Nothosaurus*–"*Paranothosaurus*" clade. Synapomorphies shared by "*Silvestrosaurus*" and the *Nothosaurus*–"*Paranothosaurus*" clade are 19(1), 27(1), 29(1), and 33(1) with ACCTRAN character optimization, and 14(1), 27(1), 29(1), and 33(1) with DELTRAN character optimization. Rooting all taxa included in Storr's (1993) data matrix on an all-0-ancestor using the same search settings again yielded four MPTs (TL = 189, CI = 0.672, RC = 0.546), with identical results with respect to the position of "*Silvestrosaurus.*"

Whereas the unresolved position of "*Silvestrosaurus*" in the strict consensus tree might raise doubts as to its generic identity, its pairing with the *Nothosaurus*–"*Paranothosaurus*" clade in the 50% majority rule consensus tree would seem to contradict its status as a junior synonym of *Lariosaurus*. Closer inspection of the data matrix published by Storrs (1993) indicates a number of characters for which "*Silvestrosaurus*" is coded differently than *Lariosaurus*. These are as follows: nasals contact prefrontals in *Lariosaurus*, but not in "*Silvestrosaurus*" (14); postfrontal enters upper temporal fenestra in *Lariosaurus*, but not in "*Silvestrosaurus*" (19—mistaken coding?); pineal foramen displaced posteriorly in *Lariosaurus*, but not in "*Silvestrosaurus*" (28—but see the juvenile *Lariosaurus* described by Renesto [1993]); rostrum not constricted in *Lariosaurus*, constricted in "*Silvestrosaurus*" (33); sacral ribs distally expanded in "*Silvestrosaurus*," distally reduced in Lariosaurus (52); rib pachyostosis present in *Lariosaurus*, but not in "*Silvestrosaurus*" (53); supracoracoid foramen/notch present in *Lariosaurus*, but not in "*Silvestrosaurus*" (64);

entepicondylar foramen present in *Lariosaurus*, but not in "*Silvestrosaurus*" (76); ulna broad in *Lariosaurus*, but not in "*Silvestrosaurus*" (83). Many of these characters, as well as those cited by Kuhn-Schnyder (1990) in support of "*Silvestrosaurus*," require greater scrutiny, as discussed below.

Character Analysis

General Morphology

"*Ceresiosaurus*" *calcagnii* is known from several specimens, all but one of which are currently not accessible for detailed investigation. "*Silvestrosaurus*" *buzzii* is known from a single, incomplete, and disarticulated specimen described in detail by Tschanz (1989). Specimens referred to the genus *Lariosaurus* are frequent throughout Ladinian deposits of the Alpine Triassic and, because of a variable degree of pachyostosis, bear a superficial resemblance to pachypleurosaurs often found at the same localities. The detailed morphology of lariosaurs is distinct from that of pachypleurosaurs, however, and rather closely resembles that of *Nothosaurus*. The general morphological description of the skeletal anatomy of lariosaurs provided in this section will be followed by a more detailed analysis of selected characters important for cladistic analysis of lariosaur interrelationships.

The skull of *Lariosaurus* is distinctly depressed and elongated, with an elongated postorbital region characterized by large upper temporal fossae distinctly larger than the orbits. The rostrum is elongated and constricted, and the premaxillary and anterior dentary teeth are distinctly enlarged (fanglike) and strongly procumbent. Kuhn-Schnyder (1987, p. 18) found the *Lariosaurus* specimen from the Montral–Alcover locality kept at the Museum of the Solnhofer Aktien-Verein, Maxberg, to show certain "anomalies," and he may have referred to seemingly aberrant skull proportions, as they appear in Sanz (1983b, Pl. 5, Fig. 1). However, this is a false impression created by the difficulties in photographing the specimens from the Montral–Alcover locality. Investigation of the original specimen showed the skull to share the elongated, distinctly constricted rostrum. *Lariosaurus* shares with *Nothosaurus* the presence of paired maxillary fangs located at a level between the external naris and the orbit. And as in *Notho-*

saurus, the parietal and squamosal are elaborated into an occipital crest rising above the occiput. The occiput is closed and platelike, with the supraoccipital more or less horizontally oriented. Unfortunately, the detailed morphology of the occiput remains incompletely known for *Lariosaurus*, in particular the taxonomically important relations of the basioccipital to the dermal palate (Rieppel, 1994c), although these are assumed to be similar to *Nothosaurus*. The lower jaw of *Lariosaurus* is a slender and delicate structure without a distinct coronoid process. The surangular bears a laterally protruding flange for the insertion of superficial jaw adductor muscle fibers (Tschanz, 1989). The retroarticular process is distinct.

The vertebrae of *Lariosaurus* show swollen or dome-shaped (pachyostotic) pre- and postzygapophyses and a very low neural spine, much like pachypleurosaurs. *Lariosaurus balsami* shows 43 to 45 presacrals (42 in the holotype of *L. valceresii*; 47 in the Basel specimen of "*Ceresiosaurus*"), of which 19–23 are cervicals (located in front of the clavicular–interclavicular complex; 22 cervicals in the holotype of *L. valceresii*; 23 in the Basel specimen of "*Ceresiosaurus*"). Cervical ribs are present throughout the cervical vertebral column with the probable exception of the atlas (Peyer, 1933–1934, Pl. 35). They are, however, often incompletely exposed and visible in the posterior cervical region only. The cervical ribs bear a distinct anterior process. The dorsal ribs show a variable degree of pachyostosis, as discussed in detail below. The sacrum is defined by a cluster of tightly juxtaposed ribs converging with a tapering distal end toward the dorsal process of the ilium. The number of sacral ribs varies from four to five pairs. The tail is completely preserved in the Frankfurt specimen (SMF R-13), but the exact vertebral count is difficult to establish. Dislocation of the pelvic elements obscures the proximal caudal region, and individual vertebrae are difficult to distinguish at the tapering tip of the tail, but 32 caudal vertebrae can unequivocally be identified, the total probably being 37 or 38. The Maxberg specimen shows a total of 36 caudal vertebrae with few, if any, missing. The proximal caudal ribs differ from the posterior sacral ribs by their greater length and by their orientation in a posterolateral rather than anterolateral direction. Posteriorly, the caudal ribs rapidly decrease in size, the last ones assuming a knoblike shape; they do not seem to be present beyond the 15th or 16th caudal. The closely juxtaposed gastral ribs

form a sturdy ventral armor. There are two gastral ribs per vertebral segment. Each gastral rib is composed of five elements: a median, slightly angulated rib flanked by two slightly curved and overlapping elements on either side.

The clavicular–interclavicular complex of the pectoral girdle shows pronounced anterolateral corners, emphasized by pachyostosis of the clavicula. The interclavicle bears no trace of a posterior stem or process. As in other eosauropterygians, the clavicle is applied against the anteromedial surface of the dorsal wing of the scapula. The humerus of *Lariosaurus* is morphologically distinct. It is distinctly curved and characterized by a weak development of the deltopectoral crest (in *Lariosaurus balsami*), as well as by the absence of a distinct crest for the insertion of the latissimus dorsi muscle on its postaxial surface. The width of the humerus increases gradually toward the distal end. A distinct sexual dimorphism is expressed in the proportions of the humerus in pachypleurosaurs (Rieppel, 1989a, 1993b; Sander, 1989), but no such dimorphic proportions of the humerus can be detected in the sample of lariosaurs deposited in public repositories. The distinctly broadened ulna is very characteristic in *Lariosaurus*. The radius is slightly shorter than the ulna and much more slender. Between radius and ulna remains a distinct spatium interosseum, distal to which lies the intermedium. The number of carpal ossifications varies in a pattern discussed in detail below. The manus shows a tendency toward hyperphalangy, which reflects the general observation that the forelimb is more strongly developed than the hind limb in *Lariosaurus*.

The pelvic girdle is notable for the further reduction of the dorsal wing of the ilium, reduced to a stocky dorsal process. The obturator foramen in the distinctly waisted pubis is slitlike and remains open in the adult. The fenestra thyroidea separates the pubis from the ischium. The ischium has a relatively narrow, rounded dorsal head but shows a distinct ventral expansion. Its ventral margin is strongly convex.

The femur is a slender, slightly sigmoidally curved bone that in general is much more lightly built than the humerus but remains slightly longer than the humerus in *Lariosaurus*, including the large neotype of *L. balsami* (BSP AS I 802); the humerus is longer than the femur in the large (adult) "*Ceresiosaurus*" specimens due to its allometric growth. Tibia and fibula show no particular differentiation, and they enclose a spatium interosseum distal to which lies the astragalus.
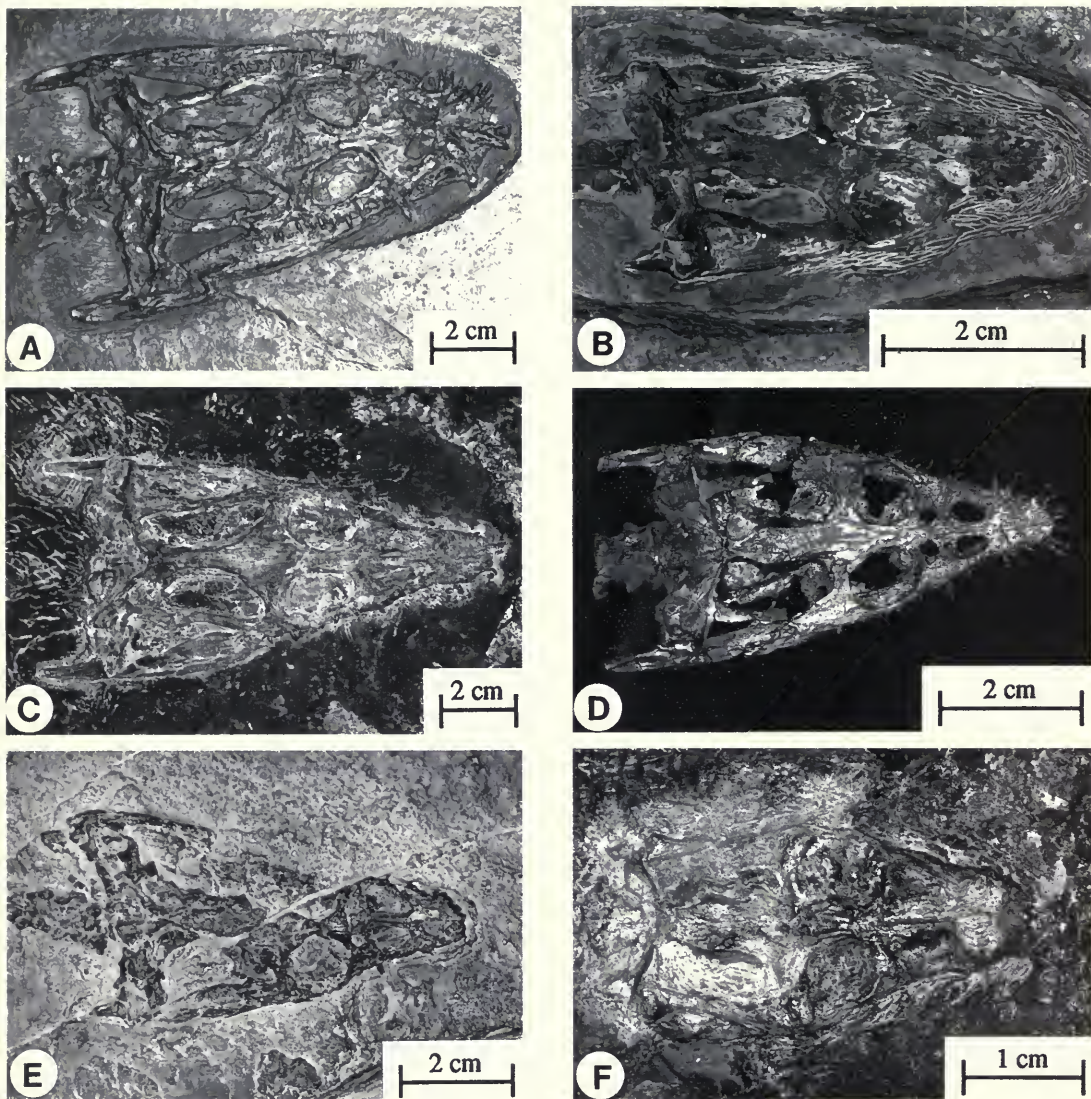
FIG. 10. The skull of *Lariosaurus* in dorsal view. **A,** *Lariosaurus balsami* (neotype, BSP ASI 802); **B,** *L. balsami* (SMF R-13, original of Boulenger, 1898); **C,** *L. valceresii* (holotype, Museo Civico di Szienze Naturali di Induno Olona P 500); **D,** *L. curionii* n. sp. (holotype, PVHR 1); **E,** *L. balsami* (MCSNM uncatalogued, original of Mariani, 1923); **F,** *Lariosaurus* sp. Museo (Civico di Szienze Naturali di Induno Olona P 550, original of Renesto, 1993).

Tarsal ossifications vary in a pattern discussed in detail below. Hyperphalangy in the pes is restricted to specimens referred to "*Ceresiosaurus.*"

The Skull

The morphological analysis of lariosaurs is rendered difficult by the often poor preservation and/or preparation of the sometimes incomplete and always dorsoventrally compressed material (Fig. 10). Information on sutural characteristics of the skull will therefore remain limited.

PREMAXILLA-FRONTAL CONTACT—In "*Silvestrosaurus,*" fused nasals form a relatively broad dorsal bridge between the external nares (the nasals appear paired in Kuhn-Schnyder, 1974, Fig. 12). The posterior (nasal) process of the premaxilla appears unusually short due to breakage of its posterior tip, and as preserved, the premaxilla remains widely separated from the frontal. This is in contrast to other lariosaurs, where the dorsal

bony bridge between the external nares is relatively narrower, the posterior (nasal) processes of the premaxillae are more elongate, and the nasals are paired. Dividing the dorsal bridge between the orbits (width of the frontal) by the dorsal bridge between the external nares yields a ratio of 1.1 for "*Silvestrosaurus*" and values ranging from 1.2 to 2.1 in *Lariosaurus*; the only exception is the *Lariosaurus* described by Kuhn-Schnyder (1987, PMZ T4288), with a corresponding ratio of 1.0, which reflects the relatively large orbits in this juvenile specimen. In PVHR 1 and PMZ T4288, the posterior (nasal) processes of the premaxillae contact the anteromedial process of the frontal, whereas the nasals seem to contact each other behind the premaxillary processes in the holotype of *L. valceresii*. A similar variation in the relations of the premaxillae, nasals, and frontal is observed in *Neusticosaurus* (Sander, 1989) and *Nothosaurus* (Rieppel & Wild, 1996), where the nasals may cover the contact between premaxilla and frontal to a variable degree. The relatively broad and fused nasal is an autapomorphy of "*Silvestrosaurus.*"

PREFRONTAL–NASAL CONTACT—In "*Silvestrosaurus,*" an anterolateral process of the frontal contacts the ascending (medial) process of the maxilla, thus separating the nasal from the prefrontal. The only other specimen that shows sutural details in the preorbital skull is PMZ T4288, where the nasals are seen to contact the prefrontal. In this specimen, the frontal is figured without anterolateral processes, which, if correct, is a condition highly unusual in Sauropterygia. The only other sauropterygian with no anterolateral processes of the frontal is the Chinese pachypleurosaur *Keichousaurus*. As figured, the anterior end of the frontal is asymmetrical in PMZ T4288, which appears to be the result of breakage. The best preserved *Lariosaurus* skull, PVHR 1 (Fig. 11), shows a distinct yet short anterolateral process of the frontal on the left side, leaving enough room for the nasal to contact the prefrontal. Unfortunately, the presence of such a contact cannot be ascertained, owing to damage of the bone surface in the critical area on both sides of the skull. Skulls of *Simosaurus* (Rieppel, 1994b) and *Nothosaurus* (Rieppel & Wild, 1996) show bilateral asymmetry of the presence versus absence of a contact of nasal and prefrontal.

POSTFRONTAL RELATIONS—In "*Silvestrosaurus*" and *Lariosaurus,* the pre- and postfrontal remain separated at the dorsal margin of the orbit. "*Silvestrosaurus*" shows a broad postfrontal, which
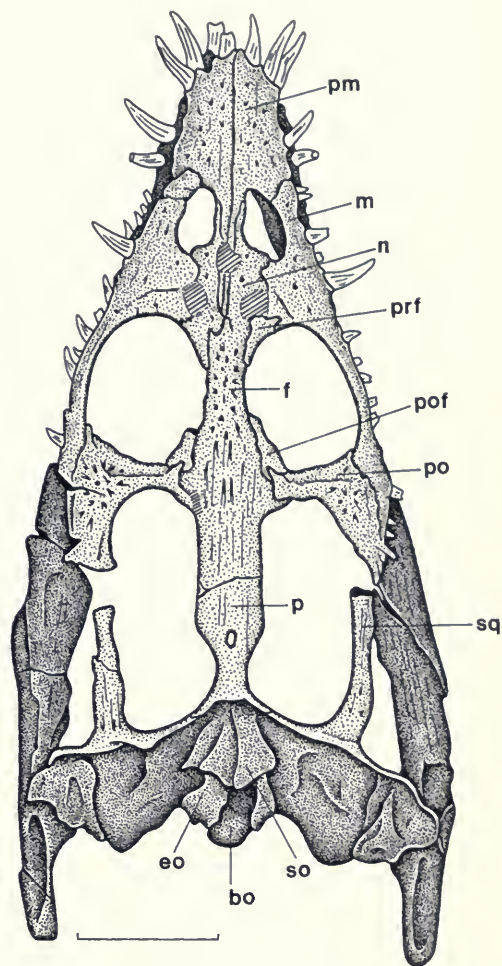
FIG. 11. The skull of *Lariosaurus curionii* n. sp. in dorsal view (holotype, PVHR 1). Abbreviations: bo, basioccipital; eo, exoccipital; f, frontal; m, maxilla; n, nasal; p, parietal; pm, premaxilla; po, postorbital, pof, postfrontal; prf, prefrontal; so, supraoccipital; sq, squamosal. Scale bar = 10 mm.

defines the anteromedial margin of the upper temporal fossa. A similar postfrontal is reconstructed for *L. valceresii* by Tintori and Renesto (1990), and the entry of the postfrontal into the anteromedial margin of the upper temporal fossa is distinct in SMF R-13 (right side). Interestingly, this contrasts with PVHR 1 (Fig. 11), where the postfrontal appears as a much smaller element located at the posteromedial margin of the orbit, excluded from the upper temporal fossa by the postorbital. The latter element reaches high up in the postorbital arch to meet a lateral extension of the parietal, a condition otherwise not known in sauropterygians.

JUGAL RELATIONS—"*Silvestrosaurus*" was originally figured with a jugal extending anteriorly along the ventral margin of the orbit (Tschanz, 1989), restricting the maxilla to an anterior position (same in Kuhn-Schnyder, 1974, Fig. 12). This is a highly unusual configuration of the jugal and maxilla for a nothosaurian eosauropterygian. In fact, the jugal cannot be identified unequivocally in "*Silvestrosaurus*" (Tschanz, 1989, p. 159) or *Lariosaurus* (Peyer, 1933–1934, p. 24, identified a jugal in the Munich specimen BSP AS I 802, currently mounted for permanent exhibit and hence difficult to analyze). Indeed, the jugal seems to be absent in the relatively well-preserved and acid-prepared specimen PVHR 1 (Fig. 11). For lack of adequate preservation of other specimens, it remains unknown whether the absence of a jugal is unique to specimen PVHR 1 or shared by other *Lariosaurus*. A jugal bone is present in "*Ceresiosaurus*," indicating that loss of the jugal could be a derived character of *Lariosaurus* that is shared by "*Silvestrosaurus*." Corroboration of this hypothesis requires better preserved specimens, however.

PARIETAL MORPHOLOGY—"*Silvestrosaurus*" shows an unusually broad parietal skull table with the pineal foramen shifted to a position only slightly behind the midpoint of the parietal. Dorsoventral compression may add to the impression of a wide parietal skull table, which nevertheless shows some constriction behind the pineal foramen. This constriction is much more pronounced in *Lariosaurus*, where the parietal has a distinct morphology, at least in the smaller specimens. It is relatively broad anteriorly, with straight and parallel lateral edges between the anterior two-thirds of the upper temporal fenestrae. The degree of posterior displacement of the pineal foramen is somewhat variable. The foramen may lie in a rather forward position as in SMF R-13, which in this respect is comparable to "*Silvestrosaurus*," or its posterior displacement may be more pronounced, but it never reaches the immediate proximity of the posterior margin of the parietal skull table as in "*Ceresiosaurus*" and in some *Nothosaurus* specimens. Behind the pineal foramen, the parietal skull table shows a marked constriction that is distinctly set off from the anterior part of the skull table in smaller *Lariosaurus*; in larger specimens (BSP AS I 802, and holotype of *L. valceresii*), this posterior parietal constriction appears less abrupt. It is interesting to note that the juvenile specimen of *Lariosaurus* described by Renesto (1993) resembles "*Silvestrosaurus*" rather closely by showing a broad parietal skull table and a relatively anterior position of the pineal foramen. Parietal morphology in "*Silvestrosaurus*" is reversed (on the basis of DELTRAN character optimization; see discussion of cladistic analysis below), seemingly as a result of paedomorphosis.

ROSTRUM CONSTRICTION—The elongated rostrum is distinctly constricted in "*Ceresiosaurus*," "*Silvestrosaurus*," and *Lariosaurus*, as is also the case in *Nothosaurus*. In juvenile *Lariosaurus* specimens, rostral constriction may be weakly pronounced (Renesto, 1993), and a rostral constriction is absent in the skull from the Pyrenees (Fig. 11; PVHR 1, original of Mazin, 1985). Dividing the width of the skull at the level in front of the orbits by the width of the skull at the rostral constriction yields a ratio of 1.8 in "*Silvestrosaurus*," 1.2–2.0 in *Lariosaurus*. Dividing the maximal width of the premaxillary rostrum by the width of the skull at the rostral constriction yields a ratio of 1.0 in "*Silvestrosaurus*," 0.9–1.4 in *Lariosaurus*. Dividing the distance from the tip of the snout to the anterior margin of the external naris by the width of the skull at the rostral constriction yields a ratio of 0.9 in "*Silvestrosaurus*," 0.6–1.2 in *Lariosaurus*.

RELATIVE ROSTRUM LENGTH—The relative length of the rostrum is similar in "*Silvestrosaurus*" and *Lariosaurus*. Dividing the distance from the tip of the snout to the anterior margin of the orbit by the distance from the tip of the snout to the anterior margin of the external naris yields 2.0 for "*Silvestrosaurus*," 1.8–2.1 for *Lariosaurus*. Dividing the distance from the tip of the snout to the anterior margin of the upper temporal fossa by the distance from the tip of the snout to the anterior margin of the external naris yields 3.7 for "*Silvestrosaurus*," 2.8–3.9 for *Lariosaurus*.

RELATIVE SIZE OF THE UPPER TEMPORAL FOSSA—The relatively small upper temporal fossa of "*Silvestrosaurus*" has played a major role in discussions of the validity of that genus (Tschanz, 1989; Kuhn-Schnyder, 1990). The difficulty here is that the size of the temporal fossa has been compared to skull length or to the size of the orbit, respectively, which may be problematic in view of the negative allometric growth of the orbit and the possibility of allometric growth of the rostrum. On the other hand, the size of the temporal fossae cannot be compared to a standard measurement of the postcranial skeleton (such as the length of the last four presacral centra), since the postcranial skeleton of "*Silvestrosaurus*" is completely disarticulated.

Keeping these provisions in mind, the division of the longitudinal diameter of the orbit by the distance from the tip of the snout to the back end of the supraoccipital (the posterior cranial landmark most easily identified in the specimens from Montral–Alcover) yields 0.2 for "*Silvestrosaurus*" and all *Lariosaurus* included in the analysis. Division of the longitudinal diameter of the upper temporal fossa by the distance from the tip of the snout to the back end of the supraoccipital yields 0.3 for "*Silvestrosaurus*" and 0.2–0.3 for *Lariosaurus*. Division of the longitudinal diameter of the upper temporal fossa by the distance from the tip of the snout to anterior margin of the upper temporal fossa yields 0.4 for "*Silvestrosaurus*" 0.3–0.6 for *Lariosaurus*. Division of the longitudinal diameter of the upper temporal fossa by the longitudinal diameter of the orbit yields 1.0 for "*Silvestrosaurus*," 1.0 (1.1)–1.8 for *Lariosaurus*.

A closer look at these values indicates that the upper temporal fossa is equal in size to the orbit in "*Silvestrosaurus*," whereas the longitudinal diameter of the upper temporal fossa is between 1.4 (in the juvenile described by Renesto, 1993) and 1.8 (in BSP AS I 802 and in the specimen described by Mariani, 1923) times the longitudinal diameter of the orbit in *Lariosaurus*. The one exception is a specimen from Montral–Alcover (SB M-501), with a lower jaw length of 50.5 mm (tip of snout to back end of supraoccipital 43.5 mm). The longitudinal diameter of the upper temporal fossa is distinct on the left side of the skull (8.7 mm), the longitudinal diameter of the orbit is 8.1 mm (left) and 8.5 mm (right) respectively, yielding a quotient of 1.02 to 1.07. The specimen is a little more than half the size of "*Silvestrosaurus*," but shows much smaller temporal fossae relative to orbital size than juvenile *Lariosaurus* (Renesto, 1993). A relatively small upper temporal fossa is plesiomorphic at the level of the Eosauropterygia, and with respect to this character, "*Silvestrosaurus*" lies at one extreme of the range of variation observed in *Lariosaurus*.

Postcranial Skeleton

VERTEBRAL COUNT—The presacral vertebral count cannot be established for "*Silvestrosaurus*." In *Lariosaurus*, the presacral vertebral count ranges from 42 (holotype of *L. valceresii*) to 44. Cervical vertebrae are defined as those lying in front of the pectoral girdle (interclavicle and clavicle), and their number ranges from 19 to 23. The number of dorsal vertebrae ranges from 20 to 24. These numbers are randomly distributed throughout the sample and do not segregate lariosaurs according to geographic locality.

SACRUM—The number of sacral vertebrae ranges from four to five in *Lariosaurus* (Fig. 12). This does not imply that four or five sacral ribs actually contact the ilium, but rather that four to five closely juxtaposed sacral ribs converge on the dorsal process of the ilium. Storrs (1993) coded the presence of distally expanded sacral ribs for "*Silvestrosaurus*," but in fact the elements identified as (disarticulated) sacral ribs by Tschanz (1989) show a broadened proximal head and a tapering, blunt distal tip, as is also seen in *Lariosaurus* (as well as in *Nothosaurus* and "*Ceresiosaurus*").

RIBS—The dorsal ribs of "*Silvestrosaurus*" show no pachyostosis, in contrast to most specimens of *Lariosaurus*. Rib pachyostosis is variably expressed in the latter genus, however, and appears to be reduced with increasing size. Rib pachyostosis is distinct in juvenile (Kuhn-Schnyder, 1987; Renesto, 1993) as well as most intermediate-sized specimens (not in the relatively small SMF R-13), but it is weak or absent in the large neotype of *L. balsami* and in the relatively large holotype of *L. valceresii*. (It was weakly expressed in the original holotype of *L. balsami*.)

PECTORAL GIRDLE (Fig. 13)—The clavicle of "*Silvestrosaurus*" differs from that of *Lariosaurus* by a generally more slender appearance and by the apparent absence of an expanded anterolateral edge (Tschanz, 1989, Fig. 6). In fact, the radiograph of the specimen shows a weak anterolateral expansion of the clavicle (Kuhn-Schnyder, 1974, Fig. 10), which is also present in *Lariosaurus* to a variable degree (compare BSP AS I 802, Fig. 13C, with a very distinct anterolateral extension of the clavicle, to the specimen Curioni VI or to the holotype of *Macromirosaurus*, with a weak expression of that character). The relatively slender shape of the clavicle in "*Silvestrosaurus*" results from the absence of pachyostosis, which inflates the clavicle in most small and intermediate-sized specimens of *Lariosaurus* (see diagnosis of the genus given by Peyer, 1933–1934). An anterolateral expansion of the clavicles is absent (Peyer, 1933–1934) or weakly expressed in "*Ceresiosaurus*" (Fig. 13D).

The clavicle of "*Silvestrosaurus*" is narrow and pointed anteromedially and hence does not seem to have met its counterpart in an anteromedial suture. The same is observed in "*Ceresiosaurus*" (Peyer, 1933–1934). In *Lariosaurus*, the
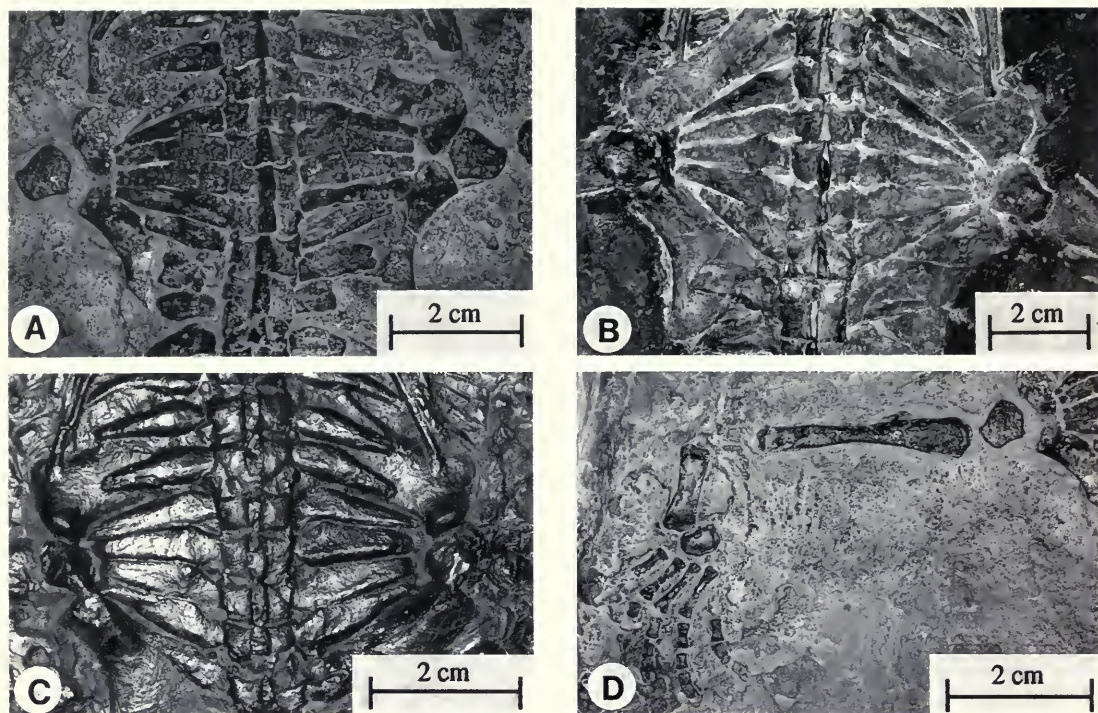
FIG. 12. The sacrum and hind limb of *Lariosaurus* in dorsal view. **A,** *Lariosaurus balsami* (MCSNM uncatalogued, original of Mariani, 1923); **B,** *L. valceresii* (holotype, Museo Civico di Szienze Naturali di Induno Olona P 500); **C,** *L. balsami* (MCL 202, original of Ticli, 1984); **D,** *L. balsami*, left hind limb (MCSNM uncatalogued, original of Mariani, 1923).

clavicles meet in an anteromedial suture in front of the interclavicle (PVHR 1, Figs. 13A, B), as is also the case in *Nothosaurus* (Rieppel, 1994b). The interclavicle of *"Silvestrosaurus"* is unknown; that of *Lariosaurus* (PVHR 1; also well exposed in the small specimen from the Natural History Museum in Lausanne) and *"Ceresiosaurus"* (Peyer, 1931) is rhomboidal and shows no rudiment of a posterior stem (Fig. 13B).

Storrs (1993) coded the supracoracoid notch absent for *"Silvestrosaurus."* In the Sauropterygia, the coracoid nerve always passes in between the scapula and coracoid (Rieppel, 1994b, as opposed to piercing the coracoid), and it must have done so in *"Silvestrosaurus,"* since a supracoracoid foramen is absent in the coracoid. The apparent absence of the supracoracoid notch (Tschanz, 1989, Fig. 6) may be due to incomplete preparation, to incomplete ossification of the endochondral pectoral girdle, and/or to compression of the scapula or coracoid, respectively.

PELVIC GIRDLE—The ilium of *"Silvestrosaurus," Lariosaurus,* and *"Ceresiosaurus"* differs from that of *Nothosaurus* by further reduction of

its dorsal wing. No praeacetabular process is formed by the ilium or by a posteriorly projecting wing (Fig. 12). The pubis of *"Silvestrosaurus"* lacks the ventral concavity characteristic for the pubis of *Simosaurus* or *Nothosaurus* (Rieppel, 1994b). As far as can be inferred from the available material, the pubis shows a convex ventral edge in *Lariosaurus*. In *"Ceresiosaurus,"* the pubis shows a weakly concave ventral edge.

LIMB PROPORTIONS—Kuhn-Schnyder (1990) emphasizes the relatively short humerus (compared to the femur) in *"Silvestrosaurus"* as a character separating this taxon from *Lariosaurus*. In *Lariosaurus,* as in all other Sauropterygia, the humerus grows with positive allometry. Dividing the length of the humerus by standard length (defined as the length of the last four presacral vertebrae) yields 1.0 in juvenile specimens (Kuhn-Schnyder, 1987; Renesto, 1993), and a ratio of 1.4–1.6 for larger specimens. The corresponding value remains unknown for *"Silvestrosaurus"* due to complete disarticulation of the postcranial skeleton.

Dividing humerus length by femur length

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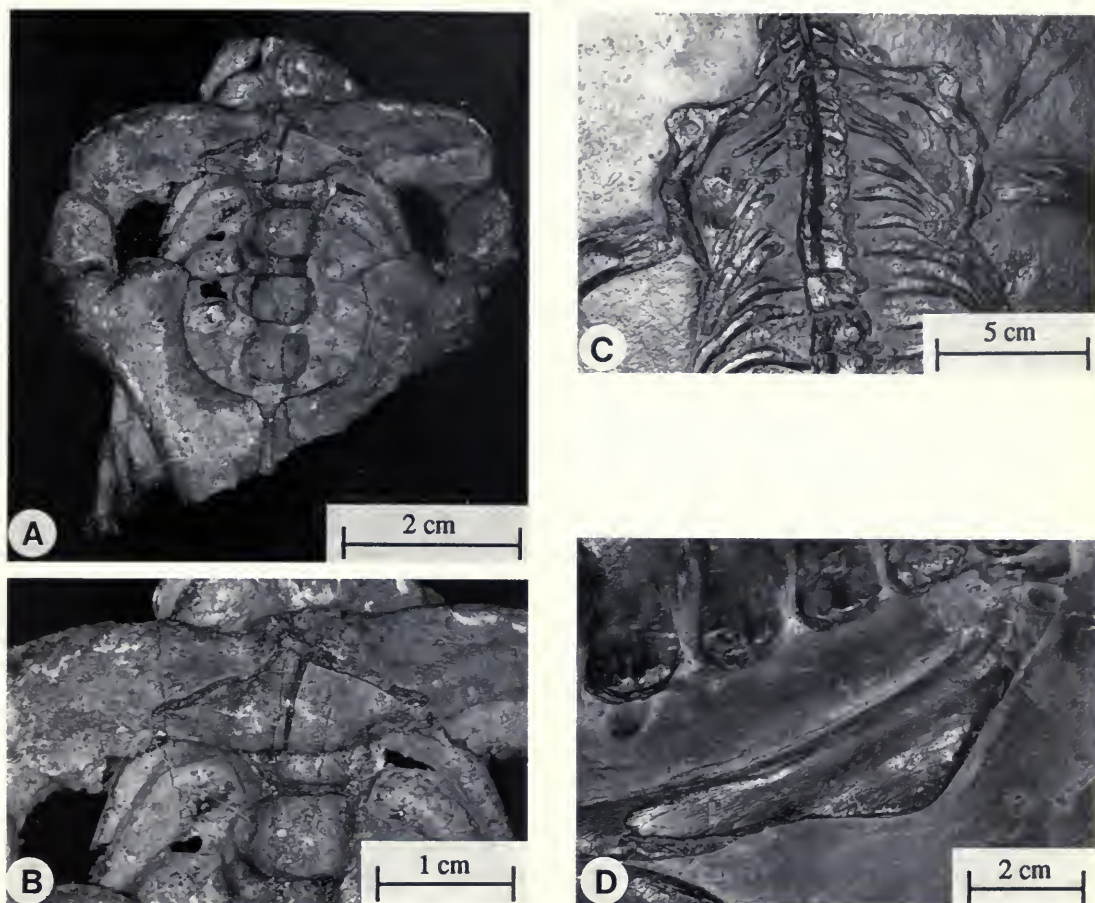
FIG. 13. **A,** The pectoral girdle of *Lariosaurus curionii* n. sp. in ventral view (holotype, PVHR 1); **B,** interclavicle of *L. curionii* n. sp. in ventral view (holotype, PVHR 1); **C,** pectoral girdle of *L. balsami* in dorsal view (neotype, BSP ASI 802); **D,** right clavicle of *L. calcagnii* in dorsal view (MBS, uncatalogued).

yields 0.74 for "*Silvestrosaurus*," 0.74–0.77 for juvenile *Lariosaurus* (Kuhn-Schnyder, 1987; Renesto, 1993), and 0.76–0.96 for other *Lariosaurus*. Since "*Silvestrosaurus*" is larger than the juvenile *Lariosaurus,* its humerus is relatively somewhat shorter (compared to the femur) than that of *Lariosaurus* of comparable size. The humerus is smaller than the femur in all *Lariosaurus,* with the exception of the holotype of *L. valceresii,* where the two bones are of almost equal size.

A relatively short humerus (or a relatively long zeugopodium) is also indicated for "*Silvestrosaurus,*" as humerus length divided by radius length yields 0.7 (0.8–1.0 in *Lariosaurus*). Finally, a relatively short forelimb in "*Silvestrosaurus*" (as compared with the hind limb) is documented by the ratio obtained when the combined lengths of

humerus and radius are divided by the combined lengths of the femur and tibia. This ratio is 0.78 in "*Silvestrosaurus*" and 0.79–0.93 in *Lariosaurus,* except for the holotype of *L. valceresii,* which has a ratio of 1.02, indicating relatively long forelimbs in the latter species (Tintori & Renesto, 1990). The forelimb of "*Ceresiosaurus*" is distinctly longer than the hind limb, at least in adult specimens (Kuhn-Schnyder, 1974, Fig. 40), an effect probably due to strong positive allometric growth of the humerus in this large species.

The ulna is slightly longer than the radius, or the two bones are of equal length, in *Lariosaurus* (radius length divided by ulna length equals 0.8–1.0), whereas the ulna is slightly shorter than the radius in "*Silvestrosaurus*" (radius length divided by ulna length equals 1.1). The fibula, on the other hand, is either slightly longer than the tibia or of
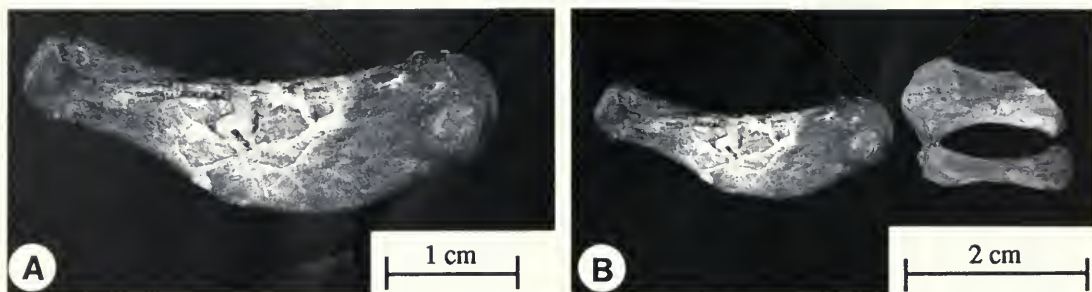
Fig. 14. The left forelimb of *Lariosaurus curionii* n. sp. in dorsal view (holotype, PVHR 1). **A,** humerus; **B,** humerus, radius, and ulna.

equal length both in "*Silvestrosaurus*" and *Lariosaurus* (tibia length divided by fibula length yields 0.8–1.0).

HUMERUS MORPHOLOGY—In most specimens of *Lariosaurus,* and in some specimens of "*Ceresiosaurus,*" humerus morphology (Figs. 14–16) is distinctly different from that seen in *Nothosaurus.* The latter genus shows a distinct outer angulation of the shaft of the humerus caused by the deltopectoral crest, whereas the inner margin of the shaft of the humerus is concave, with the insertional crest for the latissimus dorsi muscle projecting from its postaxial surface (only weakly developed in smaller specimens, but distinct in large specimens [Sanz, 1984; see also Rieppel, 1994b, Fig. 59B]). The middiaphyseal region is waisted in the humerus of *Nothosaurus* and hence always more slender than either the proximal or the distal parts. In most *Lariosaurus* and in at least some "*Ceresiosaurus,*" the humerus lacks the angulation on its anterior edge because of lesser development of the deltopectoral crest, and the insertional crest for the latissimus dorsi muscle is never distinct. This results in a more evenly curved appearance of the bone (Figs. 14–15). In addition, the middiaphyseal region is not waisted, as the cross-sectional diameter of the humerus gradually increases in a proximodistal direction. The middiaphyseal region is therefore wider than the proximal end, but it is not as expanded as the distal end of the humerus. These proportional differences are best expressed in the ratio that results if the diameter of the proximal head is divided by the diameter of the middiaphyseal region.

Throughout the sample of *Lariosaurus,* this ratio varies from 0.8 to 1.4, indicating that in some specimens the humerus is waisted, but not quite as strongly as in some *Nothosaurus* (where the corresponding ratio ranges from 1.0 to 1.7, with the large humeri of *Nothosaurus giganteus* show-

ing minimal middiaphyseal constriction). Among *Lariosaurus,* the most distinctly waisted humerus is seen in the holotype of *L. valceresii* with the ratio 1.4, which accordingly also shows a rather distinct angulation of the proximal part of the humerus at its anterior margin (Fig. 15D). The humerus of the holotype of *L. valceresii* compares closely to that of "*Silvestrosaurus,*" again with a distinctly angulated appearance and a proximal width/middiaphyseal width ratio of 1.4. The humerus of the holotype of *L. valceresii* is further characterized by a notched ectepicondylar groove, absent in other *Lariosaurus* and in "*Silvestrosaurus.*"

Storrs (1993) coded the entepicondylar foramen as present in *Lariosaurus* and absent in "*Silvestrosaurus.*" The presence of an entepicondylar foramen may be variable in *Lariosaurus.* It is present in the holotype of *L. valceresii* and in SMF R-13, but it is absent in the juvenile specimens (Kuhn-Schnyder, 1987; Renesto, 1993; Fig. 16A, this work), probably due to incomplete ossification of the humerus. I was unable to positively identify an entepicondylar foramen in the neotype of *L. balsami* (BSP AS I 802), in the specimens 'Curioni V.I.' and 'Curioni VI', or in the specimen described by Mariani (1923). In all of these latter specimens, the entepicondylar foramen may have been obscured by crushing (as assumed by Peyer, 1933–1934).

ULNA MORPHOLOGY—A diagnostic character of *Lariosaurus* is the distinctly broadened ulna (Figs. 14B, 16A; Table 1). A broadened ulna is also observed in the pachypleurosaurs *Keichousaurus* and in "*Ceresiosaurus*" (Fig. 17).

In comparison to *Lariosaurus,* the ulna of "*Silvestrosaurus*" appears rather narrow but still distinctly broader than the radius. The values listed in Table 1 indicate that the ulnas of "*Silvestrosaurus*" and "*Ceresiosaurus*" are not as broad as
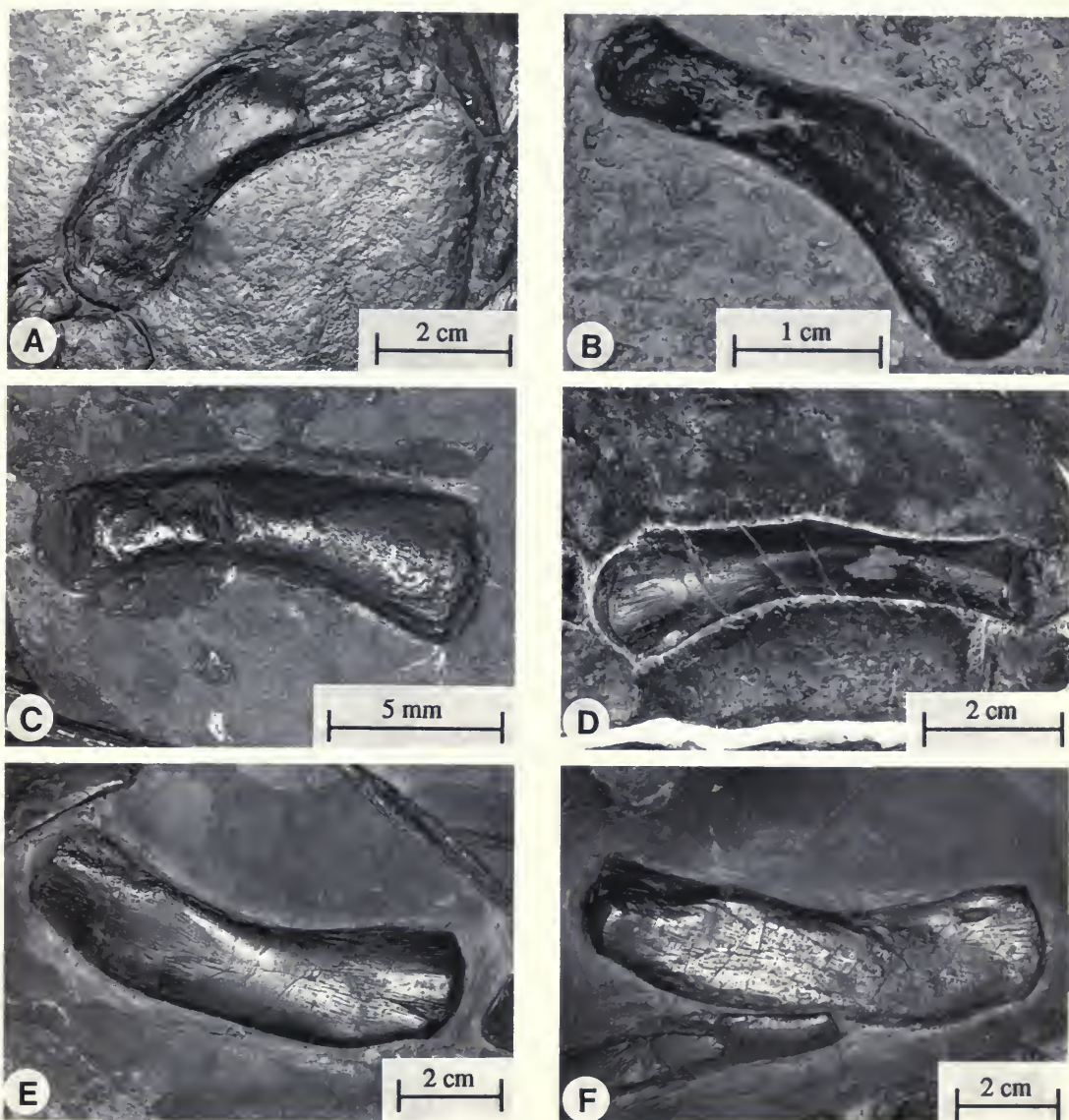
FIG. 15. The humerus of *Lariosaurus*. **A,** *Lariosaurus balsami,* left humerus in dorsal view (neotype, BSP ASI 802); **B,** *L. balsami,* right humerus in dorsal view (MCSNM uncatalogued, original of Mariani, 1923); **C,** *L. balsami,* right humerus in dorsal view (MCL 663, original of Ticli, 1984); **D,** *L. valceresii,* left humerus in dorsal view (holotype, Museo Civico di Szienze Naturali di Induno Olona P 500); **E,** *L. calcagnii,* left humerus in dorsal view (MBS, uncatalogued); **F,** *L. calcagnii,* right humerus in dorsal view (MBS, uncatalogued).

that of *Lariosaurus* but are still distinctly broader than that of *Northosaurus* in the middiaphyseal region. The proximal head of the ulna is distinctly less expanded in "*Silvestrosaurus*" than in *Lariosaurus* or "*Ceresiosaurus.*" Peyer (1933–1934) emphasized the proximal expansion of the ulna in his diagnosis of *Lariosaurus,* yet it should be noted that the proximal expansion of the ulna relative to its length in *Nothosaurus* (Schröder, 1914; and even more so in *Simosaurus* [Rieppel, 1994b, Fig. 30]) closely approaches that of *Lariosaurus* and exceeds that of "*Ceresiosaurus.*" Relative expansion of the distal head of the ulna of "*Silvestrosaurus*" falls into the range of variation observed in *Lariosaurus.*

CARPAL AND TARSAL OSSIFICATIONS—The number of carpal ossifications remains unknown in "*Silvestrosaurus.*" The specimens referred to
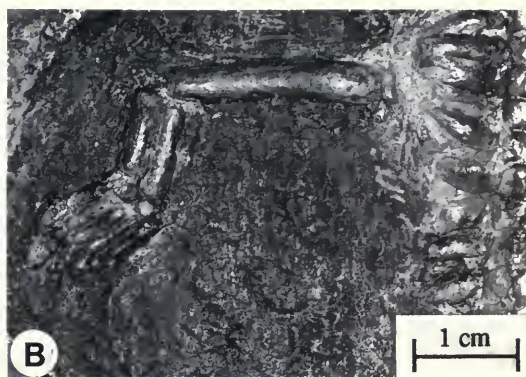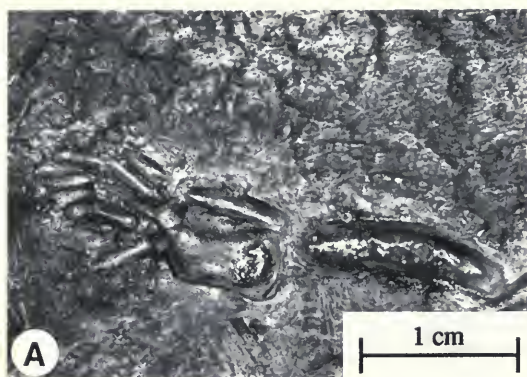
FIG. 16. *Lariosaurus balsami* (Museo Civico di Szienze Naturali di Induno Olona P 550, original of Renesto, 1993). **A,** left forelimb; **B,** left hind limb.

"*Ceresiosaurus*" (Fig. 17) show a good correlation of the number of carpal (tarsal) ossifications and absolute body size (Rieppel, 1989b), but such is not the case for the specimens referred to *Lariosaurus.* The maximum number of carpal elements ossifying in *Lariosaurus* is six (SMF R-13; five or six carpals are ossified in the holotype of *L. valceresii*), and six carpals ossify in adult "*Ceresiosaurus*" (Rieppel, 1989b). The maximum number of tarsal ossifications in *Lariosaurus* is four; there are three in "*Ceresiosaurus,*" where distal tarsal 3 remains cartilaginous (Rieppel, 1989b). The sequence of ossification is intermedium > ulnare > distal carpal (dc) 4 > dc3 > dc2 > dc5 in the carpus, astragalus > calcaneum > distal tarsal (dt) 4 > dt 3 in the tarsus. There are notable exceptions to the correlation of carpal/tarsal ossifications and absolute body size. The neotype of *Lariosaurus balsami* (BSP AS I 802; glenoid–acetabulum length 246 mm, Figs. 18A,C) shows only three ossified carpals (intermedium, ulnare, and distal carpal 4) and tarsals (astragalus, calcaneum, and distal tarsal 4), and a relatively large isolated foot (specimen Lucas II, original of Sanz, 1983a, Pl. 3C), again shows only three tarsal ossifications. By contrast, the much smaller

specimen SMF R-13 (Boulenger, 1898, glenoid–acetabulum length 70 mm, Figs. 18B,D) has six carpals (including distal carpals 2 through 5) and four tarsals (including distal tarsal 3, well exposed in left tarsus), and the even smaller specimen kept at the Natural History Museum in Lausanne (uncatalogued, glenoid–acetabulum length 54 mm) shows four ossified carpals. The question may be raised as to whether these specimens represent two separate species (or different sexes of the same species) distinguished by different adult size, the smaller one retaining more carpal (five to six) and tarsal (four) ossifications in the adult than the larger species. However, the original material of Curioni (1863) includes specimen Cu-

TABLE 1. Proportions of the ulna in *Lariosaurus.* See text for further discussion.

	$\frac{\text{ul-lg}}{\text{mw}}$	$\frac{\text{ul-lg}}{\text{pw}}$	$\frac{\text{ul-lg}}{\text{dw}}$
Nothosaurus "raabi"	4.2	2.2	3.4
"*Ceresiosaurus*"	3.1	2.3	2.8
"*Silvestrosaurus*"	3.4	2.6	2.2
Lariosaurus	2.2 - 3.5	1.7 - 2.1	1.8 - 2.3

FIG. 17. Left zeugopodium and carpus of *Lariosaurus calcagnii* (MBS, uncatalogued).
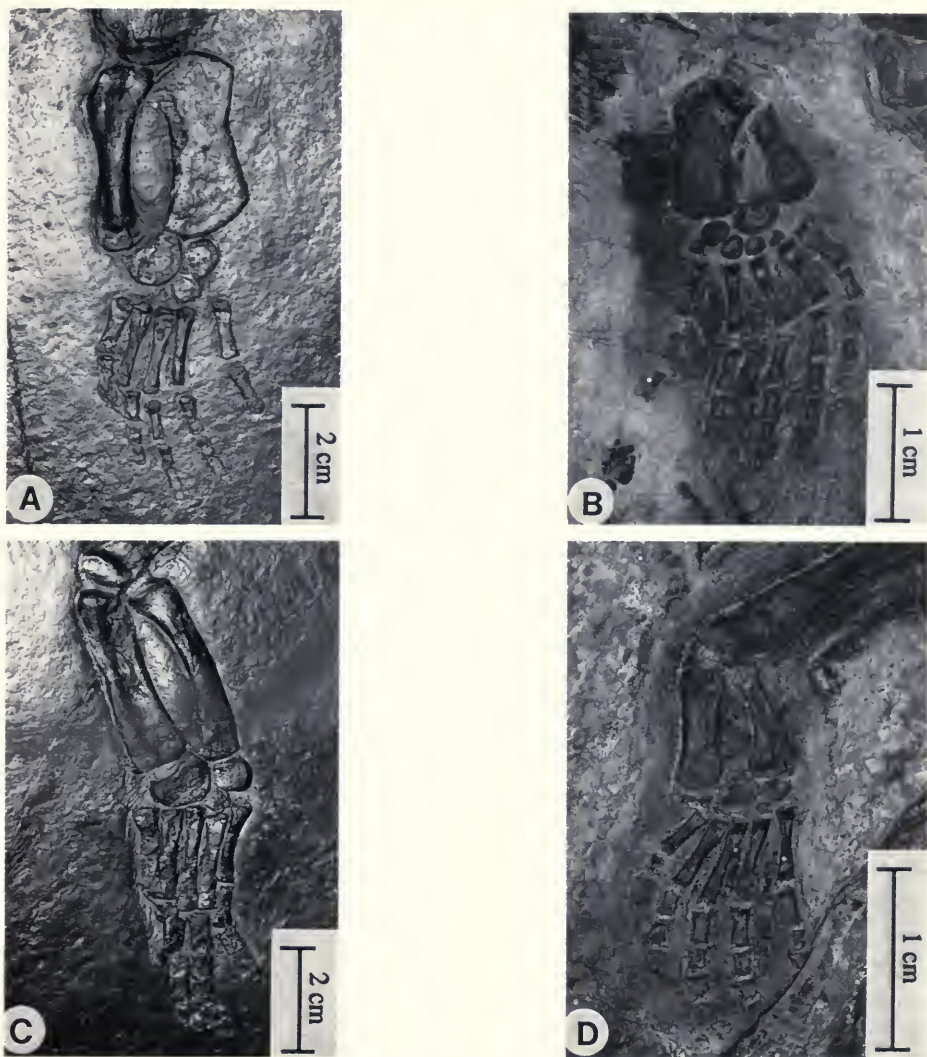
Fig. 18. The manus and pes of *Lariosaurus balsami*. **A,** Zeugopodium and left manus in dorsal view (neotype, BSP ASI 802); **B,** zeugopodium and left manus in ventral view (SMF R-13, original of Boulenger, 1898); **C,** zeugopodium and left pes in dorsal view (neotype, BSP ASI 802); **D,** zeugopodium and right pes in ventral view (SMF R-13, original of Boulenger, 1898).

rioni V.I., represented by the anterior trunk, neck, and skull of similar size as the neotype of *Lariosaurus balsami* (BSP AS I 802), which has a total of five carpal ossifications; the specimen Curioni VII.I. is an isolated foot, again similar in size to the Munich specimen (BSP AS I 802) with a total of four tarsal ossifications. Specimen 'Curioni VI' (glenoid–acetabulum length 194 mm) is the second largest known specimen of *Lariosaurus balsami,* with a total of five carpal and three tarsal ossifications. In fact, a comparison of all adequately preserved *Lariosaurus* specimens kept in public repositories (Table 2) indicates a poor correlation of the degree of ossification in the carpus and tarsus with glenoid–acetabulum (trunk) length. The number of carpal or tarsal ossifications by itself does not allow the distinction of two separate taxa of different adult body size within the entire sample, and other than the total number of carpal or tarsal ossifications in the adult (three versus five or six carpals; four versus three tarsals), there is no character supporting the hypothesis that more than one taxon might be represented by the specimens referred to *L. balsami.*

TABLE 2. Number of carpal and tarsal ossifications in relation to body size in *Lariosaurus*. See text for further discussion.

specimen number	specimen description	trunk length	carpals	tarsals
PMZ uncatalogued	*"Ceresiosaurus"*	545	6	3
PMZ uncatalogued	*"Ceresiosaurus"*	520	6	3
PMZ T2460	*"Ceresiosaurus"*	260	4	3(4)
BSP AS I 802	Neotype *L. balsami*	246	3	3
Induno-Olona P 500	Holotype *L. valceresii*	215.5	5(6)	3
PMZ T2462	*"Ceresiosaurus"*	125	3(4)	3
UGR 4428P	"Curioni VI"	193.8	5	4
Maxberg uncatalogued	Sanz, 1983 Pl. 5, Fig. A	116	?	3
MCSNM uncatalogued	Mariani, 1923	114.5	3	3
MCL 202	Ticli, 1984	109	5(6)	4
SB M-501	Sanz, 1983 Pl. 2, Fig. B	74.3	2	2
SMF R-15	Boulenger, 1898	70	6	4
SB M-506	Sanz, 1983 Pl. 2, Fig. A	62	2	2
PMZ T4288	holotype *"L. lavizzarii"*	58	2(1)	1(0)
Induno-Olona P550	Renesto, 1993	57.5	1	2
MHNL uncatalogued		54	4	?
UGR 4427P	holotype *"Macromirosaurus"*	52.2	4	2

Peyer (1933–1934, p. 115) arrived at the same conclusion.

PHALANGEAL FORMULA—Due to incomplete preservation, the accurate phalangeal formula can be established in very few specimens only. An exact count of phalanges is possible in the right manus of the specimen "Curioni V.I.", where the formula is 4–5–5–4 (5?)–3; a similar formula is likely for SMF R-13. Specimen SB M-501 from Montral–Alcover shows at least four phalanges in the fifth digit of the left manus. Hyperphalangy in the manus of *Lariosaurus* is therefore well established. The pes of *Lariosaurus* retains the primitive phalangeal formula 2–3–4–5–4 (specimens 'Curioni VI' and SMF R-13), with the exception of the holotype of *L. valceresii*. In the latter specimen, all four autopodia are incomplete, but the second digit of the left foot shows four phalanges with the ungual in situ, indicating the possibility of mild hyperphalangy in the pes. "Ceresiosaurus" is characterized by hyperphalangy both in manus and pes (Tschanz, 1989).

Discussion

Lariosaurs, a monophyletic clade including "*Ceresiosaurus*," *Lariosaurus,* and "*Silvestrosaurus,*" differ from their sister group, the genus *Nothosaurus,* by a relatively smaller temporal opening with a longitudinal diameter that equals between one and two times the longitudinal diameter of the orbit. In *Nothosaurus,* the longitudinal diameter of the upper temporal fossa is always longer than twice that of the orbit. Other relatively plesiomorphic features of lariosaurs that are shared with basal species within the genus *Nothosaurus* (*N. marchicus* [Rieppel & Wild, 1996]) are a relatively short and broad but distinctly constricted rostrum and a relatively forward position of the pineal foramen (which is still located behind the midpoint of the parietal, however). The maxillary tooth row does not extend backward beyond the first third of the temporal fossa. The anterior part of the parietal skull table remains relatively broad, but behind the pineal foramen, the parietal skull table may be strongly constricted without ever being developed into a sagittal crest. Carpal and tarsal ossifications may exceed three in the adult.

Lariosaurs differ from *Nothosaurus* in a number of derived features, most notably the morphology of the humerus with no constriction in its middiaphyseal part (in some but not all specimens or species), the broadened ulna, the absence of all traces of a posterior stem on the interclavicle, the presence of four or five sacral ribs (three in *Nothosaurus*), the reduced dorsal wing of the ilium (with no praeacetabular process and without posterior process), and the potential for hyperphalangy in manus and pes.

Within the lariosaur clade, "*Silvestrosaurus*" is characterized by relatively small upper temporal fenestrae (equal in size to the orbit), a broad parietal skull table that shows only a weak constriction in its posterior part, the pineal foramen located close behind the midpoint of the parietal, the anterolateral corner of the clavicle only weakly expanded, and the absence of pachyostosis. The anteromedial tip of the clavicle is narrow and pointed, suggesting the absence of an anteromedial suture between the two clavicles as in "*Ceresiosaurus*" (Peyer, 1931, Pl. 1) but unlike *Lariosaurus.* "*Silvestrosaurus*" also differs from *Lariosaurus* by a relatively short humerus, absence of the entepicondylar foramen, and a relatively narrow ulna (yet broader than in *Nothosaurus*). The close resemblance of "*Silvestrosaurus*"

to the juvenile specimen of *Lariosaurus* described by Renesto (1993) suggests that the broad skull table in "*Silvestrosaurus*" is either a paedomorphic feature or, alternatively, that the holotype of "*Silvestrosaurus*" is a juvenile. Paedomorphosis or a juvenile specimen may also explain the relatively short humerus and, correlated therewith, the absence of the entepicondylar foramen, also absent in juvenile *Lariosaurus*. Manus and pes of "*Silvestrosaurus*" are not known.

Within lariosaurs, the genus *Lariosaurus* is characterized by pachyostosis affecting not only the ribs but also the clavicle (with the exception of the holotype of *L. valceresii*, weakly expressed in large specimens of *L. balsami*), by a strongly expanded proximal head of the ulna, and by hyperphalangy in the manus (not known in "*Silvestrosaurus*"). *Lariosaurus valceresii* differs from *L. balsami* by a relatively longer forelimb and by a distinctly waisted humerus with an open and notched ectepicondylar groove. The specimen PVHR 1, which is from the eastern Pyrenees (Mazin, 1985), is unique among *Lariosaurus* by the absence of a rostral constriction and by the exclusion of the postfrontal from the anteromedial margin of the upper temporal fossa.

To evaluate the status of "*Ceresiosaurus*" among lariosaurs is difficult at this time because critical material remains inaccessible for analysis. The genus is derived as compared to *Lariosaurus* by the relatively large forelimbs in the adult, by the presence of hyperphalangy in the pes, and by an increased height of the neural spines in the proximal caudal region (Kuhn-Schnyder, 1974, Fig. 40).

To assess the systematic status of the taxa included in the lariosaur clade, a phylogenetic analysis using parsimony is required to critically address the significance of the characters distilled from the morphological comparison detailed above.

A Case for Monophyly

To investigate the interrelationships of lariosaurs, I conducted a phylogenetic analysis using parsimony using the software package PAUP (version 3.1.1), developed by David L. Swofford (Swofford, 1990; Swofford & Begle, 1993). The analysis builds on the data matrix developed by Rieppel (1994b, 1997), with new characters added and old ones redefined as detailed in Appendix I.
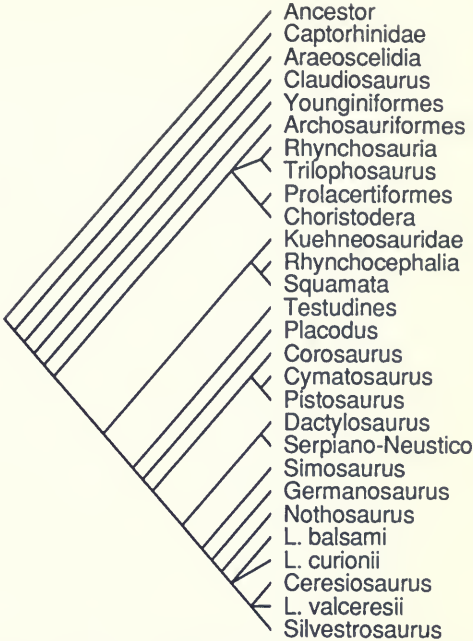
FIG. 19. Strict consensus tree of 10 equally parsimonious trees (TL = 479, CI = 0.630, and RI = 0.762), indicating lariosaur interrelationships.

The data matrix (Table 3) includes a total of 27 taxa plus the all-0-ancestor, and a total of 122 characters. Character codings for lariosaurs follow the morphological description given above.

In a first run, the Sauropterygia were treated as a monophyletic ingroup rooted on a paraphyletic outgroup that included the Captorhinidae, Testudines, Araeoscelidia, YouNginiformes, and *Claudiosaurus*. Deletion of all other taxa rendered a number of characters uninformative (2, 5, 24, 28, 34, 40, 53, 63, 66, 111, and 117), which were consequently ignored in the analysis. Character 27 was the only multistate character treated as an ordered transformation series because it implies a logical interdependence of the character states: a lower temporal fenestra must have formed before the lower temporal arch could be lost (Rieppel, 1994b; the alternative of ventral emargination of the cheek in sauropterygians is discussed in this paper). A heuristic search, employing random stepwise addition (10 replications) and branch swapping (on minimal trees only) by tree bisection and reconnection, yielded a total of 10 most parsimonious trees (MPTs) with a tree length (TL) of 310 steps, a consistency index (CI) of 0.645, and a retention index (RI) of 0.746. All 10 trees support the monophyly of lariosaurs (including

1		1	2	3	4	5	6	7	8	9	10
1	Ancestor	0	0	0	0	0	0	0	0	0	0
2	Captorhinidae	0	0	0	0	0	0	0	0	0	0
3	Testudines	0	0	0	0	0	0	0	0	1	0 & 1
4	Araeoscelidia	0	0	0	0	0	0	0	0	0	0
5	Younginiformes	0	0	0	0	0	0	0	0	1	0
6	Kuehneosauridae	0	0	0	0	0	0	0	0	1	0
7	Rhynchocephalia	0	0	0	0	0	0	0	0	1 & 2	0
8	Squamata	0	0	0	0	0	0	0	0	1 & 2	0 & 1
9	Rhynchosauria	1	1	0	0	0	0	0	0	1	0
10	Prolacertiformes	1	1	0	0	1	0	0	0	1	0
11	Trilophosaurus	1	?	0	0	0	0	0	0	?	1
12	Choristodera	1	1	0	0	1	0	0	0	1	0
13	Archosauriformes	1	1	0	0	1	0	0	0	1	0
14	Claudiosaurus	0	0	0	0	0	0	0	0	1	0
15	Dactylosaurus	1	0	0	0	0	0	0	0	2	0
16	Serpiano-Neustico	1	0	0	0	0	0	0	0 & 1	2	0
17	Simosaurus	1	0	0	0	0	1	0	1	2	0
18	Nothosaurus	1	0	1	1	0	0	0	0 & 1	2	0
19	Ceresiosaurus	1	0	1	1	0	0	0	0	2	0
20	L. balsami	1	0	1	1	0	0	0	1	2	0
21	L. curionii	1	0	0	1	0	0	0	1	2	0
22	L. valceresii	1	0	1	1	0	0	0	0	2	0
23	Silvestrosaurus	1	0	1	1	0	0	0	0	2	0
24	Corosaurus	1	0	0	0	0	0	0	0	2	0
25	Cymatosaurus	1	0	1	0	0	2	0 & 1	1	2	0 & 1
26	Germanosaurus	1	0	1	1	0	1	0	1	2	0
27	Pistosaurus	1	0	0	0	0	2	1	1	2	0
28	Placodus	1	0	1	0	1	0	0	0	2	1

"*Ceresiosaurus*," *Lariosaurus*, and "*Silvestrosaurus*"), and in all 10 trees, *Lariosaurus valceresii*, "*Ceresiosaurus*" *calcagnii*, and "*Silvestrosaurus*" *buzzii* from a monophyletic group (internally unresolved in the strict consensus tree), which in turn falls into an unresolved trichotomy with *Lariosaurus balsami* and specimen PVHR 1 (described as *Lariosaurus curionii* n. sp. below) in the strict consensus tree. In six out of these 10 trees, *Lariosaurus balsami* is the sister taxon of specimen PVHR 1; these two in turn are the sister group to a second lariosaur clade within which "*Ceresiosaurus*" *calcagnii* is the sister taxon to *Lariosaurus valceresii* plus "*Silvestrosaurus*" *buzzii*. Tree topology of the 50% majority rule consensus tree is: ((*balsami*, PVHR 1) (*calcagnii* (*buzzii*, *valceresii*))). Implementation of identical search options but treating character 27 as unordered yielded five MPTs (TL = 309; CI = 0.647, RI = 0.747), with identical lariosaur interrelationships in the strict consensus and 50% majority rule consensus trees.

In a second analysis, all 26 taxa were treated as the monophyletic ingroup (Reptilia) rooted on an all-0-ancestor. Heuristic search settings were identical, and of all multistate characters, only character 27 was treated as ordered. All characters were informative. One hundred replications yielded a total of 10 MPTs, with TL = 479, CI = 0.630, and RI = 0.762. Lack of resolution was restricted to archosauromorph taxa and lariosaurs. All 10 trees again support the monophyly of lariosaurs (including "*Ceresiosaurus*," *Lariosaurus*, and "*Silvestrosaurus*"). Within lariosaurs, *Lariosaurus valceresii*, "*Ceresiosaurus*" *calcagnii*, and "*Silvestrosaurus*" *buzzii* again form a monophyletic group (internally unresolved in the strict consensus tree), which in turn falls into an unresolved trichotomy with *Lariosaurus balsami* and specimen PVHR 1 in the strict consensus tree (Fig. 19). In six out of these 10 trees, *Lariosaurus balsami* is the sister taxon of specimen PVHR 1; these two in turn are the sister group to a second lariosaur clade within which "*Ceresiosaurus*" *calcagnii* is the sister taxon to *Lariosaurus valceresii* plus "*Silvestrosaurus*" *buzzii* (Fig. 20B). Tree topology of the 50% majority rule consensus tree again is: ((*balsami*, PVHR 1) (*calcagnii* (*buzzii*, *valcere-*

TABLE 3. *Extended.*

2		11	12	13	14	15	16	17	18	19	20
1	Ancestor	0	0	0	0	0	0	0	0	0	0
2	Captorhinidae	0	0	0	0	0	?	0	0&3	0	0
3	Testudines	0	0&2	0	0	0	?	0	4	0	1
4	Araeoscelidia	0	1	1	0	1	0	0	0	0	0
5	Younginiformes	0	1	1	0	1	0	0	0	0	0
6	Kuehneosauridae	0	0	1	0	1	0	0	3	0	1
7	Rhynchocephalia	0	0	1	0&1	0&1	0	0&1	0&3	0&2	1
8	Squamata	0	0&1&2	1	0&1	0	0	0&1	0&3&4	0&2	1
9	Rhynchosauria	0	0	1	0	0	0	1	4	3	1
10	Prolacertiformes	0	1	1	0	0&1	0	0&1	3&4	0	1
11	Trilophosaurus	0	1	1	0	0	1	0	4	3	1
12	Choristodera	0	2	1	0	0	0	0	4	1	1
13	Archosauriformes	0	0&1	1	0&1	0&1	0&1&2	0&1	0&4	0&2	1
14	Claudiosaurus	0	1	1	0	1	0	0	0	0	1
15	Dactylosaurus	0	1	3	0	1	0	0	0	0	1
16	Serpiano-Neustico	0	1	3	0	1	0	0	0	0	1
17	Simosaurus	0	2	2	1	0	0	2	1	1	1
18	Nothosaurus	1	2	2	1	1	0	2	1&2	2&3	1
19	Ceresiosaurus	1	2	2	1	1	0	2	2	2	1
20	L. balsami	1	2	2	1	1	0	2	1&2	1&2	1
21	L. curionii	1	2	2	1	1	0	2	1	2	1
22	L. valceresii	1	2	2	1	1	0	2	1&2	1&2	1
23	Silvestrosaurus	1	2	1	1	1	0	2	1	0	1
24	Corosaurus	0	0	1	0	1	1	0	0	1	1
25	Cymatosaurus	0	2	2	0	1	1&2	1&2	0	2&3	1
26	Germanosaurus	1	2	2	0	1	1	1	1	1	1
27	Pistosaurus	0	1	2	0	1	2	1	3	3	1
28	Placodus	0	0	2	0&1	1	0	0&2	3	0	1
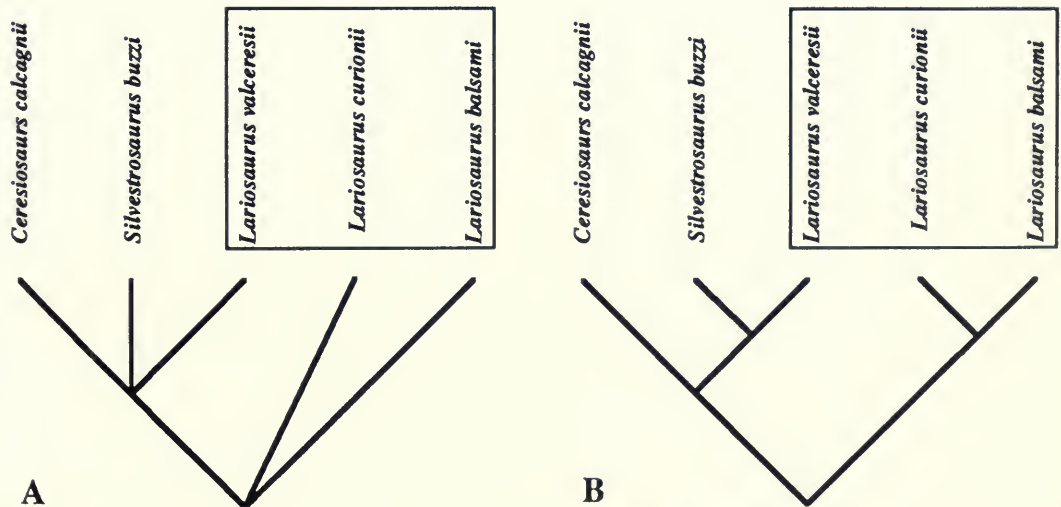
FIG. 20. Strict consensus (**A**) and majority rule consensus tree (**B**; six out of 10 equally parsimonious trees), indicating lariosaur interrelationships. For further discussion, see text.

TABLE 3. *Extended.*

	3	21	22	23	24	25	26	27	28	29	30
1	Ancestor	0	0	0	0	0	0	0	0	0	0
2	Captorhinidae	1	0	0	0	0	0	0	0	0	0
3	Testudines	1	0&1	0	0	0	?	0	1	0	0
4	Araeoscelidia	0	0	0	0	0	1	0&1	0	0	0
5	Younginiformes	0&1	0	0	0	0	1	1	0	0	0
6	Kuehneosauridae	1	1	0	0	0	1	2	1	1	1
7	Rhynchocephalia	1	0&1	0&1	1	0	1	1&2	0	0	1
8	Squamata	1	0&1	0&1	0	0	1	2	1	1	?
9	Rhynchosauria	1	1	0	1	0	1	1	1	0	0
10	Prolacertiformes	1	0&1	0	0&1	0	1	2	1	0&1	1
11	Trilophosaurus	1	?	0	?	0	1	0	?	0	?
12	Choristodera	1	1	0	0	0	1	1	1	0&1	0
13	Archosauriformes	1	0&1	0	1	0	1	1	1	0	0
14	Claudiosaurus	1	1	0	0	0	1	2	0	0	1
15	Dactylosaurus	1	1	?	0	0	2	2	0	0	1
16	Serpiano-Neustico	1	1	0	0	0	2	2	0	0	1
17	Simosaurus	1	1	0	0	1	1	2	0	0	1
18	Nothosaurus	1	1	1&2	0	1	1&2	2	0	0&1	1
19	Ceresiosaurus	1	1	1&2	0	1	2	2	0	?	?
20	L. balsami	1	1	?	0	1	2	2	0	?	?
21	L. curionii	1	1	?	?	?	2	2	0	?	?
22	L. valceresii	1	1	?	0	1	2	2	0	?	?
23	Silvestrosaurus	1	1	?	0	1	1	2	0	?	?
24	Corosaurus	1	1	?	0	0	1	2	0	?	?
25	Cymatosaurus	1	1	1	0	0	1	2	0	1	?
26	Germanosaurus	1	1	2	0	1	1	2	0	?	?
27	Pistosaurus	1	1	?	0	1	1	2	0	1	?
28	Placodus	1	1	0	0	1	1	2	0	0	0

sii))). Treating character 27 unordered in an otherwise equivalent search (10 replications) yielded 15 MPTs (TL = 478, CI = 0.632, RI = 0.762), with identical lariosaur interrelationships but decreased resolution among archosauromorph taxa.

Listing of synapomorphies for lariosaur taxa was identical in the two searches. The implementation of DELTRAN character optimization will minimize the number of synapomorphies diagnostic at any node that will subsequently be lost again within that same clade. For this reason, it will generally indicate synapomorphic characters (character states) at a level of minimal inclusiveness, rather than maximal inclusiveness as ACCTRAN character optimization would. Synapomorphy listing will here be based on DELTRAN character optimization (also in the diagnoses given below). The consistency index (CI) for the individual characters is derived from the comprehensive analysis (second run). Derived characters shared by the genera *Germanosaurus, Nothosaurus,* "*Ceresiosaurus,*" *Lariosaurus,* and "*Silvestrosaurus*" are: 3(1) [CI = 0.25], 4(1) [CI = 1.0], 11(1) [CI = 1.0], 23(2) [CI = 1.0], 55(1) [CI =

0.5]. Synapomorphies shared by the genera *Nothosaurus,* "*Ceresiosaurus,*" *Lariosaurus,* and "*Silvestrosaurus*" are 14(1) [CI = 0.833], 19(2) [CI = 0.714], 35(1) [CI = 0.667], 36(1) [CI = 0.625], 45(1) [CI = 0.5], 51(2) [CI = 0.5], 56(0) [CI = 0.333], 67(1) [CI = 0.5], 74(1) [CI = 0.5], 83(2) [CI = 0.75]. Lariosaurs are diagnosed by the following characters: 26(2) [CI = 0.6], 69(1) [CI = 0.667], 73(2) [CI = 0.75], 82(0) [CI = 0.667], 98(0) [CI = 0.6]; 99(3) [CI = 0.667], 101(1) [CI = 0.667], 120(1) [CI = 1.0], 122(1) [CI = 1.0]. "*Ceresiosaurus,*" "*Silvestrosaurus,*" and *Lariosaurus valceresii* share the following synapomorphies: 8(0) [CI = 0.6], 77(1) [CI = 0.5], 79(0) [CI = 0.5].

The evidence currently at hand does not support the monophyly of the genus *Lariosaurus* as currently conceived, including the two species *Lariosaurus balsami* Curioni, 1847, and *Lariosaurus valceresii* Tintori and Renesto, 1990. Nor does the available evidence allow the separation of three distinct genera, viz. "*Ceresiosaurus,*" *Lariosaurus,* and "*Silvestrosaurus.*" Instead, *Lariosaurus valceresii,* "*Ceresiosaurus*" *calcagnii,*

TABLE 3. *Extended.*

	4	3 1	3 2	3 3	3 4	3 5	3 6	3 7	3 8	3 9	4 0
1	Ancestor	0	0	0	0	0	0	0	0	0	0
2	Captorhinidae	0	0	0	?	0	0	0	0	0	0
3	Testudines	0	0	0&2	0	0	0	1	1	0	0
4	Araeoscelidia	0	0	0	1	0	0	0	0	?	0
5	Younginiformes	0	0	0	1	0	0	1	1	?	0
6	Kuehneosauridae	0	0	0	1	0	1	1	1	?	1
7	Rhynchocephalia	0 & 1	0	0	1	0	0 & 1	1	1	1	0 & 1
8	Squamata	0	0	0&1&2	0&1	0&1	0&1	1	1	1	1
9	Rhynchosauria	1	0	0	0	0	0	1	1	1	0
1 0	Prolacertiformes	1	0	0	1	0	0	1	1	?	0
1 1	Trilophosaurus	1	0	2	?	0	?	1	1	0	0
1 2	Choristodera	1	0	1	1	0	1	1	1	?	0
1 3	Archosauriformes	0 & 1	0	0&1&2	1	0	0 & 1	1	1	?	0
1 4	Claudiosaurus	0	0	0	?	0	0	0	0	?	0
1 5	Dactylosaurus	2	0	0	?	1	0	1	1	1	0
1 6	Serpiano-Neustico	2	0	0	?	1	0	1	1	1	0
1 7	Simosaurus	2	0	1	1	0	0	0	1	0	0
1 8	Nothosaurus	2	0	0 & 1	1	1	1	0	1	0	0
1 9	Ceresiosaurus	2	0	0	1	1	1	0	1	0	0
2 0	L. balsami	2	0	0	1	1	1	0	1	?	0
2 1	L. curionii	2	0	0	1	1	1	0	1	?	0
2 2	L. valceresii	2	0	0	1	1	1	0	1	?	0
2 3	Silvestrosaurus	2	0	0	1	1	1	0	1	?	0
2 4	Corosaurus	1	1	1	1	0	1	0	1	1	0
2 5	Cymatosaurus	1	1	1	?	0	0 & 1	0	1	?	0
2 6	Germanosaurus	?	?	?	?	?	0	0	1	?	0
2 7	Pistosaurus	1	?	1	?	0	1	0	1	1	0
2 8	Placodus	1	0	0	1	0	0	1	1	1	0

and "*Silvestrosaurus*" *buzzii* group in a monophyletic clade (itself unresolved), which in turn falls into an unresolved trichotomy with *Lariosaurus balsami* and PVHR 1 in the strict consensus tree.

As shown in Figure 20, the genus *Lariosaurus* as currently conceived is paraphyletic. Monophyly of the genus *Lariosaurus* Curioni, 1847, senior synonym of all three generic names (with *L. balsami* as the genotypical species), requires the inclusion of all four terminal taxa in that genus, a procedure that renders *Ceresiosaurus* Peyer, 1931, and *Silvestrosaurus* Kuhn-Schnyder, 1990, junior synonyms of *Lariosaurus*.

Systematic Paleontology

Sauropterygia Owen, 1860
Eosauropterygia Rieppel, 1994b
Nothosauridae Baur, 1889

DEFINITION—A monophyletic taxon including the genera *Germanosaurus* Nopcsa, 1928a,b, *Noth-*osaurus Münster, 1834, and *Lariosaurus* Curioni, 1847.

DIAGNOSIS—Small to large eosauropterygians with a distinctly constricted snout; temporal region of skull strongly depressed; dorsal exposure of prefrontal reduced; jugal restricted to position behind the orbit without entering the latter's posterior margin; premaxillary and anterior dentary fangs present.

DISTRIBUTION—Lower to Upper Triassic, Europe and Israel.

Nothosaurinae Nopcsa, 1923

DEFINITION—A monophyletic taxon, including the genera *Nothosaurus* Münster, 1834, and *Lariosaurus* Curioni, 1847.

DIAGNOSIS—Frontals fused in adult; parietal skull table strongly constricted (at least posteriorly); occipital crest present; maxillary canines present; dorsal centra not constricted in ventral view; sacral ribs without distal expansion.

TABLE 3. *Extended.*

5		41	42	43	44	45	46	47	48	49	50
1	Ancestor	0	0	0	0	0	0	0	0	0	0
2	Captorhinidae	0	0	0	0	0	1	0	0	0	0
3	Testudines	0&1	0	1	0	0&1	1	0	0&1	0	0
4	Araeoscelidia	0	0	1	0	0	0	0	0	0	0
5	Younginiformes	0	0	1	0	0	0	0	1	1	0
6	Kuehneosauridae	0	0	1	0	?	?	0	1	0	0
7	Rhynchocephalia	0	0	1	0	0	0	0	1	1	0
8	Squamata	0	0	1	0	0&1	0	0	1	1	0
9	Rhynchosauria	0	0	1	0	1	0	0	1	1	0
10	Prolacertiformes	0	0	1	0	0	0	0	1	0&1	0
11	Trilophosaurus	0	0	1	0	0	0	0	1	1	0
12	Choristodera	?	0	1	0	1	0	0	1	0	0
13	Archosauriformes	0&1	0	1	0	0&1	0&1	0	1	0&1	0
14	Claudiosaurus	0	0	1	1	0	0	0	0	0	?
15	Dactylosaurus	1	?	0	1	0	1	?	1	0	0
16	Serpiano-Neustico	1	?	0	1	0	1	?	1	0	0
17	Simosaurus	1	2	0	1	0	0	1	1	0	1
18	Nothosaurus	1	2	0	0&1	1	0	1	1	0	1
19	Ceresiosaurus	1	2	0	1	1	0	?	1	0	1
20	L. balsami	1	2	0	1	1	0	?	1	0	1
21	L. curionii	1	2	0	1	1	0	?	1	0	1
22	L. valceresii	1	2	0	1	1	0	?	1	0	1
23	Silvestrosaurus	1	2	0	1	1	0	?	1	0	1
24	Corosaurus	1	?	0	0	?	0	?	1	1	1
25	Cymatosaurus	1	?	0	0	1	0	1	?	0	?
26	Germanosaurus	1	?	?	?	?	?	?	?	?	?
27	Pistosaurus	1	?	0	0	?	0	?	?	?	?
28	Placodus	1	1	0	0	1	0	0	1	1	0

DISTRIBUTION—Lower to Upper Triassic, Europe and Israel.

Lariosaurus Curioni, 1847

1847	*Lariosaurus,* Curioni, p. 166.
1847	*Macromirosaurus,* Curioni, p. 161.
1854	*Lariosaurus,* Cornalia, p. 54.
1854	*Macromerosaurus,* Cornalia, p. 54.
1854	*Deirosaurus,* Owen, p. 68.
1863	*Lariosaurus,* Curioni, Pls. 1–3.
1863	*Macromerosauro,* Curioni, p. 266.
1886	*Lariosaurus,* Bassani, p. 21.
1886	*Macromirosaurus,* Bassani, p. 22.
1886	*Lariosaurus,* Baur, p. 247 *ff.*
1886	*Macromirosaurus,* Baur, p. 247 *ff.*
1886	*Lariosaurus,* Deecke, p. 171 *ff.*
1886	*Macromerosaurus,* Deecke, p. 189 *f.*
1887	*Lariosaurus,* Zittel, p. 486.
1887	*Macromirosaurus,* Zittel, p. 486.
1889	*Lariosaurus,* Lydekker, p. 284.
1889	*Macromerosaurus,* Lydekker, p. 284.
1889	*Macromirosaurus,* Lydekker, p. 284.
1890	*Lariosaurus,* Dames, p. 78 *ff.*
1891	*Eupodosaurus,* Boulenger, p. 293.
1898	*Lariosaurus,* Boulenger, p. 1 *ff.*
1898	*Macromerosaurus,* Boulenger, p. 2.
1898	*Palaeosaurus,* Boulenger, p. 2.
1924	*Lariosaurus,* Arthaber, p. 498 *f.*
1924	*Macromerosaurus,* Arthaber, p. 489 *f.*
1924	*Palaeosaurus,* Arthaber, p. 499.
1924	*Proneusticosaurus* (partim), Arthaber, p. 498 *f.*
1927	*Lariosaurus,* Broili, p. 220 *f.*
1927	*Macromerosaurus,* Broili, p. 223.
1927	*?Rhaeticonia,* Broili, p. 205 *ff.*
1928a	*Lariosaurus,* Nopcsa, p. 43.
1928a	*Macromerosaurus,* Nopcsa, p. 43.
1928b	*Lariosaurus,* Nopcsa, p. 173.
1928b	*Macromerosaurus,* Nopcsa, p. 173.
1931	*Ceresiosaurus,* Peyer, p. 3 *ff.*
1933–34	*Lariosaurus,* Peyer, p. 4 *ff.*
1934	*Ceresiosaurus,* Kuhn, p. 46.
1934	*Lariosaurus,* Kuhn, p. 46.
1950	*Ceresiosaurus,* Peyer, p. 184 *f.*
1955	*Ceresiosaurus,* Saint-Seine, pp. 424, 428.

TABLE 3. *Extended.*

6		51	52	53	54	55	56	57	58	59	60
1	Ancestor	0	0	0	0	0	0	0	0	0	0
2	Captorhinidae	0	0	0	0	?	0	0	0	0	0
3	Testudines	0	1	?	?	?	?	?	0	0&1	0&2
4	Araeoscelidia	0	1	0	0	0	0	0	0	0	0
5	Younginiformes	0	?	0	0	0	1	0	0	0	0
6	Kuehneosauridae	0	?	0	0	0	1	0	1	1	0
7	Rhynchocephalia	0	1	1	0	0	1	0	1	0&1	0
8	Squamata	0	1	1	0	0	1	0	1	1	0&2
9	Rhynchosauria	0	0	0	?	0	1	0	1	1	0
10	Prolacertiformes	0	1	0	0	0	1	0	0&1	1	0&2
11	Trilophosaurus	0	?	0	?	0	1	0	1	1	1&2
12	Choristodera	0	1	0	0	0	1	0	0	1	1
13	Archosauriformes	0	1	0	0	0	1	0	0&1	1	0&1&2
14	Claudiosaurus	0	1	0	0	0	1	0	0	?	0
15	Dactylosaurus	0	?	0	0	0	1	0	1	1	0
16	Serpiano-Neustico	0	?	0	0	0	1	0	1	1	0
17	Simosaurus	0	1	0	1	0	1	2	1	1	1
18	Nothosaurus	2	1	0	1	1	0	2	1	1	1
19	Ceresiosaurus	2	1	0	1	1	0	2	1	1	1
20	L. balsami	2	1	0	1	1	0	2	1	1	1
21	L. curionii	2	1	0	1	1	0	2	1	1	1
22	L. valceresii	2	1	0	1	1	0	2	1	1	1
23	Silvestrosaurus	2	1	0	1	1	0	2	1	1	1
24	Corosaurus	1	?	0	1	1	0	1	1	1	0
25	Cymatosaurus	2	1	0	1	1	0	1	1	1	1
26	Germanosaurus	?	?	0	1	1	1	1	?	?	?
27	Pistosaurus	?	?	0	1	1	0	1	1	1	1
28	Placodus	2	0	0	1	0	1	0	1	0	0

1955   *Lariosaurus,* Saint-Seine, p. 428.
1955   *Macromerosaurus,* Saint-Seine, p. 428.
1956   *Ceresiosaurus,* Huene, p. 387.
1956   *Lariosaurus,* Huene, p. 386.
1956   *Ceresiosaurus,* Romer, pp. 410, 662.
1956   *Lariosaurus,* Romer, p. 662.
1964   *Lariosaurus,* Kuhn, p. 12.
1964   *Ceresiosaurus,* Kuhn, p. 9.
1966   *Ceresiosaurus,* Romer, p. 371.
1966   *Lariosaurus,* Romer, p. 371.
1968   *Ceresiosaurus,* Müller, p. 158.
1968   *Lariosaurus,* Müller, p. 157.
1970   *Ceresiosaurus,* Schultze and Wilczewski, p. 101 *ff.*
1970   *Lariosaurus,* Schultze and Wilczewski, p. 101 *ff.*
1987   *Lariosaurus,* Kuhn-Schnyder, p. 19.
1987   *Ceresiosaurus,* Schmidt, p. 366.
1987   *Lariosaurus,* Schmidt, p. 366.
1988   *Ceresiosaurus,* Carroll, pp. 244, 245, 584, 619.
1988   *Lariosaurus,* Carroll, pp. 584, 619.
1989b   *Ceresiosaurus,* Rieppel, p. 139 *ff.*
1989b   *Lariosaurus,* Rieppel, p. 139 *ff.*

1989   *Ceresiosaurus,* Tschanz, p. 174.
1989   *Lariosaurus,* Tschanz, p. 156.
1990   *Ceresiosaurus,* Kuhn-Schnyder, p. 315.
1990   *Lariosaurus,* Kuhn-Schnyder, p. 315.
1990   *Silvestrosaurus,* Kuhn-Schnyder, p. 315.
1991   *Ceresiosaurus,* Storrs, p. 134.
1991   *Macromerosaurus,* Storrs, p. 136.
1991   *Macromirosaurus,* Storrs, p. 136.
1991   *Lariosaurus,* Storrs, p. 136.
1991   *Silvestrosaurus,* Storrs, p. 139.
1993   *Ceresiosaurus,* Storrs, p. 179 *ff.*
1993   *Lariosaurus,* Storrs, p. 179 *ff.*
1993   *Silvestrosaurus,* Storrs, p. 179 *ff.*
1993   *Silvestrosaurus,* Renesto, p. 208.
1993b   *Ceresiosaurus,* Rieppel, p. 135.
1993b   *Lariosaurus,* Rieppel, p. 135.
1994a   *Lariosaurus,* Rieppel, p. 347.

TYPE SPECIES—*Lariosaurus balsami* Curioni, 1847, from the upper Ladinian, Middle Triassic, northern Italy.

DEFINITION—A monophyletic taxon including

TABLE 3. *Extended.*

	7	6 1	6 2	6 3	6 4	6 5	6 6	6 7	6 8	6 9	7 0
1	Ancestor	0	0	0	0	0	0	0	0	0	0
2	Captorhinidae	0	0	0	0	?	0	0	0	0	0
3	Testudines	1	0 & 1	1	0	0	0	0	0	0	0
4	Araeoscelidia	0	0	1	0	?	0	0	0	0	0
5	Younginiformes	0	0	1	0	0	0	0	0	0	0
6	Kuehneosauridae	1	1	1	0	?	1	0	0	0	1
7	Rhynchocephalia	0 & 1	0	1	1	0	0	0	0	0	0
8	Squamata	1	0	1	0 & 1	0	0	0	0	0	0 & 1
9	Rhynchosauria	0	0	1	0	?	0	0	0	0	0 & 1
1 0	Prolacertiformes	0 & 1	0 & 1	1	0	?	0	0	0	0	0
1 1	Trilophosaurus	0	0	1	0	?	0	?	0	0	0
1 2	Choristodera	1	0	1	0	1	0	0	0	0	0
1 3	Archosauriformes	0 & 1	0 & 1	1	0	0	1	0	0	0	0 & 1
1 4	Claudiosaurus	0	0	1	0	?	0	0	0	0	0
1 5	Dactylosaurus	1	1	1	1	1	0	1	0	1	0
1 6	Serpiano-Neustico	1	1	1	1	1	0	1	0	1	0
1 7	Simosaurus	1	1	1	1	1	0	0	0	0	1
1 8	Nothosaurus	1	1	1	1	1	0	1	0	0 & 1	0
1 9	Ceresiosaurus	1	1	1	1	1	0	1	0	1	0
2 0	L. balsami	1	1	1	1	1	0	1	0	1	0
2 1	L. curionii	1	1	1	1	1	0	1	0	1	?
2 2	L. valceresii	1	1	1	1	1	0	1	0	1	0
2 3	Silvestrosaurus	1	1	1	1	1	0	1	0	1	0
2 4	Corosaurus	1	1	1	0	1	0	0	1	0	1
2 5	Cymatosaurus	1	1	?	1	1	0	0	0	?	?
2 6	Germanosaurus	?	?	?	?	?	?	?	?	?	?
2 7	Pistosaurus	?	?	?	1	1	0	0	1	0	?
2 8	Placodus	1	1	1	0	0	1	0	0	0	1

the species *balsami, buzzii, calcagnii, curionii,* and *valceresii.*

DIAGNOSIS—Small to large nothosaurs; zyg-apophyseal pachyostosis present; four or more sacral ribs; interclavicle of rhomboidal (triangular) shape without any trace of a posterior stem; dorsal wing of ilium reduced to stout process; obturator foramen open in adult; ulna broadened at middiaphysis; radius somewhat shorter than ulna; hyperphalangy present in manus.

DISTRIBUTION—Uppermost Anisian and Ladinian; southern and western Europe.

COMMENTS—Curioni (1847) published a plate showing the mirror image of a specimen he described under the name *Macromirosaurus Plini* (p. 161). Later in the text (Curioni, 1847, p. 166), he introduced the name *Lariosaurus balsami* to refer to the "rettile della famiglia dei Paleosauri" described and figured, but not named, by Balsamo-Crivelli (1839). Baur (1886), Deecke (1886), and Lydekker (1889) list *Macromirosaurus (Macromerosaurus)* as a valid taxon. Zittel (1887) considered *Macromirosaurus plinii* a juvenile of *Lariosaurus balsami,* a view accepted by Boulenger

(1898), and most subsequent workers (e.g., Arthaber, 1924). Peyer (1933–1934) reviewed in detail the controversy surrounding these taxon names (see also Rieppel, 1987), and concluded that *Lariosaurus* must have priority over *Macromirosaurus (Macromerosaurus)* because the latter species was described in 1847, whereas the first genus name refers to a specimen already described and figured in 1839 (for a similar view, see Storrs, 1991).

An isolated sacrum came from the Partnachschichten (Ladinian) of the Gailtaler Alps (Austria) and was described as *Proneusticosaurus carinthiacus* by Arthaber (1924, p. 509), but was referred to *Lariosaurus* by Zapfe and König (1980).

Broili (1927) described a complete sauropterygian skeleton from the Arlbergschichten (Ladinian) of Vorarlberg (Austria) as *Rhäticonia rothpletzi.* The holotype and only known specimen can no longer be located today (destroyed in World War II, P. Wellnhofer, personal communication). Peyer (1933–1934) considered the taxonomic affinities of *Rhaeticonia* unresolved, but to judge from the illustration of the specimen (Broili,

TABLE 3. *Extended.*

	8	71	72	73	74	75	76	77	78	79	80
1	Ancestor	0	0	0	0	0	0	0	0	0	0
2	Captorhinidae	0	0	0	0	0	?	0	0	0	0
3	Testudines	0	0	0	0	0	1	0	0	0	0
4	Araeoscelidia	0	0	0	0	0	0	0	0	0	0
5	Younginiformes	0	0	0	0	0&1	0&1	1	0	0	0
6	Kuehneosauridae	?	0	0	0	1	?	?	?	?	?
7	Rhynchocephalia	0	0	0	0	1	1	1	0	0	0
8	Squamata	0	0	0	0	1	1	0&1	0	0	0
9	Rhynchosauria	0	0	0	0	0	1	1	0	0	0
10	Prolacertiformes	1	0	0	0	1	1	1	0	0	0
11	Trilophosaurus	1	0	0	0	?	1	1	0	0	0
12	Choristodera	1	0	1	0	0	1	1	1	0	0
13	Archosauriformes	1	0	0&2	0	0&1	1	1	0	0	0
14	Claudiosaurus	1	0	0	0	1	1	1	0	0	0
15	Dactylosaurus	1	0	1	1	0	1	0	1	1	1
16	Serpiano-Neustico	1	1	1	1	0	1	0	1	1	0
17	Simosaurus	1	0	1	0	0	1	0	1	1	1
18	Nothosaurus	1	0&1	1	1	0&1	1	0&1	1	1	1
19	Ceresiosaurus	1	0	2	1	0	1	1	1	0	1
20	L. balsami	1	0&1	2	1	0	1	0	1	1	1
21	L. curionii	1	1	?	?	?	1	0	1	1	1
22	L. valceresii	1	0	2	1	0	1	?	1	?	?
23	Silvestrosaurus	1	0	?	1	0	1	1	1	0	0
24	Corosaurus	1	0	1	0	1	1	1	1	0	1
25	Cymatosaurus	?	0	?	?	0	1	?	?	?	?
26	Germanosaurus	?	?	?	?	?	1	?	?	?	?
27	Pistosaurus	1	0	?	?	?	1	?	?	?	?
28	Placodus	1	0	1	0	0	1	1	1	0	0

1927, Pl. 1), *Rhaeticonia* is another probable junior synonym of *Lariosaurus*.

Boulenger (1891, pp. 292–293) erroneously described an isolated left foot of *Lariosaurus balsami* from Esino close to Perledo, first described by Curioni (1863, Pl. 7, Fig. 1), as a new taxon, *Eupodosaurus longobardicus*. In correcting his error, Boulenger (1891, p. 407) referred to the cast of *Lariosaurus* from the same area and deposits kept at the College of Surgeons, London. The cast he mentioned must be a specimen that Owen (1854, p. 68) referred to under the name of *Deirosaurus italicus*, which here is treated as a junior synonym of *Lariosaurus balsami*.

Lariosaurus balsami Curioni, 1847

1847   *Lariosaurus balsami*, Curioni, p. 161.
1854   *Deirosaurus italicus*, Owen, p. 68.
1863   *Lariosaurus Balsami*, Curioni, p. 266.
1886   *Macromerosaurus Plini*, Baur, p. 247.
1886   *Lariosaurus balsami*, Bassani, p. 22.

1886   *Macromerosaurus Plinii*, Bassani, p. 22.
1886   *Lariosaurus balsami*, Deecke, p. 171 *ff*.
1886   *Macromerosaurus Plinii*, Deecke, p. 171 *ff*.
1887   *Lariosaurus balsami*, Zittel, p. 485, Figs. 461–462.
1889   *Lariosaurus balsami*, Lydekker, p. 284.
1889   *Macromerosaurus plinii*, Lydekker, p. 284.
1891   *Eupodosaurus longobardicus*, Boulenger, p. 293.
1891   *Lariosaurus balsami*, Boulenger, p. 407.
1898   *Lariosaurus balsami*, Boulenger, p. 1 *ff*., Pl. 1.
1898   *Macromerosaurus plinii*, Boulenger, p. 1.
1899   *Lariosaurus balsami*, Schrammen, Pl. 25, Fig. 13.
1923   *Lariosaurus balsami*, Mariani, p. 218 *ff*., Fig. 1.
1924   *Lariosaurus balsami*, Arthaber, Figs. 23–29.

TABLE 3. *Extended.*

9	81	82	83	84	85	86	87	88	89	90
1 Ancestor	0	0	0	0	0	0	0	0	0	0
2 Captorhinidae	0	0	?	0	?	0	1	0	0	0
3 Testudines	0	1	0	0	?	?	0	0	1	0
4 Araeoscelidia	0	1	0	0	?	0	1	0	0	0
5 Younginiformes	0	0 & 1	0	0	?	1	0	0	0	0
6 Kuehneosauridae	?	?	?	1	?	1	0	0	0	0
7 Rhynchocephalia	0	1	0	0	?	1	0	0	0	0
8 Squamata	0	1	0 & 1	0	?	1	0	0	0	0
9 Rhynchosauria	0	1	0	0	?	1	0	0	0 & 1	0
10 Prolacertiformes	0	0	?	0	?	1	0	0	0	0
11 Trilophosaurus	0	1	0	0	?	1	0	0	0	0
12 Choristodera	0	1	0	0	?	1	0	0	0	0
13 Archosauriformes	0	1	0	0	?	1	0	0	0 & 1	0
14 Claudiosaurus	0	1	0	0	?	1	0	0	0	0
15 Dactylosaurus	1	?	?	1	0	1	0	2	1	1
16 Serpiano-Neustico	1	0 & 1	2	1	0	1	0	2	1	1
17 Simosaurus	1	1	1	1	0	1	0	2	1	1
18 Nothosaurus	1	0 & 1	2	1	0	1	0	2	1	1
19 Ceresiosaurus	1	0	2	1	0	1	0	2	1	1
20 L. balsami	1	0	2	1	0	1	0	2	1	1
21 L. curionii	1	0	2	1	0	1	0	2	1	1
22 L. valceresii	1	?	?	1	0	1	0	2	1	1
23 Silvestrosaurus	1	?	?	1	0	1	0	2	1	1
24 Corosaurus	1	1	1	1	1	1	0	1	1	1
25 Cymatosaurus	?	?	?	?	?	?	0	?	?	?
26 Germanosaurus	?	?	?	?	?	?	0	?	?	?
27 Pistosaurus	?	?	?	1	1	1	0	3	?	?
28 Placodus	1	1	1	0	?	1	0	0	1	1

1924 *Proneusticosaurus carinthiacus,* Arthaber, p. 509, Figs. 34–35.

1927 *Lariosaurus balsami,* Broili, p. 215, Fig. 5.

1927 *Macromerosaurus Plinii,* Broili, p. 215, Fig. 2.

1928a *Proneusticosaurus carinthiacus,* Nopcsa, p. 32.

1933–34 *Lariosaurus balsami,* Peyer, p. 121, Figs. 1, 3–14; Pls. 31; 32; 33, Figs. 1, 3; 34–37; 38, Figs. 1, 1a; 40; 41, Fig. 3.

1933–34 *Lariosaurus balsami* var. *plinii,* Peyer, p. 121 *f.,* Fig. 2; Pl. 41, Fig. 1.

1934 *Lariosaurus balsami,* Kuhn, p. 46.

1934 *Lariosaurus balsami* var. *plinii,* Kuhn, p. 46.

1956 *Lariosaurus balsami,* Huene, p. 386.

1959 *Lariosaurus balsami,* Kuhn-Schnyder, p. 655.

1964 *Lariosaurus balsami,* Kuhn, p. 12.

1974 *Lariosaurus balsami,* Kuhn-Schnyder, p. 65, Fig. 42.

1976 *Lariosaurus balsami,* Sanz, pp. 547 *ff.,* Figs. 1–6, 10.

1980 *Lariosaurus* cf. *balsami,* Zapfe and König, p. 72.

1980 "*Proneusticosaurus carinthiacus,*" Zapfe and König, p. 78, Pl. 1, Fig. 1; Pl. 2, Fig. 3.

1983a *Lariosaurus balsami,* Sanz, p. 205 *ff.,* Pls. 2, 3A, C, 4, 5A.

1984 *Lariosaurus balsami,* Ticli, p. 69 *ff.,* Figs. 1–3.

1984 *Lariosaurus* cf. *balsami,* Warch, p. 81 *f.*

1987 *Lariosaurus balsami,* Kuhn-Schnyder, p. 19, Figs. 10–11.

1989b *Macromirosaurus Plini,* Rieppel, p. 140.

1990 *Lariosaurus balsami,* Kuhn-Schnyder, p. 315.

1989 *Lariosaurus balsami,* Tschanz, p. 157.

1991 *Lariosaurus balsami,* Pinna and Teruzzi, p. 32, figure on p. 33.

TABLE 3. *Extended.*

	10	9 1	9 2	9 3	9 4	9 5	9 6	9 7	9 8	9 9	100
1	Ancestor	0	0	0	0	0	0	0	0	0	0
2	Captorhinidae	0	0	0	0	0	0	0	0	0	0
3	Testudines	0	0	0	0	0&1	0&2	1	0	1&2	0
4	Araeoscelidia	1	0	0	0	0	0	0	0	0	0
5	Younginiformes	1	0	0	0	0	0&2	0	0&1	0	0
6	Kuehneosauridae	1	0	0	0	0	2	1	2	0	0
7	Rhynchocephalia	1	0	0	0	0	2	0	0	0	0
8	Squamata	1	0	0	0	0	0&2	1	0	0	0
9	Rhynchosauria	1	0	0	0	0	0	1	0	0	0
1 0	Prolacertiformes	1	0	0	0	0	0	1	1&2	0	0
1 1	Trilophosaurus	1	0	0	?	0	0	1	0	0	0
1 2	Choristodera	1	0	0	0	0	0&2	1	2	0	0
1 3	Archosauriformes	1	0	0	0	0&1	0	1	0	0	0
1 4	Claudiosaurus	0	0	1	1	1	1	0	0	0	0
1 5	Dactylosaurus	0	1	0	1	0	0	0	1	3	0
1 6	Serpiano-Neustico	0	1	0	1	0&1	0&1	0	1&2	3	0&1
1 7	Simosaurus	0	1	0	1	1	1	1	2	2	1
1 8	Nothosaurus	0	1	0&1	0&1	1	0&1	0	2	2	1
1 9	Ceresiosaurus	0	1	1	1	1	1	0	?	3	1
2 0	L. balsami	0	1	1	1	1	1	0&1	0&2	3	0
2 1	L. curionii	0	1	1	1	1	1	0	0	?	?
2 2	L. valceresii	0	1	0	1	1	0	0	0	3	0
2 3	Silvestrosaurus	0	1	0	1	1	1	1	1	3	0
2 4	Corosaurus	0	1	1	1	1	0	0	2	1	0
2 5	Cymatosaurus	0	0	0	0	0	0	0	?	?	0
2 6	Germanosaurus	?	?	?	?	?	?	?	?	?	?
2 7	Pistosaurus	0	1	?	1	1	1	1	2	0	?
2 8	Placodus	0	1	1	1	1	0	1	2	1	0

1993 *Lariosaurus balsami,* Sanz et al., p. 157 f., Figs. 8–13.

1993 *Lariosaurus balsami,* Renesto, p. 199 ff., Fig. 4A.

1994a *Lariosaurus balsami,* Rieppel, p. 347, Figs. 2–3.

HOLOTYPE—A large specimen from Perledo represented by the cervical and anterior dorsal region with parts of the forelimbs preserved was first described by Balsamo-Crivelli (1839) and named by Curioni (1847). The specimen was destroyed during World War II. A cast is preserved at the Museo Civico di Storia Naturale, Milano. Kuhn-Schnyder (1987) designated a complete specimen from Perledo (Bayerische Staatssammlung für Paläontologie und Historische Geologie, BSP AS I 802) as neotype.

LOCUS TYPICUS—Calcare di Perledo, Perledo-Varenna Formation, upper Ladinian, Perledo above Varenna, Lake Como, northern Italy.

DIAGNOSIS—A medium-sized species of *Lariosaurus* with a temporal fenestra typically between 1.4 and 1.8 times the size of the orbit; marked parietal constriction behind pineal foramen; humerus distinctly curved, with reduced deltopectoral crest; up to six carpal and four tarsal ossifications in the adult; hyperphalangy in manus only.

DISTRIBUTION—Middle Triassic (middle to upper Ladinian), southern and western Europe.

COMMENTS—*Lariosaurus lavizzarii* Kuhn-Schnyder, 1987 (referred to *Lariosaurus balsami* in Kuhn-Schnyder, 1974, p. 65), is based on a juvenile specimen and was treated as a subjective junior synonym of *Lariosaurus balsami* by Tschanz (1989, p. 157). As a juvenile, the specimen is not diagnostic (see also Renesto, 1993), and *Lariosaurus lavizzarii* is therefore here considered a *nomen dubium.* Similarly, the juvenile specimen described by Renesto (1993) is not diagnostic and cannot be referred to any species of *Lariosaurus* with certainty. As noted by Renesto (1993), both these juvenile specimens were collected in equivalent deposits (Kalkschieferzone) and in close geographic proximity. The Kalkschieferzone has otherwise yielded the holotype of *Lariosaurus valceresii,* and it must remain questionable whether these juvenile specimens are

TABLE 3. Extended.

11		101	102	103	104	105	106	107	108	109	110
1	Ancestor	0	0	0	0	0	0	0	0	0	0
2	Captorhinidae	0	0	0	0	0	0	0	0	0	0
3	Testudines	0	1	0	0	0	0	1	1	1	0
4	Araeoscelidia	0	0	0	0	0	0	0	0	0	0
5	Younginiformes	0	0	1	1	0	1	0	1	0	0
6	Kuehneosauridae	0	1	1	1	0	1	0	1	?	0
7	Rhynchocephalia	0	1	1	1	0	1	0	1	1	0
8	Squamata	0	1	1	1	0	1	0	1	1	0
9	Rhynchosauria	0	0	1	1	0	1	0	1	1	0
10	Prolacertiformes	0	0&1	1	1	0	1	0	1	0	0
11	Trilophosaurus	0	0	1	1	0	1	0	1	0	0
12	Choristodera	0	0	1	1	0	1	1	1	?	0
13	Archosauriformes	0	0	1	1	0	1&2	0&1	1	0	0
14	Claudiosaurus	0	0	1	1	0	1	1	1	0	0
15	Dactylosaurus	0	1	1	?	1	?	?	?	?	0
16	Serpiano-Neustico	0&1	1	1	1	1	2	1	1	1	1
17	Simosaurus	0	1	1	1	1	2	1	1	1	1
18	Nothosaurus	0	1	1	1	1	2	1	1	1	1
19	Ceresiosaurus	1	1	1	1	1	2	1	1	1	1
20	L. balsami	1	1	1	1	1	2	1	1	1	1
21	L. curionii	?	?	?	?	?	?	?	?	?	?
22	L. valceresii	?	1	1	1	1	2	1	1	1	1
23	Silvestrosaurus	1	1	1	1	1	2	1	1	1	?
24	Corosaurus	1	1	1	1	0	1	1	1	1	1
25	Cymatosaurus	1	1	1	1	0	1	1	1	?	?
26	Germanosaurus	?	?	?	?	?	?	?	?	?	?
27	Pistosaurus	?	?	?	1	1	?	?	?	?	?
28	Placodus	0	1	1	1	0	1	1	1	1	0

to be referred to the latter species or to *Lariosaurus balsami* (see Renesto, 1993, for further comments).

Although distinct, the genotypical species *Lariosaurus balsami* unfortunately is the only one of all lariosaur species that lacks uniquely derived autapomorphies, and it may thus be considered a metaspecies (Archibald, 1994). This may be the reason why all other specimens of *Lariosaurus* deposited in public repositories (see Appendix II), except for the holotypes of *L. buzzii,* specimen PVHR 1, of *L. valceresii,* and of the specimens referred to *L. calcagnii,* have to be referred to this species. *Lariosaurus balsami* correspondingly seems to be the most abundant and the most geographically widespread species of its genus. Interestingly, a congruent pattern is observed in the *Serpianosaurus–Neusticosaurus* clade of pachypleurosaurs from the Alpine Triassic (Ladinian), within which *Neusticosaurus pusillus* is the most abundant and geographically most widespread of five (perhaps six) diagnosable species. Nevertheless, some doubt persist as to whether this large assemblage of specimens referred to *Lariosaurus*

balsami might not, in fact, represent two or more separate species. However, as discussed above, there is no morphological feature known to substantiate such supposition other than the absolute number of carpal (and tarsal) ossifications (see also Peyer, 1933–1934).

Among the specimens from the Ladinian of northern Italy, the number of carpal (and tarsal) ossifications varies in a pattern that suggests only a very poor correlation of overall size and degree of ossification. This contrasts with observations of both extant (e.g., Rieppel, 1992) and other fossil (Caldwell, 1994, 1996) taxa, where a good correlation of the number of carpal (and tarsal) ossifications with absolute body size is usually observed. Using these observations as a basis for the a priori assumption that a strict control of the degree of ossification in relation to individual age (and overall size) also existed in lariosaurs, it would seem possible to distinguish two species, one with six, the other with only three carpal ossifications. Such a conclusion leaves most of the relatively small specimens indistinct with respect to their specific status, neglects the alternative hy-

TABLE 3. *Extended.*

12		111	112	113	114	115	116	117	118	119	120
1	Ancestor	0	0	0	0	0	0	0	0	0	0
2	Captorhinidae	0	0	0	0	0	0	0	0	0	0
3	Testudines	0	0	0 & 1	1	0	1	1	0	?	0
4	Araeoscelidia	0	1	0	0	0	0	0	1	0	0
5	Younginiformes	0	1	0	0	0	1	0	1	0	0
6	Kuehneosauridae	?	?	?	?	?	?	?	?	?	0
7	Rhynchocephalia	0	1	0 & 1	1	0	1	1	1	0	0
8	Squamata	0	1	1	1	0	1	1	1	?	0
9	Rhynchosauria	1	1	0	1	0	1	1	?	0	0
10	Prolacertiformes	0 & 1	1	0 & 1	1	0	1	0 & 1	1	0	0
11	Trilophosaurus	1	1	0	1	0	1	1	?	?	0
12	Choristodera	1	1	0	1	0	1	1	?	?	0
13	Archosauriformes	1	1	0 & 1	1	0	1	1	1	0	0
14	Claudiosaurus	0	1	0	0	0	0	0	?	0	0
15	Dactylosaurus	?	?	?	?	?	?	?	0	0	0
16	Serpiano-Neustico	0	0	1	1	2	0	0	0	0	0
17	Simosaurus	0	0	1	1	1	0	0	0	1	0
18	Nothosaurus	0	0	1	1	1	0	0	0	1	0
19	Ceresiosaurus	0	0	1	1	1	0	0	0	0	1
20	L. balsami	0	0	1	1	0	0	0	0	0	1
21	L. curionii	?	?	?	?	?	?	?	0	?	1
22	L. valceresii	0	0	1	1	1	0	0	0	0	1
23	Silvestrosaurus	0	0	?	?	?	?	?	0	0	1
24	Corosaurus	0	0	1	1	1	?	?	0	1	0
25	Cymatosaurus	?	?	?	?	?	?	?	0	0	0
26	Germanosaurus	?	?	?	?	?	?	?	0	?	0
27	Pistosaurus	?	?	?	?	?	?	?	0	?	0
28	Placodus	0	0	1	1	2	0	0	0	0	0

pothesis of possible sexual dimorphism (no sexual dimorphism is expressed by humerus proportions in *Lariosaurus,* in contrast to pachypleurosaurs), and creates the difficulty of explaining, in ecological terms, how two separate species of very similar morphology and adult body size coexisted in restricted habitats as are, for example, represented by the deposits at Perledo.

The peculiar preservation of the fossils from Montral–Alcover renders it impossible to study the skeletal anatomy of lariosaurs from that locality in detail. Their general anatomy allows their identification as *Lariosaurus balsami* (Sanz, 1983b), but in view of their occurrence in a separate locality and facies, the possibility still remains that these specimens, like the one from the eastern Pyrenees, represent a separate species.

Lariosaurus buzzii Tschanz, 1989

1989   *Lariosaurus buzzii,* Tschanz, p. 157, Figs. 1–8.
1990   *Silvestrosaurus buzzii,* Kuhn-Schnyder, p. 313 *ff.*

1990   *Silvestrosaurus buzzii,* Tintori and Renesto, p. 310 *ff.*
1991   *Lariosaurus buzzii,* Storrs, p. 139.
1993   *"Lariosaurus" buzzii,* Storrs, p. 179, Fig. 1.
1993   *Lariosaurus buzzii,* Renesto, p. 208.
1993b   *Lariosaurus buzzii,* Rieppel, p. 135.

HOLOTYPE—Disarticulated skeleton kept at the Paläontologisches Institut und Museum der Universität Zürich (PMZ T 2804).

LOCUS TYPICUS—Grenzbitumenzone (Anisian–Ladinian boundary), Point 902, Monte San Giorgio, Switzerland.

DIAGNOSIS—A small species of *Lariosaurus* with an upper temporal fossa equal in size to the orbit; nasals fused; parietal broad, not distinctly constricted behind the pineal foramen; anterolateral corner of clavicle reduced; entepicondylar foramen absent; radius slightly longer than ulna; pachyostosis absent.

DISTRIBUTION—Middle Triassic (Anisian–Ladinian boundary), southern Europe.

COMMENTS—This species is known from the

TABLE 3. *Extended.*

		13	121	122
1	Ancestor	0	0	
2	Captorhinidae	0	0	
3	Testudines	0	0	
4	Araeoscelidia	0	0	
5	Younginiformes	0	0	
6	Kuehneosauridae	0	0	
7	Rhynchocephalia	0	0	
8	Squamata	0	0	
9	Rhynchosauria	0	0	
1 0	Prolacertiformes	0	0	
1 1	Trilophosaurus	0	0	
1 2	Choristodera	0	0	
1 3	Archosauriformes	0	0	
1 4	Claudiosaurus	0	0	
1 5	Dactylosaurus	0	0	
1 6	Serpiano-Neustico	0	0	
1 7	Simosaurus	1	0	
1 8	Nothosaurus	1	0	
1 9	Ceresiosaurus	0	1	
2 0	L. balsami	1	1	
2 1	L. curionii	1	?	
2 2	L. valceresii	1	?	
2 3	Silvestrosaurus	?	?	
2 4	Corosaurus	?	?	
2 5	Cymatosaurus	?	?	
2 6	Germanosaurus	?	?	
2 7	Pistosaurus	?	?	
2 8	Placodus	?	0	

holotype only. The species is unequivocally diagnosed by uniquely derived autapomorphies such as the relatively small upper temporal fossa, the broad parietal skull table, and the fused nasals.

Lariosaurus curionii n. sp.

1985   *Lariosaurus balsami,* Mazin, p. 168, Figs. 1–8.

HOLOTYPE—Skull and partial postcranial skeleton, kept at the Université Paris VI, Laboratoire de Paléontologie et de Paléoanthropologie, Paris (PVHR 1, original of Mazin, 1985).

LOCUS TYPICUS—Middle Triassic (probably Ladinian), Amélie-les-Bains, eastern Pyrenees, France.

DIAGNOSIS—A medium-sized species of *Lariosaurus* with no rostral constriction; postfrontal small, excluded from the upper temporal fossa by a contact of the parietal with the postorbital; jugal absent; marked parietal constriction behind pineal

foramen; dorsal ribs pachyostotic; deltopectoral crest reduced.

DISTRIBUTION—Middle Triassic (Ladinian), southern Europe.

COMMENTS—This species is known from the holotype only. The species is unequivocally diagnosed by uniquely derived autapomorphies such as the absence of the rostral constriction and the exclusion of the postfrontal from the upper temporal fossa.

Lariosaurus calcagnii (Peyer), 1931

1931   *Ceresiosaurus calcagnii,* Peyer, p. 3 *ff.*; Figs. 1–16, 18–22, 29.2, 30–31; Pls. 18–24.
1934   *Ceresiosaurus calcagnii,* Kuhn, p. 50.
1949   *Ceresiosaurus calcagnii,* E. v. Huene, p. 118, Figs. 14–16, 18.
1955   *Ceresiosaurus calcagnii,* Saint-Seine, Figs. 1, 7–8.
1956   *Ceresiosaurus calcagnii,* F. v. Huene, p. 387, Fig. 425.
1964   *Ceresiosaurus calcagnii,* Kuhn, p. 9.
1968   *Ceresiosaurus calcagnii,* Müller, Figs. 190–191.
1974   *Ceresiosaurus calcagnii,* Kuhn-Schnyder, p. 62, Figs. 39–40.

HOLOTYPE—Complete skeleton, specimen A of Peyer (1931), kept at the Paläontologisches Institut und Museum der Universität Zürich.

LOCUS TYPICUS—Lower Meridekalke (lower Ladinian), Acqua del Ghiffo near Serpiano, Monte San Giorgio, Switzerland.

DIAGNOSIS—A large species of *Lariosaurus* with the pineal foramen displaced to the posterior extremity of parietal skull table; front limbs much larger than hind limbs in the adult; humerus not constricted in middiaphyseal region in adult; deltopectoral crest reduced; ulna without distinctly broadened proximal head; pubis with slightly concave ventral margin; hyperphalangy in pes; height of neural spines increased in anterior caudal region.

DISTRIBUTION—Middle Triassic (Ladinian), southern Europe.

COMMENTS—Since Peyer's (1931) monograph, additional specimens of *Lariosaurus calcagnii* have been collected (Kuhn-Schnyder, 1974) that document ontogenetic variation and sexual dimorphism, if not taxic diversity. Unfortunately, this material remains inaccessible for study. The

diagnosis for *L. calcagnii* given above is likely to change once this new material is described in detail. Nevertheless, the species is unequivocally diagnosed by uniquely derived autapomorphies such as the hyperphalangy in the pes and the heightened neural spines in the proximal caudal region.

Lariosaurus valceresii Tintori and Renesto, 1990

1990   *Lariosaurus valceresii,* Tintori and Renesto, p. 314, Figs. 1–7, Pl. 1–2.
1993   *Lariosaurus valceresii,* Renesto, p. 205 *ff.,* Fig. 4B.

HOLOTYPE—Complete skeleton, kept at the Museo Civico di Szienze Naturali di Induno Olona (P 500).

LOCUS TYPICUS—Kalkschieferzone, upper Meridekalke (upper Ladinian), Cà del Frate near Viggiù, Varese, northern Italy.

DIAGNOSIS—A medium-sized species of *Lariosaurus* with an upper temporal fossa twice the size of the orbit; forelimbs somewhat longer than hind limbs; ectepicondylar groove open and distinctly notched; rib pachyostosis absent. Possible hyperphalangy in pes.

DISTRIBUTION—Middle Triassic (upper Ladinian), southern Europe.

COMMENTS—This species is known from the holotype only. The species is unequivocally diagnosed by uniquely derived autapomorphies such as the relatively large upper temporal fossa and the notched ectepicondylar groove.

Evolution and Paleobiogeography of the Genus *Lariosaurus*

The Nothosauridae is a well-corroborated clade within the Sauropterygia (Eosauropterygia) which, on the basis of present knowledge, is restricted to the shallow, warm-water epicontinental seas of the western Pacific (China: Young, 1959, 1960, 1965, 1978) and western Tethyan (Europe and Middle East: Rieppel, 1997; Rieppel & Wild, 1996; Brotzen, 1957) Province. An earlier analysis of the stratigraphic and geographic distribution of Eosauropterygia in the Germanic Triassic indicated that the Muschelkalk sauropterygians reached the Germanic basin with a marine trans-gression at the time of transition from the upper Buntsandstein (Röt [so_2], Scythian) to the lower Muschelkalk (mu_1, Anisian) through an eastern gateway (Rieppel & Hagdorn, 1996; Rieppel, 1997; Fig. 21). This scenario will be tested by the projected review of the Chinese nothosaurs.

The earliest appearance of the Nothosauridae in the Germanic Triassic coincides with the occurrence of *Germanosaurus* (Arthaber, 1924) and *Nothosaurus* (Kunisch, 1888) in the lower Gogolin layers of the lowermost Muschelkalk of Upper Silesia. *Germanosaurus* is known from an isolated occurrence (skull only: Rieppel, 1997). *Nothosaurus* remains are fragmentary and rare in the basal lower Muschelkalk of the eastern part of the Germanic basin. More abundant and better preserved *Nothosaurus* material (undescribed; kept in private collections: Oosterink, 1986; Oosterink & Diepenbroek, 1990) is known from the basal lower Muschelkalk of the western part of the Germanic basin. In the eastern Muschelkalk basin, the abundance of *Nothosaurus* picks up in the late lower Muschelkalk and basal middle Muschelkalk, with the appearance of *Nothosaurus marchicus* and an incompletely known, larger species (Rieppel & Wild, 1996). The genus *Nothosaurus* persists throughout the Germanic Muschelkalk (the Anisian–Ladinian boundary corresponds to the boundary between lower [mo_1] and middle [mo_2] upper Muschelkalk), and into the Keuper up to the Gipskeuper, i.e., into the uppermost Ladinian (Rieppel & Wild, 1994). Taxonomic diversification of the genus *Nothosaurus* starts to increase with the upper Muschelkalk (Rieppel & Wild, 1996). In spite of abundant material, no sauropterygian remains diagnostic for the genus *Lariosaurus* are known from the entire Muschelkalk.

Sauropterygians are exceedingly rare in the Anisian of the Alpine Triassic. Singular occurrences are *Cymatosaurus* in the lower Anisian of the northern Alpine facies (Rieppel, 1995b), as well as scarce pachypleurosaur remains plus a vertebra probably referable to *Cymatosaurus* from the lower Anisian of the southern Alpine facies (Rieppel & Hagdorn, 1997). A partial and rather poorly preserved *Nothosaurus* skeleton from the lower S-charl-Formation of the (eastern) Alpine facies (transition from Anisian to Ladinian: Furrer et al., 1992) may be referred to *Nothosaurus marchicus* on the basis of skull proportions. The invasion of the (southern) Alpine facies by the genus *Nothosaurus* at the time of the Anisian–Ladinian boundary (Rieppel & Hagdorn, 1997) is further documented by the occurrence of *Nothosaurus gigan-*
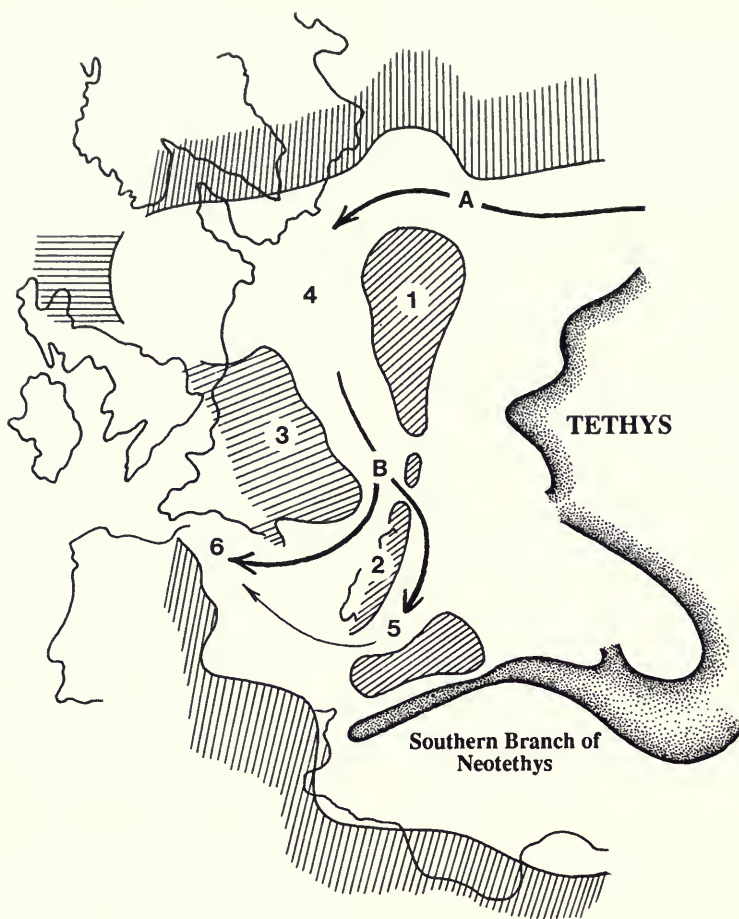
FIG. 21. Paleogeography of the genera *Nothosaurus* and *Lariosaurus*. **A,** Entry of Sauropterygia into the Germanic basin through the East Carpathian Gate and/or Silesian–Moravian Gate during the basal Anisian. **B,** Exit of Sauropterygia from the Germanic basin through the Burgundy Gate at the Anisian–Ladinian boundary to reach the southern Alpine platform and the Spanish Muschelkalk basin. **1,** Bohemian Massif; **2,** Vindelician Ridge; **3,** Central Massif; **4,** Germanic (Muschelkalk) basin; **5,** Southern Alpine platform; **6,** Spanish (Muschelkalk) basin. Paleoreconstructions are those of Marcoux et al. (1993).

teus (senior synonym for *Paranothosaurus amsleri* Peyer, 1939; see Rieppel & Wild, 1996, for further discussion) and other nothosaur remains (currently not available for study) in the Grenzbitumenzone of Monte San Giorgio. Although *Nothosaurus* successfully invaded the Alpine intraplatform basin facies (Fig. 21), as documented by isolated records from the middle Ladinian Prosanto Formation (Bürgin et al., 1991) or from the Ladinian of the Province Udine, Italy (Dalla Vecchia, 1993), it remains a very rare faunal component in an otherwise abundant fossil record (Furrer, 1995).

The Grenzbitumenzone of Monte San Giorgio (Anisian–Ladinian boundary) yielded the first record of *Lariosaurus* (*Lariosaurus buzzii* Tschanz,

1989), sister group of the genus *Nothosaurus*. Somewhat later, in the lower Ladinian Meridekalke (Furrer, 1995), *Lariosaurus calcagnii* makes its first appearance. *Lariosaurus* becomes abundant in the middle and upper Ladinian deposits of the Alpine facies. The type locality for *Lariosaurus balsami* is the Calcare di Perledo, Perledo-Varenna Formation, of the upper Ladinian of the southern Alps. The type locality for *Lariosaurus valceresii* is the Kalkschieferzone of Cà del Frate near Viggiù, northern Italy, again in the upper Ladinian of the southern Alps. The type locality for *Lariosaurus curionii* n. sp. is the Middle Triassic (Ladinian) of Amélie-les-Bains in the eastern Pyrenees. Other middle to upper Ladinian occurrences of *Lariosaurus* (in the northern Alpine

facies, and in the Spanish Muschelkalk) are summarized above. The stratigraphic and geographic distribution of the genus suggests that *Lariosaurus* originated in the Alpine Triassic sometime around the Anisian–Ladinian boundary, i.e., at a time when its sister group, the genus *Nothosaurus,* had invaded the Alpine realm. The slightly later appearance of lariosaurs in the Ladinian of the Spanish Muschelkalk and in the eastern Pyrenees corresponds to the marine reptile speciation and migration scenario reconstructed by Rieppel and Hagdorn (1997): From early Ladinian times onward, the southern Alpine realm was differentiated into a patchy facies pattern of deeper basins, carbonate platforms, and intraplatform basins. From this speciation center situated offshore from the main passages to both the Germanic and Spanish Muschelkalk, sauropterygians may have spread over the western Tethys and Peritethys domain during the Ladinian as long as a high sea level flooded these areas. It is interesting to note (as summarized above) that in those localities where *Lariosaurus* is frequent, it may occur together with pachypleurosaurs, which share the same phylogenetic and paleobiogeographic history (Rieppel & Hagdorn, 1997), but not with its sister taxon *Nothosaurus.* The exception is the rare occurrence of *Lariosaurus* in the Keuper, which documents the return of the genus from the Alpine into the Germanic Triassic by upper Ladinian times, a distributional pattern that again is congruent with the stratigraphic and geographic occurrence of the pachypleur genus *Neusticosaurus* (Rieppel & Hagdorn, 1997). The genus *Neusticosaurus* originated and diversified in the Alpine Triassic, with *Neusticosaurus pusillus* invading the Germanic Triassic during late Ladinian times. The congruence of the evolutionary pattern observed in the genera *Neusticosaurus* and *Lariosaurus* extends to the fact that in spite of appreciable diversification at the species level, there is one species in both genera (*Neusticosaurus pusillus* and *Lariosaurus balsami,* respectively) that is the most abundant and, geographically, the most widespread.

The lack of geographic and stratigraphic overlap in the distribution of *Lariosaurus* and *Nothosaurus* may reflect similar ecological requirements of the two sister taxa. But as is the case with *Nothosaurus* in the Germanic Triassic (Muschelkalk and lower Keuper; Rieppel & Wild, 1996), the species of *Lariosaurus* segregate into different size classes in the Alpine Triassic. The only known specimen of *Lariosaurus buzzii* is relative-ly small, and *Lariosaurus calcagnii* grows to distinctly larger size than *Lariosaurus balsami, Lariosaurus curionii* n. sp., and *Lariosaurus valceresii.* Different adult size presumably indicates different ecological preferences with respect to diet and may reduce competition between otherwise morphologically very similar species, at least as adults. But whereas species of different body size of *Nothosaurus* are known to show overlapping occurrence both geographically and stratigraphically, the only locality where species of *Lariosaurus* of different body size (*L. balsami* and *L. calcagnii*) are known to co-occur is the Spanish Muschelkalk of Montral–Alcover.

Acknowledgments

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Appendix I: Character Definitions for the Data Matrix Shown in Table 3

See Rieppel (1994a, 1997) for a complete discussion of characters and for references.

1. Premaxillae small (0) or large (1), forming most of snout in front of external nares.

2. Premaxilla without (0) or with (1) postnarial process, excluding maxilla from posterior margin of external naris.

3. Snout unconstricted (0) or constricted (1).

4. Temporal region of skull relatively high (0) or strongly depressed (1).

5. Nasals shorter (0) or longer (1) than frontal(s).

6. Nasals not reduced (0), somewhat reduced (1), or strongly reduced or absent (2).

7. Nasals do (0) or do not (1) enter external naris.

8. Nasals meet in dorsomedial suture (0) or are separated from one another by nasal processes of the premaxillae extending back to the frontal bone(s)(1).

9. Lacrimal is present and enters the external naris (0), or remains excluded from the external naris by a contact of maxilla and nasal (1), or is absent (2).

10. Prefrontal and postfrontal are separated by the frontal along the dorsal margin of the orbit (0), or a contact of prefrontal and postfrontal excludes the frontal from the dorsal margin of the orbit (1).

11. Dorsal exposure of prefrontal large (0) or reduced (1).

12. Preorbital and postorbital region of skull: of subequal length (0), preorbital region distinctly longer than postorbital region (1), or postorbital region distinctly longer (2).

13. Upper temporal fossa absent (0), present and subequal in size or slightly larger than the orbit (1), present and distinctly larger than orbit (2), or present and distinctly smaller than orbit (3).

14. Frontal(s) paired (0) or fused (1) in the adult.

15. Frontal(s) without (0) or with (1) distinct posterolateral processes.

16. Frontal widely separated from the upper temporal fossa (0), narrowly approaches the upper temporal fossa (1), or enters the anteromedial margin of the upper temporal fossa (2).

17. Parietal(s) paired (0), fused in their posterior part only (1), or fully fused (2) in adult.

18. Pineal foramen close to the middle of the skull table (0), weakly displaced posteriorly (1), strongly displaced posteriorly (2), displaced anteriorly (3), or absent (4).

19. Parietal skull table broad (0), weakly constricted (1), strongly constricted (at least posteriorly) (2), or forms a sagittal crest (3).

20. Postparietals present (0) or absent (1).

21. Tabulars present (0) or absent (1).

22. Supratemporals present (0) or absent (1).

23. The jugal extends anteriorly along the ventral margin of the orbit (0), is restricted to a position behind the orbit but enters the latter's posterior margin (1), or is restricted to a position behind the orbit without reaching the latter's posterior margin (2).

24. The jugal extends backward no farther than to the middle of the cheek region (0) or nearly to the posterior end of the skull (1).

25. The jugal remains excluded from (0) or enters (1) the upper temporal arch.

26. Postfrontal large and platelike (0), with distinct lateral process overlapping the dorsal tip of the postorbital (1), or postfrontal with reduced lateral process and hence more of an elongate shape (2).

27. Lower temporal fossa absent (0), present and closed ventrally (1), or present but open ventrally (2).

28. Squamosal descends to (0) or remains broadly separated from (1) ventral margin of skull.

29. Quadratojugal present (0) or absent (1).

30. Quadratojugal with (0) or without (1) anterior process.

31. Occiput with paroccipital process forming the lower margin of the posttemporal fossa and extending laterally (0), paroccipital processes trending posteriorly (1), or occiput platelike with no distinct paroccipital process and with strongly reduced posttemporal fossae (2).

32. Squamosal without (0) or with (1) distinct notch to receive distal tip of paroccipital process.

33. Mandibular articulations approximately at level with occipital condyle (0), or displaced to a level distinctly behind occipital condyle (1), or positioned anterior to the occipital condyle (2).

34. Exoccipitals do (0) or do not (1) meet dorsal to the basioccipital condyle.

35. Supraoccipital exposed more or less vertically on occiput (0) or exposed more or less horizontally at posterior end of parietal skull table (1).

36. Occipital crest absent (0) or present (1).

37. Quadrate with straight posterior margin (0) or quadrate shaft deeply excavated (concave) posteriorly (1).

38. Quadrate covered by squamosal and quadratojugal in lateral view (0), or quadrate exposed in lateral view (1).

39. Dorsal wing of epipterygoid broad (0) or narrow (1).

40. Lateral conch on quadrate absent (0) or present (1).

41. Palate kinetic (0) or akinetic (1).

42. Basioccipital tubera free (0) or in complex relation to the pterygoid as they extend ventrally (1) or laterally (2).

43. Suborbital fenestra absent (0) or present (1).

44. Pterygoid flanges well developed (0) or strongly reduced (1).

45. Premaxillae enter internal naris (0) or are excluded (1).

46. Ectopterygoid present (0) or absent (1).

47. Internal carotid passage enters basicranium (0) or quadrate ramus of pterygoid (1).

48. Retroarticular process of lower jaw absent (0) or present (1).

49. Distinct coronoid process of lower jaw absent (0) or present (1).

50. Surangular without (0) or with (1) strongly projecting lateral ridge defining the insertion area for superficial adductor muscle fibers on the lateral surface of the lower jaw.

51. Mandibular symphysis short (0), somewhat enforced (1), or elongated and scooplike (2).

52. Splenial bone enters the mandibular symphysis (0) or remains excluded therefrom (1).

53. Teeth set in shallow or deep sockets (0) or superficially attached to bone (1).

54. Anterior (premaxillary and dentary) teeth upright (0) or strongly procumbent (1).

55. Premaxillary and anterior dentary fangs absent (0) or present (1).

56. One or two caniniform teeth present (0) or absent (1) on maxilla.

57. The maxillary tooth row is restricted to a level in front of the posterior margin of the orbit (0), or extends backward to a level below the posterior corner of the orbit and/or the anterior corner of the upper temporal fossa (1), or extends backward to a level below the anterior one-third to one-half of the upper temporal fossa (2).

58. Teeth on pterygoid flange present (0) or absent (1).

59. Vertebrae notochordal (0) or nonnotochordal (1).

60. Vertebrae amphicoelous (0), platycoelous (1), or other (2).

61. Dorsal intercentra present (0) or absent (1).

62. Cervical intercentra present (0) or absent (1).

63. Cervical centra rounded (0) or keeled (1) ventrally.

64. Zygosphene–zygantrum articulation absent (0) or present (1).

65. Sutural facets receiving the pedicels of the neural arch on the dorsal surface of the centrum in the dorsal region are narrow (0) or expanded into a cruciform or butterfly-shaped platform (1).

66. Transverse processes of neural arches of the dorsal region relatively short (0) or distinctly elongated (1).

67. Vertebral centrum distinctly constricted in ventral view (0) or with parallel lateral edges (1).

68. Distal end of transverse processes of dorsal vertebrae not increasing in diameter (0) or distinctly thickened (1).

69. Zygapophyseal pachyostosis absent (0) or present (1).

70. Pre- and postzygapophyses do not (0) or do (1) show an anteroposterior trend of increasing inclination within the dorsal and sacral region.

71. Cervical ribs without (0) or with (1) a distinct free anterior process.

72. Pachyostosis of dorsal ribs absent (0) or present (1).

73. The number of sacral ribs is two (0), three (1), or four or more (2).

74. Sacral ribs with (0) or without (1) distinct expansion of distal head.

75. Sacral (and caudal) ribs or transverse processes sutured (0) or fused (1) to their respective centrum.

76. Cleithrum present (0) or absent (1).

77. Clavicles broad (0) or narrow (1) medially.

78. Clavicles positioned dorsally (0) or antero-ventrally (1) to the interclavicle.

79. Clavicles do not meet in front of the interclavicle (0) or meet in an interdigitating antero-medial suture (1).

80. Clavicles without (0) or with (1) anterolaterally expanded corners.

81. Clavicle applied to the anterior (lateral) (0) or to the medial (1) surface of scapula.

82. Interclavicle rhomboidal (0) or T-shaped (1).

83. Posterior process on (T-shaped) interclavicle elongate (0), short (1), or rudimentary or absent (2).

84. Scapula represented by a broad blade of bone (0) or with a constriction separating a ventral glenoidal portion from a posteriorly directed dorsal wing (1).

85. The Dorsal wing or process of the eosauropterygian scapula tapers to a blunt tip (0) or is ventrally expanded at its posterior end (1).

86. Supraglenoid buttress present (0) or absent (1).

87. One (0) or two (1) coracoid ossifications.

88. Coracoid of rounded contours (0), slightly waisted (1), strongly waisted (2), or with expanded medial symphysis (3).

89. Coracoid foramen enclosed by coracoid ossification (0) or between coracoid and scapula (1).

90. Pectoral fenestration absent (0) or present (1).

91. Limbs short and stout (0) or long and slender (1).

92. Humerus rather straight (0) or curved (1).

93. Deltopectoral crest well developed (0) or reduced (1).

94. Insertional crest for latissimus dorsi muscle prominent (0) or reduced (1).

95. Humerus with prominent (0) or reduced (1) epicondyles.

96. Ectepicondylar groove open and notched anteriorly (0), open without anterior notch (1), or closed (2) (i.e., ectepicondylar foramen present).

97. Entepicondylar foramen present (0) or absent (1).

98. Radius shorter than ulna (0), longer than ulna (1), or approximately of the same length (2).

99. Iliac blade well developed (0), reduced but projecting beyond level of posterior margin of acetabular portion of ilium (1), reduced and no longer projecting beyond posterior margin of acetabular portion of ilium (2), or absent, i.e., reduced to simple dorsal stub (3).

100. Pubis with convex (0) or with concave (1) ventral (medial) margin.

101. Obturator foramen closed (0) or open (1) in adult.

102. Thyroid fenestra absent (0) or present (1).

103. Acetabulum oval (0) or circular (1).

104. Femoral shaft stout and straight (0) or slender and sigmoidally curved (1).

105. Internal trochanter well developed (0) or reduced (1).

106. Intertrochanteric fossa deep (0), distinct but reduced (1), or rudimentary or absent (2).

107. Distal femoral condyles prominent (0) or not projecting markedly beyond shaft (1).

108. Anterior femoral condyle relative to posterior condyle larger and extending further distally (0) or smaller/equisized and of subequal extent distally (1).

109. Perforating artery passes between astragalus and calcaneum (0) or between the distal heads of tibia and fibula proximal to the astragalus (1).

110. Astragalus without (0) or with (1) a proximal concavity.

111. Calcaneal tuber absent (0) or present (1).

112. Foot short and broad (0) or long and slender (1).

113. Distal tarsal 1 present (0) or absent (1).

114. Distal tarsal 5 present (0) or absent (1).

115. Total number of tarsal ossifications four or more (0), three (1), or two (2).

116. Metatarsal 5 long and slender (0) or distinctly shorter than the other metatarsals and with a broad base (1).

117. Metatarsal 5 straight (0) or hooked (1).

118. Mineralized sternum absent (0) or present (1).

119. Medial gastral rib element always has only a single (1) lateral process or may have a two-pronged lateral process (1).

120. Ulna slender at middiaphysis (0) or broadened at middiaphysis (1).

121. Ulna without (0) or with (1) distinctly broadened proximal head.

122. Hyperphalangy absent (0) or present (1) in manus.

Appendix II: Material Included in the Analysis

Bayerische Staatssammlung für Paläontologie und historische Geologie, München: BSP ASI 802 (neotype for *Lariosaurus balsami*).

British Museum (Natural History), London: BMNH R-2880 (cast of *Lariosaurus balsami,* left pes; original of Boulenger, 1891; the original specimen was kept in Milano and was destroyed in World War II); BMNH R-5263 (*Lariosaurus balsami,* cast of original of Mariani, 1923).

Forschungsinstitut und Naturmuseum, Frankfurt a.M.: SMF R-13 (*Lariosaurus balsami,* original of Boulenger, 1898).

Geologische Bundesanstalt, Wien: *Proneusticosaurus carinthiacus* (holotype, original of Arthaber, 1924; uncatalogued).

Landesmuseum für Kärnten, Klagenfurt: Paläontologische Inventarnummer 5410 (*Lariosaurus balsami,* original of Zapfe & König, 1980, Pl. 1, Fig. 1).

Museo Civico, Lecco: MCL #202, #663 (*Lariosaurus balsami,* originals of Ticli, 1984).

Museo Civico di Szienze Naturali di Induno Olona: P 500 (holotype of *Lariosaurus valceresii*), P 550 (*Lariosaurus,* original of Renesto, 1993).

Museo Civico di Storia Naturale, Milano: MCSNM uncatalogued (cast of holotype of *Lariosaurus balsami,* first described by Balsamo-Crivelli, 1839); MCSNM uncatalogued (original of Mariani, 1923).

Museo y Laboratorio de Geologia, Seminario de Barcelona: M-501 (*Lariosaurus balsami,* original of Sanz, 1983b, Pl. 2, Fig. B); M-504 (*Lariosaurus balsami,* original of Sanz, 1983b, Pl. 4, Fig. A); M-506 (*Lariosaurus balsami,* original of Sanz, 1983b, Pl. 2, Fig. A); M-507 (*Lariosaurus balsami* original of Sanz, 1983b, Pl. 4, Fig. B).

Museum beim Solnhofer Aktien-Verein, Maxberg: uncatalogued (*Lariosaurus balsami,* original of Sanz, 1983b, Pl. 5, Fig. A).

Muséum d'Histoire Naturelle, Lausanne: MHNL uncatalogued (*Lariosaurus balsami,* juvenile). Perledo.

Naturhistorisches Museum, Basel: uncatalogued (*Lariosaurus calcagnii,* adult specimen).

Paläontologisches Institut und Museum der Universität, Zürich: PMZ T 2804 (holotype of *Lariosaurus buzzii*); PMZ T 4288 (holotype of *Lariosaurus lavizzarii*).

Servicio Geologico d'Italia, Ufficio Geologico di Roma: UGR #4423 P (*Lariosaurus balsami,* specimen Curioni V.I.); UGR #4425 P and UGR #4427 P (holotype of *Maromirosaurus Plini* Curioni, 1947, part and counterpart); UGR #4428 P (*Lariosaurus balsami,* specimen Curioni VI); UGR #4429 P (*Lariosaurus balsami,* specimen Curioni VII.I.); UGR #4430 P (*Lariosaurus balsami,* specimen Curioni V.3.).

Université Paris VI, Laboratoire de Paléontologie et de Paléonthropologie, Paris: PVHR 1 (*Lariosaurus balsami,* original of Mazin, 1985).

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